Magill's
Encyclopedia of Science:
Animal Life

Carl W. Hoagstrom, Ph.D.,
Editor

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MAGILL'S ENCYCLOPEDIA OF SCIENCE

ANIMAL LIFE

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Volume 1
Aardvarks–Endoskeletons

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PUBLISHER'S NOTE

Animals have always been a source of fascination for humans. We have sought to explain the origin and evolution of life, to classify the planet's many organisms in a logical manner, and to study the forms and behavior of creatures as diverse as jellyfish and elephants. *Magill's Encyclopedia of Science: Animal Life* offers accessible, easy-to-understand scientific information for high-school, undergraduate, and general readers on a subject of significant popular and academic interest. This illustrated, four-volume encyclopedia refocuses and expands on *Magill's Survey of Science: Life Science*. *Animal Life* revises and updates 108 articles from that 1991 set and its 1998 *Supplement* and then adds 277 new main entries, as well as more than three hundred textual sidebars, fact boxes, and biographies. Photographs, tables, and maps complement the text.

Animal Life concentrates on science in its discussion of nonhumans from the kingdom Animalia: invertebrates, insects, arthropods, amphibians, reptiles, fish, birds, and mammals. The 385 entries, ranging from 1,000 to 3,000 words each, survey a wide range of topics: anatomy (*Antennae*, *Feathers*, and *Tails*); behavior (*Defense mechanisms*, *Hibernation*, and *Nesting*); classification (*Bears*, *Crustaceans*, and *Mammoths*); ecology (*Herbivores*, *Poisonous animals*, and *Symbiosis*); evolution (*Fossils*, *Mutations*, and *Natural selection*); fields of study (*Biogeography*, *Paleontology*, and *Zoology*); geography and habitats (*Fauna: Australia*, *Fauna: Galápagos Islands*, *Deserts*, and *Rain forests*); physiology (*Cold-blooded animals*, *Reflexes*, and *Smell*); reproduction and development (*Asexual reproduction*, *Life spans*, and *Metamorphosis*); and scientific methods (*Breeding programs* and *Population analysis*). The emphasis of this encyclopedia is on animals in nature; the entries on domestic animals also cover their wild kin (*Chickens, turkeys, pheasant, and quail*; *Pigs and hogs*; and *Dogs, wolves, and coyotes*), and while there are entries on *Domestication* and *Zoos*, pets and farm animals are not discussed as such. Early humans are addressed in an evolutionary context, and modern humans are included only for interspecies comparison or for their efforts to coexist with other species.

All entries begin with ready-reference information about type of animal science and fields of study. Next is a list of principal terms, with brief definitions. Numerous creative subheads guide the reader through the main text of the entry. Every essay ends with an annotated bibliography; those reused from *Magill's Survey of Science* have been updated with recent sources. Species overviews, at 1,000 or 2,000 words, discuss notable anatomy and physiology, habitat, behavior (food sources, social groups), and reproduction and include an "Animal Facts" sidebar listing classification, geographical location, habitat, gestational period, life span, and special anatomy. Numerous biographical entries—on such prominent figures in the study of the natural world as John James Audubon, Charles Darwin, and Jane Goodall—appear as 500-word sidebars within main entries, as do some issue-oriented discussions such as habitat destruction and poaching. In addition, most longer entries provide one or more brief sidebars highlighting interesting subjects relating to the text.

A complete Alphabetical List of contents appears in the back of all four volumes, as does a Category List using the following headings: amphibians, anatomy, arthropods, behavior, birds, carnivores, cell biology, classification, ecology, evolution, fields of study, fish, genetics, geography, habitats, herbivores, human origins, insects, invertebrates, mammals, marine biology, marsupials, omnivores, physiology, population biology, prehistoric animals, primates, reproduction and development, reptiles, and scientific methods.

Volume 4 offers many useful appendices. The Glossary provides important terms with succinct definitions. A table of Animal Terminology gives the names applied to the males, females, young, and groups of various animals. The Time Line is a graphic depiction of the evolutionary tree across geological periods. The Classification Table lists all phyla, subphyla, superclasses, classes, subclasses, superorders, orders, infraclasses, suborders, superfamilies, and families in the kingdom Animalia. A Geographical List of Animals breaks species down into various areas: All continents (except Antarctica), all oceans, Africa, Antarctica, the Arctic, Asia, the Atlantic Ocean, Australia, the Caribbean, Central America, Europe, the Galápagos Islands, Madagascar, the Middle East, North America, the Pacific Islands, the Pacific Ocean, and South America. The Biographical List of Scientists consists of brief profiles of fifty-one important figures in animal science, past and present. A General Bibliography offers annotated sources, and both the Journals and the Organizations appendices provide contact and general information. The encyclopedia concludes with a comprehensive subject Index.

The contributors to this work are academicians from a variety of disciplines in the life sciences. We thank them for generously sharing their expertise; their names and affiliations are listed in the front matter to volume 1. Special acknowledgment is extended to the Editor, Carl W. Hoagstrom, Ph.D., from Ohio Northern University, for his invaluable guidance.

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AARDVARKS

Type of animal science: Classification
Fields of study: Anatomy, zoology

The aardvark is the only member of the order Tubulidentata and is found only on the continent of Africa.

Principal Terms

NOCTURNAL: active at night
TUBULE: filled with cavities of pulp

The aardvark differs from the anteater, sloth, armadillo, and all other mammals. It is the only member of the order Tubulidentata (tubule toothed), so named because of a permanent set of twenty teeth that have tubular pulp cavities extending through them from top to bottom. The teeth are rootless. Dutch farmers who first encountered the animal in South Africa called it an aardvark, which means "earth pig" in the Dutch language. It is also sometimes called the African ant bear. It looks like a giant, hump-backed rat with the head of an anteater, the nose of a pig, and the ears of a rabbit. It is unrelated, however, to any other mammal.

Physical Characteristics of Aardvarks

The typical aardvark is about 7.5 feet long and weighs between 110 and 150 pounds, though the largest may weigh up to 180 pounds. It has a long, ratlike tail and a foot-long, sticky tongue that usually hangs out of its mouth. The tongue is curled like a coiled spring and is unleashed quickly as the aardvark sucks in its meal of ants or termites. It is perfectly suited for inserting into nests, and the termites adhere to the sticky surface. Adult aardvarks have one- to two-inch-long whitish hairs growing from each nostril, and twenty teeth along the sides of the mouth, that are always growing. The nose hairs protect aardvarks from dust and dirt while they are digging. Young aardvarks have front teeth that fall out as the animals reach maturity. Aardvark teeth are unique in the animal kingdom, as they are rootless, lack dentine, and have hollow tubes running through them.

Thick brown hair covers aardvarks' pinkish-gray skin. The hair serves to protect members of the species from insect bites. They have short, stocky legs and small feet with long, straight, very strong, blunt claws. Their front feet have four toes, while rear feet have five toes. The rear toes are webbed at the bottom. An aardvark looks like no other animal on earth.

The Life Cycle of Aardvarks

During most of the day, aardvarks live in burrows in the ground. They live singly or in small groups. They usually come out only at night, when they begin searching for termites and ants, which are the major part of their diets. They can rip open ant and termite nests and quickly lap up the insects with their sticky tongues. Aardvarks have tremendous ability to dig burrows in the ground very quickly. One aardvark can dig much faster than several human beings armed with shovels. Their powerful front claws can tear through hard ground and mud-covered termite nests with very little difficulty. They dig like dogs, pushing dirt and mud backward under their bodies.

They have a very good sense of hearing but very poor eyesight. When frightened, they usually run as quickly as possible for their burrows, but as they run, they frequently crash into trees and bushes. Sometimes they fight by using their powerful tails to hit their attackers, or by standing up on their back legs and slashing an opponent—usually a lion or a leopard—with their claws.

Aardvark Facts

Classification:
Kingdom: Animalia
Subkingdom: Eumetazoa
Phylum: Craniata
Subphylum: Vertebrate
Class: Mammalia
Subclass: Theria
Order: Tubulidentata (tubule-toothed)
Family: Orycteropodidae (ant bear)
Genus and species: Orycteropus afer
Geographical location: Africa, from Egypt to the Cape of Good Hope
Habitat: Open woodland, scrub, brushland
Gestational period: Seven months
Life span: Eight to ten years
Special anatomy: Chisel-shaped claws to break open hard clay of termite nests; a sticky tongue; twenty teeth that grow continually throughout its lifetime

Aardvark mothers usually give birth to only one or two offspring a year, usually in May, June, or July. They nurse their young in their burrows and spend most of the day with them, curled up in a tight circle. Aardvarks are able to dig their own burrows by time they are six months of age.

Aardvarks were formerly classified with anteaters, sloths, and armadillos in the order Edentata, but this is no longer the case. The order under which they are now classified, Tubulidentata, is at least sixty million years old, though its origins are unknown. Evidence of fossil remains indicates that the aardvark ranged over Europe and Asia until about five million years ago. At that time, a close relative lived on the island of Madagascar. Today there is only one order, one family (Orycteropodidae), one genus (*Orycteropus*), and, remarkably, only one species (*afer*), and it is exclusively African. It exists in relatively small numbers and does not respond well to captivity, but has survived in zoos for ten years.

Aardvarks and Humans

The chief importance of aardvarks is their keeping in check enormous, ever-multiplying hordes of termites. Some African peoples hunt aardvarks for food and claim the meat is very tasty. Aardvark burrows are large enough for a small-sized man to crawl into, but the hunter must kill the animal before it has time to escape by burrowing deeper. The animal can dig faster than the man and can throw up a wall of packed dirt between itself and the hunter—and then it is gone. Some African peoples believe that a bracelet of aardvark teeth can protect an individual against evil forces.

—Leslie V. Tischauser

See also: Ants; Armadillos, anteaters, and sloths; Claws, nails, and hooves; Fauna: Africa; Mammals; Teeth, fangs, and tusks; Termites.

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ADAPTATIONS AND THEIR MECHANISMS

Type of animal science: Ecology
Fields of study: Evolutionary science, genetics, invertebrate biology, zoology

Adaptations are structures, physiological mechanisms, or behaviors that are shaped by the environment and enable organisms to cope with specific environmental conditions. Studying adaptations helps scientists understand how organisms live with environmental constraints and allows them to examine the mechanisms of evolution.

Principal Terms

COEVOLUTION: joint evolutionary change caused by the close interaction of two or more species; each species serves as the natural selection agent for the other(s)

COMPETITION: striving for a limited resource

EVOLUTION: a process, guided by natural selection, that changes a population's genetic composition and results in adaptations

FITNESS: the ability of an organism to produce offspring that, in turn, can reproduce successfully; the fitness of organisms increases as a result of natural selection

NATURAL SELECTION: the elimination of individuals with hereditary characteristics that hinder the organism's ability to survive and reproduce, and the preservation of those with traits beneficial to survival

POPULATION: a group of individuals of the same species in a particular location

SPECIES: a group of organisms that can successfully interbreed to produce living, successfully reproducing offspring

Many of the features that are most interesting and beautiful in biology are adaptations. Adaptations are the result of long evolutionary processes in which succeeding generations of organisms become better able to live in their environments. Specialized structures, physiological processes, and behaviors are all adaptations when they allow organisms to cope successfully with the special features of their environments. Adaptations ensure that individuals in populations will reproduce and leave well-adapted offspring, thus ensuring the survival of the species.

Mutation and Natural Selection

Adaptations arise through mutations—inheritable changes in an organism's genetic material. These rare events are usually harmful, but occasionally they give specific survival advantages to the mutated organism and its offspring. When certain individuals in a population possess advantageous mutations, they are better able to cope with their specific environmental conditions and, as a result, will contribute more offspring to future generations compared with those individuals in the population that lack the mutation. Over time, the number of individuals that have the advantageous mutation will increase in the population at the expense of those that do not have it. Individuals with an advantageous mutation are said to have a higher "fitness" than those without it, because they tend to have comparatively higher survival and reproductive rates. This is natural selection.

Over very long periods of time, evolution by natural selection results in increasingly better adaptations to environmental circumstances. Natural selection is the primary mechanism of evolutionary change, and it is the force that either favors or selects against mutations. Although natural selection acts on individuals, a population gradually changes as those with adaptations become better represented in the total population. Predaceous fish, for example, which rely on speed to pursue and overtake prey, would benefit from specific adaptations that would increase their swimming speed. Therefore, mutations causing a more sleek and hydrodynamically efficient form would be beneficial to the fish predator. Such changes would be adaptations if they resulted in improved predation success, improved diet, and subsequently greater reproductive success, compared with slower members of the population. Natural selection would favor the mutations because they confer specific survival advantages to those that carry the mutations and impose limitations on those lacking these advantages. Thus, those individuals with special adaptations for speed would have a competitive advantage over individuals that can only swim more slowly. These attributes would be passed to their more numerous offspring and, in evolutionary time, speed and hydrodynamic efficiency would increase in the population.

Environment and Survival

Although natural selection serves as the instrument of change in shaping organisms to very specific environmental features, highly specific adaptations may ultimately be a disadvantage. Adaptations that are specialized may not allow sufficient flexibility (generalization) for survival in changing environmental conditions. The degree of adaptative specialization is ultimately controlled by the nature of the environment. Environments, such as the tropics, that have predictable, uniform climates and have had long, uninterrupted periods of climatic stability are biologically complex and have high species diversity. Scientists generally believe that this diversity results, in part, from complex competition for resources and from intense predator-prey interactions. Because of these factors, many narrowly specialized adaptations have evolved when environmental stability and predictability prevail. By contrast, harsh physical environments with unpredictable or erratic climates seem to favor organisms with general adaptations, or adaptations that allow flexibility. Regardless of the environment type, organisms with both general and specific adaptations exist because both types of adaptation enhance survivorship under different environmental circumstances.

Structural adaptations are parts of organisms that enhance their survival ability. Camouflage, which enables organisms to hide from predators or prey; specialized mouth parts that allow organisms to feed on specific food sources; forms of appendages, such as legs, fins, or webbed toes, that allow efficient movement; protective spines that

Image Not Available

make it difficult for the organism to be eaten—these are all structural adaptations. These adaptations enhance survival because they assist individuals in dealing with the rigors of the physical environment, obtaining nourishment, competing with others, hiding, or confusing predators.

Physiological Versus Behavioral Adaptation

Metabolism is the sum of all chemical reactions taking place in an organism, whereas physiology consists of the processes involved in an organism carrying out its function. Physiological adaptations are changes in the metabolism or physiology of organisms, giving them specific advantages for a given set of environmental circumstances. Because organisms must cope with the rigors of their physical environments, physiological adaptations for temperature regulation, water conservation, varying metabolic rate, and dormancy or hibernation allow organisms to adjust to the physical environment or respond to changing environmental conditions.

Desert environments, for example, pose a special set of problems for organisms. Hot, dry environments require physiological mechanisms that enable organisms to conserve water and resist prolonged periods of high temperature. Highly efficient kidneys and other excretory organs that assist organisms in retaining water are physiological adaptations related to the metabolisms of desert organisms. The kangaroo rat is a desert rodent extremely well adapted to its habitat. Kangaroo rats do not drink, but rather can obtain all of their water from the seeds they eat. They produce highly concentrated urine and feces with very low water content.

Adaptation to a specific temperature range is also an important physiological adaptation. Organisms cannot live in environments with temperatures beyond their range of thermal tolerance, but some organisms are adapted to warmer and others to colder environments. Metabolic response to temperature is quite variable among animals, but most animals are either homeothermic (warm-blooded) or poikilothermic (cold-blooded). Homeotherms maintain constant body temperatures at specific temperature ranges. Although a homeotherm's metabolic heat production is constant when the organism is at rest and when environmental temperature is constant, strenuous exercise produces excess heat that must be dissipated into the environment, or overheating and death will result. Physiological adaptations that enable homeotherms to rid their bodies of heat are the ability to increase blood flow to the skin's surface, sweating, and panting, all of which promote heat loss to the atmosphere.

Behavioral adaptations allow organisms to respond appropriately to various environmental stimuli. Actions taken in response to various stimuli are adaptive if they enhance survival. Migrations are behavioral adaptations because they ensure adequate food supplies or the avoidance of adverse environmental conditions. Courtship rituals that help in species recognition prior to mating, reflex and startle reactions allowing for quick retreats from danger, and social behavior that fosters specialization and cooperation for group survival are behavioral adaptations.

Because organisms must also respond and adapt to an environment filled with other organisms—including potential predators and competitors—adaptations that minimize the negative effects of biological interactions are favored by natural selection. Many times the interaction between species is so close that each species strongly influences the others in the interaction and serves as the selective force causing change. Under these circumstances, species evolve together in a process called coevolution. The adaptations resulting from coevolution have a common survival value to all the species involved in the interaction. The coevolution of flowers and their pollinators is a classic example of these tight associations and their resulting adaptations.

Adaptation in Theory and Practice

Charles Darwin and Alfred Russel Wallace, the mid-nineteenth century biologists who formulated the theory of evolution by natural selection, found much of the evidence for their theory in the adaptations they observed in nature. They reasoned that organisms with similar body forms and structures were closely related evolutionarily and had common ancestors which are now extinct. The modern study of relatedness among species and the evolutionary history of organisms is called systematics, and this discipline aids in understanding evolution and adaptations.

The methods used to study adaptations are largely the same as those used to examine the theory of evolution. Evolution, however, is a slow process, and, as a result, it is extremely difficult to test the theory. Instead, evidence must be collected from the past, and closely related organisms must be examined carefully to reconstruct how adaptations may have come into being. Scientists can then speculate on how adaptations occurred and how they helped organisms to survive.

Fossils, because they are a historical record of evolutionary change, are used by scientists to reconstruct evolutionary histories. Similar structures in different living organisms with essentially the same function are used by comparative anatomists to show how adaptations for a specific mode of life arose. The fins of some ancient fish and the limbs of mammals, for example, have strikingly similar bones that have a common origin, but the appendages have been modified for locomotion in very different environments. Adaptations are also studied in relation to biogeography, the geographical distribution of organisms. On the Galápagos Islands, fourteen species of finches now known as Darwin's finches are distributed geographically on the basis of their adaptations. Although the species that gave rise to these fourteen species is extinct, the existing species and their distributions suggest how evolution proceeded and how the adaptations came about.

A classic example of recent evolutionary change and adaptation comes from England. The peppered moth, with a mottled gray color, is well adapted to resting quietly on pale tree bark, with which it blends nicely. This adaptive coloration (camouflage) enhanced the moth's survival because the moths could remain largely undetected by predators during daylight hours. Between 1850 and 1950, however, industrialization near urban centers blackened tree trunks with soot, making the gray form disadvantageous, as it stood out on the contrasting background. During this period, the gray moths began to disappear from industrial areas, but a black-colored variant, previously rare, became increasingly common in the population. These circumstances made it possible for scientists to test whether the peppered moth's camouflage was adaptive.

In a simple experiment, moths were raised in the laboratory, and equal numbers of gray and black moths were released in both industrial and unpolluted rural areas. Sometime later, only half of the gray-colored moths could be recovered from the industrial sites, while only half of the black forms could be recovered from the rural sites, compared with the total number released. These results enabled the scientists to conclude that increased predation on the gray moths in industrial areas led to a greater fitness of the black moths, so the frequency of black moths increased in the population. The reverse was true at the rural sites. This is the first well-documented case of natural selection causing evolutionary change, and it illustrates the adaptive significance of camouflage.

The various ways of examining adaptations (by evolutionary history, comparative anatomy, and biogeography) demonstrate how adaptations are structurally and functionally important. These approaches also give scientists insight into the survival benefits of various adaptations.

The Function of Adaptation

Adaptations can be general or highly specific. General adaptations define broad groups of organisms whose general lifestyle is similar. For example, mammals are homeothermic, provide care for their young, and have many other adaptations in common. At the species level, however, adaptations are more specific and give narrow definition to those organisms that are more closely related to one another. Slight variations in a single characteristic, such as bill size in the seed-eating Galápagos finches, are adaptive in that they enhance the survival of several closely related species. An understanding of how adaptations function to make species distinct also furthers the knowledge of how species are related to one another.

Why so many species exist is one of the most intriguing questions of biology. The study of adaptations offers biologists an explanation. Because there are many ways to cope with the environment, and because natural selection has guided the course of evolutionary change for billions of years, the vast variety of species existing on the earth today is simply an extremely complicated variation on the theme of survival.

—*Robert W. Paul*

See also: Adaptive radiation; Beaks and bills; Biodiversity; Coevolution; Convergent and divergent evolution; Defense mechanisms; Development: Evolutionary perspective; Ecological niches; Evolution: Animal life; Evolution: Historical perspective; Extinction; Extinctions and evolutionary explosions; Gene flow; Genetics; Habitats and biomes; Hardy-Weinberg law of genetic equilibrium; Mutations; Natural selection; Nonrandom mating, genetic drift, and mutation; Population genetics; Punctuated equilibrium and continuous evolution; Respiration and low oxygen; Symbiosis.

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ADAPTIVE RADIATION

Type of animal science: Evolution
Fields of study: Ecology, genetics, invertebrate biology, zoology

Adaptive radiation is a process by which new species can emerge from a common ancestor. If members of one population travel (or radiate) to new environments and are sufficiently isolated from other populations of their species, they may gradually adapt to their new environments and evolve into new species.

Principal Terms

ALLELE: an alternative form of a gene that is located at the same position on a chromosome

FOSSIL: any recognizable remains of an organism preserved in the earth's crust; it may be a footprint, bones, or even feces

GENE: the biological unit of heredity, which is composed of DNA and is located on a chromosome

GENOTYPE: the total genetic composition of an organism

HABITAT: the place where an organism normally lives or where individuals of a population live

NATURAL SELECTION: the process of evolution whereby organisms that are the best adapted are the most successful in reproducing and therefore in passing along their genotypes to successive generations

NICHE: the role of an organism in an ecological community—its unique way of life and its relationship to other biotic and abiotic factors

PHENOTYPE: the visible expression of the genetic makeup of an individual

SPECIES: a taxonomic subdivision of a genus, containing populations of similar organisms that interbreed and that usually do not interbreed with other species

In 1898, Henry F. Osborn developed the concept of adaptive radiation. According to Osborn, many different forms of evolutionary adaptations may occur among animals that started with a common ancestor. In this way evolutionary divergences can take place, and the occupation of a variety of ecological niches is made possible according to the adaptive nature of the invading species. As may be seen with certain forms of animal life, however, the ability to adapt is not shared by all species. Therefore, in many instances, either evolutionary divergence has been modest or the species involved has become extinct.

The Principles of Natural Selection

In order to understand how adaptive radiation operates, it is necessary to become familiar with the principles of natural selection. The concept of natural selection, frequently expressed as "survival of the fittest," is at the core of Charles Darwin's theory of evolution. Darwin did not mean to suggest that there was a physical struggle among organisms in order to survive. Instead, he meant that organisms compete for food, space, shelter, water, and other things necessary for existence. Only those organisms best adapted for a particular habitat will survive. According to the concept of natural selection, all organisms of a given species will show variation in color, size, physiology, and many other characteristics; in nature, all organisms produce more offspring than can survive, so the offspring must therefore compete for the limited environmental resources. Organisms that are the best adapted (most fit) to compete will live to reproduce and pass their successful traits on to their offspring. The others, which are less fit, will die without reproducing. When different parts of an animal population are faced with slightly different environments, they will diverge from one another and in time will become different enough to form new species. Natural selection also has the effect of producing different patterns of evolution. It may bring about widely different phenotypes (variable characteristics) in closely related animals, for example, or similar phenotypes in distantly related organisms. The organisms themselves may also become forces of selection through their interrelationships with other species.

The process of adaptive radiation illustrates how natural selection operates. The most frequently cited example is the evolution of Darwin's finches on the Galápagos Islands, off the west coast of South America. The islands were formed from volcanic lava about one million years ago. At first they were devoid of life, but bit by bit, several species of plants and animals migrated to them from the South American mainland. Since the nearest island is about 950 kilometers from the coast of Ecuador, it is anybody's guess how the different species arrived. It has been suggested that the birds may have been carried to the islands by strong winds, since finches are not known for their lengthy flights. Other organisms may have been carried by floating debris. In any event, the islands became populated. The mainland ancestor of the finches is not known, but it was no doubt a nonspecialized finch (a finch is about the size of a sparrow). Since there were no other birds with which to compete on the islands, the original population of finches began to adapt to the various unoccupied niches. The early off-

The evolution of white, arctic-dwelling, almost completely carnivorous polar bears from the largely vegetarian, forest-dwelling brown bear is a classic example of adaptive radiation. (PhotoDisc) shoots of the original population were modified again and again as adaptations continued. This process resulted in the evolution of fourteen species of finches. The main feature that makes each species different is the size of their beaks, which have adapted for the various types of available foods. Today the finches live on fifteen different islands. Some of the species are found in the same area (sympatric), while others occur in different areas (allopatric). The most noteworthy example of an adaptation to a particular niche is the woodpecker finch. A true woodpecker has an extremely long tongue that it uses to probe for insects. Since the woodpecker finch does not have a long tongue, it has learned to use a cactus spine for insect probing, and it can therefore occupy a niche normally filled by true woodpeckers.

A more recent example of adaptive radiation in its early stages has taken place in an original population of brown bears. The brown bear can be found throughout the Northern Hemisphere, ranging from the deciduous forests up into the tundra. During one of the glacier periods, a small population of the brown bear was separated from the main group; according to fossil evidence, this small population, under selection pressure from the Arctic environment, evolved into the polar bear. Although brown bears are classified as carnivores, their diets are mostly vegetarian, with occasional fish and small animals eaten as supplements. On the other hand, the polar bear is mostly carnivorous. Besides its white coat, the polar bear is different from the brown bear in many ways, including its streamlined head and shoulders and the stiff bristles that cover the soles of its feet, which provide traction and insulation, enabling it to walk on ice.

Evolution

All the genes of any population of living organisms at any given time make up its gene pool, and the ratio of alternative characteristics (alleles) in the gene pool can change because of selection pressures during the passage of time. As the ratio of alleles changes, evolution occurs. Evolution may be a random change, or it may occur because of the directive influences of natural selection. In the former case, occasional and unpredictable permanent random changes called mutations take place in the DNA molecules that compose the genes. These mutations also may be selected for by the environment or selected against by the environment. It is simply an accident if the newly mutated genes help the organism to become better adapted to its particular habitat niche. Genes may not change or become mutated through several generations (the Hardy-Weinberg law), but may change in terms of survival value if the environment changes or the species population is subjected to new mutations or natural selection. The relative numbers of one form of allele decrease in a divergent population, while the relative numbers of a different gene increase. This progressive change is all-important in the evolutionary process that takes place between the origin of a new gene by random mutation and the replacement of the original form of the gene by descendants having the newer, better-adapted form of the gene. The result in the long term is that enough of the DNA changes, either slowly or rapidly, through divergent populations or organisms, that the new generations have become so different from the original population that they are considered new species. Many times in earth's history, a single parental population has given rise not to one or two new species but to an entire family of species. The rapid multiplication of related species, each with its unique specializations that fit it for a particular ecological niche, is called adaptive radiation, or divergent evolution.

Studying Adaptive Radiation

Not all scientific information is gained by experimentation: A considerable portion of science is descriptive and is based upon observation. In determining that adaptive radiation has occurred and is indeed taking place among living species, much supporting evidence has come from the study of fossils and from observations of the structural, physiological, and behavioral adaptations of current animals. Clearly, wide-scale experimentation would be out of the question. No matter how well an experiment may be designed to test the concept of adaptive radiation, the scientist could not be around thousands or millions of years from now to gather the data. Therefore, scientific observation of animal remains is the best method.

Based upon scientific observations, it has been well established that the phenomenon known as adaptive radiation is a general feature of the evolution of most organisms. Studies of the morphological features of fossilized remains help determine relationships among prehistoric animals and enable the scientist to trace adaptive radiations from a more primitive ancestral stock. In order to establish time intervals, techniques such as radioactive carbon dating, potassium-argon dating, and fluorine dating have been used.

Zoologists have also made use of the uneven distribution of blood groups (A, B, AB, and O) among different groups of animals. As more blood subgroups were discovered, they became useful in helping chart migrations and indicating relationships between species.

The Evidence and Its Implications

Adaptive radiation as an important aspect of evolution means that modern organisms have attained their diversity in form and behavior through hereditary modifications after having been separated from ancestral populations. Adaptive radiation, therefore, is attributable to the genetic changes in isolated groups of organisms or, more specifically, to a change in the relative frequency of their genes from one generation to the next that eventually results in the formation of new species.

Evidence in several areas supports the concept of adaptive radiation as an important aspect of evolution: the fossil record (the most direct evidence), biogeographic distribution of organisms, comparative anatomy and embryology, homologous and analogous structures, vestigial organs, and comparative biochemistry. Regarding comparative biochemistry, scientists agree that blood group similarities confirm evolutionary relationships among the nonhuman primates. It has been shown that the blood of higher primates, such as orangutans and chimpanzees, is closer to human blood than to that of the more primitive monkeys.

—Jon P. Shoemaker

See also: Adaptations and their mechanisms; Convergent and divergent evolution; Development: Evolutionary perspective; Ecological niches; Ecosystems; Evolution: Animal life; Evolution: Historical perspective; Extinction; Extinctions and evolutionary explosions; Gene flow; Genetics; Hardy-Weinberg law of genetic equilibrium; Mutations; Natural selection; Nonrandom mating, genetic drift, and mutation; Population genetics; Punctuated equilibrium and continuous evolution.

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AGING

Types of animal science: Development, physiology
Fields of study: Anatomy, cell biology, developmental biology, genetics, neurobiology, pathology, physiology

Aging is the process of progressive and irreversible change common to all living organisms. There are striking similarities in the physical process of aging among all animal species.

Principal Terms

AGING: a process common to all living organisms, eventually resulting in death or conclusion of the life cycle
COGNITION: ability to perceive or understand
DEATH: the cessation of all body and brain functions
FUNCTION: ability, capacity, performance
LIFE SPAN: length of life from birth to death
LONGEVITY: length of life

Progressive and irreversible change has been called the single common property of all aging systems. When change is reversible or self-maintaining, such as one would see in a forest, for example, the effects of aging are often not observable. Growth of the forest is evident, but with the right conditions, trees within the forest may grow for hundreds of years in the absence of disease. Certain conditions of the forest system help to regenerate, renew, and reverse changes that happen within that system.

However, in animals some change is not reversible. The changes in the cells of the body accumulate over time and result in a steady downward trend. The end point of this trend is the death of the organism. Aging is a normal part of the life cycle. This is known to be true because aging changes within populations are rather predictable. The changes associated with aging that are seen in all animal species may occur for similar reasons. These may include chemical aging, extracellular aging, intracellular aging, and aging of cells.

Aging occurs within body systems as a result of unseen changes at the molecular and cellular levels. Although the mechanisms through which aging occurs may be understood, the causes are less clear. The fact remains that due to changes in chemical balances such as those of hormones, and to the dying of cells within the body, each of the bodily systems shows deterioration over time.

Changes that occur in domestic animals over the life span can be similar to those that occur in humans. Dogs experience the graying of their hair, a decrease in vision, and a slowing of movement with age. They also experience cataract formation, arthritis, skin problems, cancer, and diabetes. Certain breeds of animals may demonstrate a tendency toward specific illnesses or diseases. For example, German shepherds often develop hip problems, and collies commonly develop progressive arthritis that may seriously inhibit mobility by around ten years of age.

Common Effects of Aging

There are many variations in the effects of aging among the species of animals. The life span of animals may range from a few days (among insects) to thirty years or more, with great variation depending upon many factors. Animals that live in captivity, as pets or in zoos where they are sheltered from the effects of predation, disease, and adverse climate, also tend to live significantly longer than animals in the wild.

Graying hair is a sign of aging in most mammals. The pattern of graying varies with species; in dogs, it usually begins around the muzzle. (Corbis)

Physical function or capacity tends to decline with age. This is largely due to the atrophy of muscles, which is more common as the body gets older. The joints tend to become stiffer and less mobile. Range of motion may be restricted. Changes in bone density may lead to loss of teeth, osteoporosis, and subsequent fractures. Tooth loss and osteoporosis have been documented in monkeys over the age of twenty years. Pictures of such older monkeys reveal a stooped posture, with shoulders hunched forward, similar to the kyphosis observed in many older human women.

Physical function among animals has been less studied than that in humans, but certain physiological characteristics are similar. For example, survival times after severe physical injury with blood loss and trauma decreases in both humans and animals as age increases. Male monkeys do not lose reproductive capabilities until toward the end of the life span, while females have a more restricted period of time to bear offspring. Fertility among all females tends to decline with age after its peak.

The immune system functions less effectively as age increases. This leaves the body more susceptible to a range of illnesses and diseases. Neoplasms, or tumors, are most common among mammals as they age. An impaired immune system allows various types of tumors or cancers to spread more rapidly in the older body. Response to stress and ability to adapt to stressors also decline with age. For example, older mice become less able to adapt to cold temperatures.

Social roles and behaviors among animals may also change with age. Longitudinal studies on animals in the wild are scarce, so only generalities may be speculated upon. Even studies done within controlled laboratory settings yield only broad suggestions, since numbers of animals available for study are limited. Males generally

Very little research has been done on the aging of most animal species. The reasons for this include the difficulty of observing animals over a long period of time in their natural habitat. Aging in monkeys has been studied more than that in other animals because of the notion that aging patterns may closely reflect those of humans.

Aging monkeys show changes in their circulatory systems similar to those found in humans: There is notable atherosclerosis and arteriosclerosis, or hardening of the arteries. The heart pumps less effectively, and vessels show buildup of plaque. These changes often result in cardiac problems, including heart attacks. The respiratory system also shows a decrease in elasticity. Senile emphysema has been noted. The kidneys show signs of atrophy and sclerosis in aged monkeys. The kidneys of humans may lose up to half of the functioning nephrons with advanced age and thus become less effective in filtering waste products from the body.

tend to dominate the females in both physical strength and social ranks. Some nonhuman primates show different characteristics with advanced age. That is, some monkeys and baboons allow older males to remain part of the social group, while other species support the male leader in the group only as long as the female harem supports him, whether younger or older. Individual monkeys in stable groups have been observed to resort less frequently to aggressive behavior to maintain their status within the group.

Causes of Death

Among nonhuman primates, the leading cause of spontaneous death is digestive problems. Older animals that die do not always show advanced signs of tissue aging. Since much less research has been done on aging among animals than among humans, data about causes of death are rare. However, it appears that there is an increased probability of dying from trivial illnesses, perhaps due to decreased resistance factors, as animals age.

Predator-prey relationships among animals are particularly significant as causes of death. Thus, the effect of the environment on animal aging and death requires more investigation. Do animals age more quickly if they are objects of prey? Do animals relate to stress in ways similar to those of people, thus showing signs of wear and tear that are seen with premature aging under stress? Are there risk factors among animals that affect their life span? These are some of the questions that remain to be answered on the topic of aging among animals.

—Kristen L. Mauk

See also: Birth; Competition; Death and dying; Demographics; Diseases; Growth; Life spans; Natural selection; Physiology; Population analysis; Population fluctuations; Population genetics; Population growth; Predation; Wildlife management; Zoos.

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ALLOSAURUS

Type of animal science: Classification
Fields of study: Evolutionary science, paleontology, physiology

Allosaurus *is the archetypal allosaurid, and was the dominant carnosaur of the Late Jurassic.* Allosaurus *is best known from the remains of at least sixty specimens collected at the Cleveland-Lloyd dinosaur quarry in Utah.*

Principal Terms

CARNOSAURS: the largest meat-eating animals to have lived on land

MESOZOIC ERA: the middle era of the Phanerozoic eon, 250 million to 65 million years ago

SAUROPODA: large, quadrupedal herbivorous dinosaurs that lived from the Early Jurassic to the end of the Cretaceous

THEROPODA: "beast foot"; dinosaurs that lived from the Late Triassic to the terminal Cretaceous extinction event; most predatory and carnivorous dinosaurs belong to this group

Carnosaur theropods are divided into two principal families, the Allosauridae and Tyrannosauridae. The allosaurids include all carnosaurs of the Early Jurassic to Early Cretaceous age that have been studied thoroughly enough to be assigned a family lineage. All mature allosaurids were five meters or more in length, had large skulls, short, powerful necks, very short forelimbs, massive hind limbs, and long tails. *Allosaurus* is the best-known carnosaur genus and the archetypal allosaurid.

Remains of *Allosaurus* ("different reptile") were first recovered in Grand County, Colorado, in 1869, but a full skeleton was not discovered until 1883, in the Garden Park Quarry, Fremont County, Colorado. Since these initial discoveries, numerous allosaur remains have been recovered in North America, most notably from the Morrison Formation in the western United States. The most spectacular discovery occurred in Utah in 1927 at the Cleveland-Lloyd Quarry, where some ten thousand bones, representing at least sixty individual allosaurs, were identified. The quarry has provided examples of individual allosaurs ranging in size from twelve-meter-long adults to three-meter-long juveniles. It is speculated that the quarry may have been a predator trap, similar to the Pleistocene-age Rancho La Brea Tar Pits in Los Angeles, California. One unfortunate feature of the Cleveland-Lloyd Quarry's collection of bones is that no articulated skeleton has been recovered there. The stratigraphic range and large numbers of allosaur fossils recovered in North America suggest that packs of allosaurs pursued prey animals all across the Jurassic topography, and that allosaurs were the dominant predator for nearly twenty-five million years.

A unique feature of *Allosaurus* was its lightly constructed skull, which had distinctive sham-rimmed ridges above and along the nasals and a tall, triangular hornlet in front of and above the eye orbits. The skull in an adult was about ninety centimeters long, relatively long in comparison to both its body size and to the skulls of other carnosaurs. Allosaur skulls have loose joints between some of the lower skull bones and also between several bones of the lower jaw. These flexible jaw joints probably allowed for expansion of the gullet so that large chunks of food could be swallowed. Above the jaws, the skull was lightly constructed, with several large, lateral spaces in front of and behind the eye. These spaces may have helped to lighten the skull, making it easier

Image Not Available

for *Allosaurus* to move its head. Allosaur eyes were twice as large as those of any other carnosaur, suggesting the animal hunted in both dim light and bright sunshine. Allosaurs had back and front serrated, recurved teeth, positioned far forward in the jaws and in front of the eye sockets, that could be used for stabbing, killing, and dismembering prey. Like tyrannosaurs, allosaurs had an enlarged transverse crest at the back of the skull, atop the braincase, supporting powerful cervical muscles. These muscles allowed the head to be held almost above the shoulders rather than extended forward. Allosaur forelimbs were large and powerfully muscled, having three large, sharply pointed, curving claws, the inner being the largest. These claw-tipped arms were probably used for mating, slashing, holding prey, and dismembering carcasses. Allosaur hind limbs were massive, with five-toed feet, of which only three toes supported weight. The allosaur body was rather squat and was balanced over the hip structure by a massive, muscular tail. Allosaurs were well-adapted predators, but their physiology suggests to many paleontologists that, individually, they may not have had the power or speed to overtake and kill large Late Jurassic sauropods. It has been suggested that allosaurs may have hunted in packs, ambushed prey, or been simply advantageous predators and carrion scavengers. The Cleveland-Lloyd Quarry discoveries suggest that, in that locale, allosaurs and other predatory theropods engaged in feeding frenzies when sauropods and other theropods wandered into a muddy bog and were trapped in slimy ooze. The immobilized prey were then swarmed by predators, who in turn became trapped in the bog and died.

—Randall L. Milstein

See also: Carnivores; Dinosaurs; Fossils; Paleontology; Predation; Prehistoric animals; Reptiles; *Tyrannosaurus*.

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ALTRUISM

Type of animal science: Behavior
Fields of study: Evolutionary science, genetics, zoology

Altruistic behavior involves an individual's sacrifice of self in order to help others. In some animals, altruism appears to be genetically determined.

Principal Terms

ALTRUISM: sacrifice of self to aid another; subjugation of the needs of the individual to the needs of another or to the needs of the group

EGOISM: self-interest

HYMENOPTERA: an order of highly specialized insects (including bees, ants, flies, and wasps) that often associate in large colonies and have a complex social organization

KIN SELECTION: a phenomenon by which acts of altruism can help pass on genes for altruism by improving the survival of kin and their offspring

RECIPROCAL SACRIFICE: one explanation for acts of altruism among unrelated animals; an individual sacrifice is made under the assumption that a similar sacrifice may in turn aid the individual in the future

SELECTION: a process that prevents some individuals from surviving and propagating while allowing others to do so

TRAIT: a genetically inherited characteristic

Those who study behavior have observed that on occasion individuals act altruistically. In other words, they appear voluntarily to put the needs of their group or of another individual ahead of their own needs. According to some scientists, there have been examples in nature where a particular species might not have survived had there not been sacrifice by some on behalf of the many. One important question is whether this so-called altruism has been a matter of voluntary choice or whether it has occurred as a part of the selection process, making it, therefore, an involuntary response.

Group Dynamics

Of interest to a wide group, including psychologists, sociologists, philosophers, and political scientists, are the questions of whether altruism is desirable behavior—perhaps even to the exclusion of egoism—and whether altruism may be necessary for human survival. Some wonder whether such behavior is necessary, whether it can be learned, and whether humans will voluntarily choose to learn it. Biologists and geneticists have been left the problem of determining, if possible, whether the tendency for altruism is inherited, that is, instinctual, or learned. Unfortunately for scientists, the study of human beings in social groups in the wild is virtually impossible. However, the study of animal behavior, primarily in native habitats, has provided some insight, although it must be recognized that different species have solved problems of survival in different ways.

Animals of the same species are bound to consort, if only for mating purposes. Most species are, in fact, found to live in groups, not only for purposes of reproduction but also because sources of food attract individuals to the same places and because congregation provides better protection from predators. It is common in nature for groups to form because their individuals have the same physical needs, and such groups may stay together as long as the needs of those individuals can be met. This does not necessarily mean that there exists in the group any loyalty or even any recognition of individuals as members of the group. In more highly developed societies, however, groups such as families or tribes develop. In animal life, two or more adults and their offspring often form close bonds and tend to exclude those who are not related. Each recognizes the others as being members, and membership is restricted to those who are among the founders or who are born into the smaller group and who conform in recognizable ways to the norms of the group. Hierarchy or rank is recognized, and often there is a division of labor within the group.

It has been demonstrated that those species which spend a large amount of time providing for their young tend to have developed higher social orders. Humans, for example, must care for their young much longer, before these young are able to become independent, than must many of the lower forms of animal life. Humans are aware of a bond that almost always exists between parent and child and of the spirit of mutual support and a cooperation that may exist even in the extended family. Cooperative behavior within such a familial group may be considered to benefit all members. Because such behavior is not consistent, however—there are times when such bonds do not exist and when families are not cooperative—such behavior cannot necessarily be attributed to predisposition. Some have argued that in primitive animal societies, so-called altruism may have evolved of necessity in order to achieve reproductive success, but that in human society there may be no evolutionary explanation for the phenomenon. Indeed, it could be argued that pure altruism, for humans, might be self-defeating and therefore unlikely to have developed as an inherited trait.

Kin Selection and Reciprocal Sacrifice

Evidence has been gathered in the study of Hymenoptera, which provide food for their young, that certain members of the population forage for the group while others lay eggs and remain at the nest to guard them. Where such behavior has evolved, through the necessity of feeding and protecting those who will propagate their kind, the foragers may be labeled altruistic: They have sacrificed their own reproductive possibilities for survival of the group. Some have questioned whether this phenomenon can truly be labeled altruism, however, because the donor appears to have no choice (conscious purpose is very difficult to assess in animals). Moreover, some researchers wonder how the traits that favor altruistic behavior can survive and become dominant in a group if those having the traits deemed desirable are not allowed to reproduce. With the use of mathematical models, it has been demonstrated that such traits can be preserved only within the family unit. Among close relatives, the traits appear with enough strength that they will be reproduced in a greater concentration, thereby compensating for the loss suffered by the sacrifice of the donors. This phenomenon has been referred to as kin selection, because it occurs in groups that have strong recognition of membership—to the extent that there exists aggressive defense against intruders, even of the same species. Discrimination against outsiders is an important facet of altruism of this type. The willingness of an individual to provide for others at the expense of its own interests diminishes as the degree of relatedness decreases.

Most parental behavior would not be labeled altruistic, since it is in the interests of the parent to care for the offspring in order to ensure the survival of the parent's genes. Of perhaps more interest than what happens among closely related members of a group and even between parent and offspring is the question of what motivates sacrifice on the part of an individual when no close relationship with the recipient exists—for example, a male animal coming to the rescue of an unrelated male animal who is being attacked by a third male of the same species. One theory maintains that these acts of personal sacrifice are performed on the chance that reciprocal sacrifice may occur at some future time. Whether this type of altruism can occur through natural selection, which acts through individuals, is an interesting question.

Models have shown that in a population where individuals are likely to encounter and recognize one another on a frequent basis, it is possible that reciprocal exchanges can take place. Individual A might be the donor on the first encounter, individual B on the second. This theory requires that the two must have a high probability of subsequent encounters and that the tendency for altruism must already have been established through kin selection. Because animals are usually suspicious of strangers on first encounter, it is necessary to speculate that in its beginning, altruism was a selected-for trait in very small groups where strangers were not only nonhostile but also likely to be relatives and likely to be met again. This type of behavior, in which individuals act in a manner not to their own advantage and not in order that their own genes or the genes of relatives will survive, is done, in theory, with some expectation of imagined reciprocal gain. How this type of behavior has come about, however, is a matter requiring further study.

Another question concerns how much culture is an influence on the development of a hereditary tendency toward altruism. Some have suggested that after generations and generations of cultural emphasis on the need for altruism, it might come to have a genetic basis. There is little hard evidence that this would occur. On the other hand, humans have had a very rapid cultural evolution, and it is possible that they may have had strong genetic propensities for altruism, which have been culturally overlaid. Some argue that biology and culture evolve simultaneously—that the culture is formed as a result of the imposition of genetic factors while, at the same time, genetic traits are evolving in response to cultural change. In order to understand the source of altruism in humankind, one must study such behavior in the context of many factors in human development—biological as well as social, cultural, economic, and ecologic.

Studying Altruistic Behavior

Those investigating the sources of altruism usually begin with a thorough understanding of whatever organism is the subject of the study. When the insect or animal cannot be studied in the wild, the ethologist tries to simulate the important features of the natural habitat in a captive environment, at least in the beginning. Models are devised, based on observable data; formulas are employed; and projections are made which provide a basis for speculative argument when absolutes cannot be assured.

By observing, it is possible to determine whether various bits of evidence of altruism exist within a population. Altruism may be manifested in as simple a way as the sharing of food when there is a scarcity. In some populations, one might observe a division of labor in which some forfeit their reproductive possibilities in order to care for the offspring of others. This phenomenon introduces the question of how altruism can survive in a population in which the genetic traits favoring the behavior are most evident in the individuals that do not reproduce themselves. It has been shown that the tendency for altruism can be perpetuated only within the family unit, where the same genetic tendency exists to some degree in members that engage in reproductive activity; this can be demonstrated by a mathematical formula.

Each individual bears the inheritance coefficient or relatedness coefficient r. Offspring share with each parent an average of half of the genetic traits of each ($r = \frac{1}{2}$). Offspring share with each grandparent one-fourth of the genetic traits of each of the older generation ($r = \frac{1}{4}$); the same coefficient exists with cousins. Were the altruists not to reproduce, it would be required, in order for the trait to be passed on, that the reproductive chances of their siblings more than double or that the reproductive chances of their cousins more than quadruple. For the sacrifice to be of value, the genetic relationship must be close, according to the demonstration. The case has been made that in societies having evolved according to this principle, there is a diminishing willingness to put the interests of others ahead of one's own as the degree of kinship decreases.

In societies where males are produced from unfertilized eggs and females from fertilized ones, female offspring of a mated pair have a high relatedness coefficient ($r = \frac{3}{4}$). The altruists among the female siblings will benefit more, regarding their genetic potential, by caring for their sisters than for their own offspring, and it can again be observed that sacrifice is more likely to be made on behalf of the member that is more closely related.

The Value of Altruism

If altruism exists in nature, and if it has come about through natural selection, then one can argue that it must be a behavior with value. When applying the human connotation to the term altruism, however, one must consider the role of choice in the manifestation of the behavior. Humans claim to admire acts of unselfishness that are seemingly done with no expectation of reward. The admiration would diminish or become nonexistent, however, if there were to be proof that the act was performed because of some primitive biological predisposition rather than because of a decision on the part of the donor. Therefore, it is necessary to make the distinction, when discussing the importance of altruism, as to whether one is referring to the acts of human beings that are performed in the face of emergency or tragedy, where a sacrifice is made as a matter of choice, or whether the intent is to consider altruism as it occurs in other creatures and seems to be involuntary.

In the case of nonhuman forms, altruism as an act of voluntary sacrifice is infrequent—if indeed it exists at all. Altruism, however, as an act which is dictated by genetics, is observable, and it has been shown to have been necessary for the survival of certain species. Where animal societies have formed in which some members of the society have spent their lives caring for the offspring of others or performing other sacrificial behavior which benefits the group, there can be little doubt that such altruism has been dictated by nature for its own unique purposes. Moreover, the fact that voluntary self-sacrifice on the part of human beings does exist does not automatically make it desirable human behavior any more than aggressive, even warlike behavior is automatically undesirable. The case can be made that both types of behavior are important. Perhaps the larger question is when and under what circumstances certain types of human behavior should be acceptable or desirable for the individual and for the group, and, even more important, who is qualified to decide what type of behavior is appropriate.

—P. R. Lannert

See also: Communities; Competition; Ethology; Genetics; Groups; Herds; Infanticide; Insect societies; Instincts; Learning; Mammalian social systems; Packs; Pair-bonding; Reproductive strategies; Territoriality and aggression.

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AMERICAN PRONGHORNS

Types of animal science: Anatomy, classification, reproduction
Fields of study: Anatomy, zoology

Pronghorns live in grasslands of plains and deserts. Almost driven to extinction, protection and good wildlife management have allowed these herbivores to become more numerous.

Principal Terms

BUCK: a male pronghorn
DOE: a female pronghorn
FAWN: a newborn pronghorn
GESTATION: pregnancy or its length
HERBIVORE: an animal that eats only vegetation
KERATIN: a tough protein plentiful in hooves and outer coverings of horns
RUMINANT: a herbivore that chews and swallows food, which enters its stomach, is partly digested, is regurgitated and chewed again, and reenters the stomach for more digestion

The pronghorn, or American antelope, can sprint sixty miles per hour and run at forty miles per hour. Pronghorns are fast almost from birth. For example, two-day-old pronghorns can outrun humans. Pronghorns are the only living members of the artiodactyl sub-family Antilocapridae, related to antelope. They are not true antelope and reportedly are almost unchanged from ancestors of two million years ago.

Pronghorns inhabit open grasslands in plains and semideserts and depend on keen eyesight to detect enemies (wolves and coyotes) and on speed to escape them. When pronghorns are afraid, their white rump hairs rise and are visible for miles. An endangered pronghorn also emits warning odors from rump scent glands. This gives other pronghorns time to seek safety.

Pronghorns are ruminant herbivores. In the summer they eat herbs, sagebrush, and grasses. During winter, pronghorns dig under the snow for hidden grass and woody plant twigs. When water is scarce, they get needed moisture by eating cacti. Pronghorns are sociable creatures, and their groupings reflect living conditions. In summer, males form single-sex groups, and females live with offspring. In winter, pronghorns form large herds containing both genders

Physical Characteristics of Pronghorns

Pronghorns are graceful, tan to reddish-brown animals, with solid, chunky bodies, strong but slender legs, and short tails. Their bellies, rump patches, and throat bars are very white. Male pronghorns (bucks) grow to body lengths of 4.5 feet, shoulder heights of 3.5 feet, and weights of 155 pounds. Bucks have back-curving horns with prongs, which is the source of the species name. The horns are up to 1.5 feet long and made of a bone core over which a black horny covering grows. The covering is shed and renewed every year, and horn core is retained. Females have much smaller horns and also shed the coverings. Pronghorns are the only known animals that shed horn covers.

Pronghorns are artiodactyl herbivores (others include cattle, pigs, goats, deer, and antelope), which walk on two toes. Their ancestors had five toes, but evolution removed the first toe, and the second and fifth toes are vestigial. The support toes—the third and fourth toes—each end in a hoof. Many artiodactyls are ruminants that chew and swallow vegetation, which enters the stomach for partial digestion, is regurgitated, chewed again, and reenters the stomach for more digestion.

Bovids, including pronghorns, have true horns (called horns henceforth). They are permanent, hard, pointy skull outgrowths that usually occur only on heads of males. Horns of females, where present, are smaller. All have bone cores, and atop the core is a tough skin layer rich in keratin, a durable covering for underlying bone. In pronghorns, horn coverings are shed and regrown every year, allowing horns to enlarge.

American Pronghorn Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Artiodactyla
Family: Antilocapridae
Subfamily: Antilocaprinae
Genus and species: Antilocapra americana
Geographical location: Throughout North America
Habitat: Open grasslands in plains and semideserts
Gestational period: Eight months
Life span: Ten years in the wild, up to fourteen years in captivity
Special anatomy: Back-curving, pronged bone horns over which a black horny covering grows; the covering is shed and renewed every year, and the core is retained

The Life Cycle of Pronghorns

In the spring, pronghorn herds separate according to age and gender. Does live in small herds and bucks live in breeding territories that they mark with scent from glands under their ears. Each buck tries to attract mates and scare away rivals by bellows or charges. Sometimes very violent battles arise over territories.

In August and September, does begin to pass through individual male territories. Some stop and mate with a buck; others move to the next breeding territory. Gestation lasts eight months and usually produces twin offspring (fawns). Fawns weigh 7 to 8.5 pounds at birth. They develop quickly and are weaned in five months. Pronghorns live about ten years in the wild and up to fourteen years in captivity

When North America was settled by Europeans, over fifty million pronghorns lived on the continent. In the early twentieth century, it was estimated that their population was only twenty thousand to twenty-five thousand, due largely to indiscriminate hunting. At that time pronghorns were protected by severely limiting their hunting. This control and careful wildlife management have raised the pronghorn population to 500,000. Wyoming, Montana, and New Mexico permit limited hunting of pronghorns.

—Sanford S. Singer

See also: Antelope; Cattle, buffalo, and bison; Fauna: North America; Grasslands and prairies; Herbivores; Horns and antlers; Ruminants.

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Despite their deerlike appearance, pronghorns are more closely related to antelopes, which have permanent horns, than to deer, which shed their antlers yearly. (PhotoDisc)

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AMPHIBIANS

Type of animal science: Classification
Fields of study: Anatomy, evolutionary science, physiology, systematics (taxonomy), zoology

Amphibians are cold-blooded animals with backbones. From an evolutionary standpoint, they link aquatic fish with terrestrial reptiles. Living forms include frogs and toads, salamanders, and caecilians.

Principal Terms

ADAPTIVE RADIATION: rapid speciation that occurs as the result of a particular group being able to exploit a new resource

CONVERGENCE: a state that occurs when two forms that are not closely related evolve structures that appear similar

DISJUNCT: pertaining to the geographic distribution pattern in which two closely related groups are widely separated by areas that are devoid of either group

METAMORPHOSIS: the complex developmental process of morphological change in which larval amphibians are transformed into adults

NEOTENY: the retention of larval features by adults; this process has played a major role in the evolution of the amphibians

PHYLOGENY: the determination of the evolutionary history of a particular group of organisms

The term "amphibian" is derived from the Greek word *amphibios*, which means "to live two lives." The majority of amphibians do this by spending the first part of their lives as aquatic, gill-breathing larvae and then transforming into terrestrial adults. The larval stage can be as short as a few weeks or as long as several years. Completion of the larval stage is triggered by hormonal events that initiate some dramatic developmental processes that are collectively termed metamorphosis.

As adults, most amphibians seek out aquatic environments in which to deposit their eggs. These can range from fast-flowing mountain streams to ephemeral roadside ditches. Most male frogs have species-specific mating calls that serve both to attract females and to prevent interbreeding. Frogs have external fertilization, in which the male typically grasps the female and encourages her to deposit her eggs, which he promptly fertilizes. Normally, both parents abandon the eggs, but some variations of this pattern exist. In contrast, most salamanders have internal fertilization, accomplished after the male has performed a stereotypical species-specific courtship "dance," which culminates with the deposition of a packet of sperm cells that is called a spermatophore. The female squats on the spermatophore, transferring the spermatozoa to a specialized holding structure called a spermatheca. The spermatozoa can be used to fertilize her eggs up to several months after mating.

Evolution of Amphibians

Amphibians were the first vertebrates to possess adaptations that allowed them to spend considerable periods of time out of the water. The earliest fossil amphibians, Ichthyostegalia, appear in the geologic record during the Devonian period, about 320 million years ago. Among experts, there is a general consensus that the ancestor of the amphibians is to be found in the primitive, lobe-finned fish (class Osteichthyes, subclass Sarcopterygii). This conclusion is based on a detailed analysis of the comparative anatomy of hard body parts that fossilized, such as the vertebrae, shoulder girdles, teeth, and skulls. Characteristics that the first amphibians shared with their fish ancestors included internal nasal openings (nares); a strange, hinged skull; and a distinctive tooth structure, in which the enamel was folded into intricate patterns.

The environmental conditions that led to the abandonment of the aquatic habitats in favor of a more terrestrial existence remain a major topic of discussion. One scenario envisions the early amphibian ancestors in an environment that was gradually becoming more and more arid. To survive, it would have been advantageous to be able to crawl on land for short distances to escape drying pools in favor of more permanent bodies of water. Those that could migrate would have survived in higher numbers than those that lacked this adaptation. A second scenario suggests that heavy predation pressures from the jawed, carnivorous fish that are known to have been abundant in the shallow freshwater lakes of the time may have selected for individuals that could leave the water, even if only briefly. A third scenario depicts competition for food as strong in the aquatic environments and much weaker on land, where several groups of invertebrates were known to be abundant.

Taxonomy of Fossil Amphibians

The taxonomy of fossil amphibians is confusing because of a series of problems. First, as a whole, the group has been conservative in the range of morphological variations that its members possess. Striking differences of taxonomic value (which would have to fossilize) are not numerous. Second, many of the skeletal elements that are important in determining the relationships of living amphibians are composed of cartilage rather than bone, and this material does not fossilize well. Because of this limitation, bony elements such as the vertebrae and skull have played a major role in determining amphibian phylogeny. The molecular techniques—electrophoresis, immunology, karyotyping, and deoxyribonucleic acid (DNA) sequencing—that have greatly assisted modern taxonomists cannot be used on fossilized materials.

The class Amphibia is further divided into orders. The number of orders recognized by various authorities ranges from eight to thirteen. All but three of these are extinct. One extinct order is the order Ichthyostegalia, which included the earliest recorded fossil amphibians. Most were small, with elongate bodies and weakly developed limbs. Many were almost assuredly aquatic, but at least some were capable of spending extended periods of time out of the water. By the time they appear in the fossil record (in the Devonian period), they were already diverse, with several different genera and species present. Another extinct group is the order Temnospondyli, which was abundant during the late Permian period and persisted until the end of the Triassic period. Most in this order were of moderate size (0.5 to 1.0 meter in body length), with low, stout profiles and flattened skulls. Some were highly aquatic and had short, weak appendages. One group, the Trematosaurs, was marine, and they are apparently the only amphibians to have been successful at invading the oceans.

The order Anthracosauria appeared in the fossil record during the Carboniferous period and was extinct by the end of the Permian. Common names of members of this group include the seymouriamorphs and the embolomeres. This order contained a mixture of terrestrial and aquatic amphibians. From an evolutionary standpoint, this order is important because from it the ancestors of the reptiles arose. Members of the order Aistopoda were eel-like, aquatic amphibians that had elongate, limbless bodies. Members of this group are characterized by a large number of vertebrae (more than one hundred) that were clearly divisible into cervical, trunk, and caudal regions.

The order Nectridea consisted of fully aquatic, salamander-like amphibians that persisted during the Carboniferous period. Appendages were weak or absent, and most fossils indicate body forms that were flattened dorsiventrally. They probably persisted by slowly crawling about the bottoms of ponds and lakes, where they preyed upon unwitting animals that crossed their paths. Amphibians of the order Microsauria were a diverse group of elongate, weak-limbed amphibians. Fossils of this group are fairly abundant from habitats that were swamplike during the Carboniferous period. The remarkable similarity in the appearance of some microsaurs with some of the earliest reptiles is considered by most authorities to be the result of convergence of body form rather than a depiction of a true evolutionary relationship. The order Proanura consists of a single froglike fossil that dates from the Triassic period on the island of Madagascar. The skull is distinctly froglike, but a tail was present, and the hind limbs had not been modified for jumping.

The taxonomy of the living members of the class Amphibia is still under considerable debate. A central question revolves around whether all currently living amphibians were derived from a single common ancestor (are of monophyletic origin) or whether they could have arisen independently from two or more separate stocks of fish (polyphyletic origin). Based on the presence of unique features, such as pedicellate teeth, a distinctive part of the inner ear, and specialized eye receptors, most experts have concluded that all living amphibians are monophyletic and can be grouped in the superorder Lissamphibia. As recognized, living amphibians are placed in the orders Caudata, Anura, and Gymnophiona.

Salamanders

Salamanders are grouped in the order Caudata. They are distributed over temperate parts of Europe, Asia, and North and South America. There are approximately three hundred species recognized, which are placed into eight separate families. Eastern North America has the greatest overall diversity, with fully seven of the eight described families represented there. One family (Plethodontidae) invaded South America and underwent a period of such tremendous speciation that approximately 60 percent of the living species of salamanders are members of this family.

Amphibians, such as this bullfrog, must keep their skins moist in order to take in oxygen and expel carbon dioxide. (PhotoDisc)

Almost everyone is quick to recognize a frog, simply by its appearance, but the same cannot be said for salamanders. The families Proteidae, Cryptobranchidae, Sirenidae, and Amphiumidae are entirely aquatic. The family Cryptobranchidae is disjunctly distributed and occurs today only in eastern Asia and eastern North America; it contains the largest living salamanders (Andrias), which attain lengths of 1.5 meters. Members of the family Proteidae are today isolated in Europe and eastern North America. They are commonly called "water dogs" and are frequently dissected in comparative anatomy classes. Members of the families Sirenidae and Amphiumidae are restricted to the southeastern United States, where they are called sirens and amphiumas, respectively. Sirens have external gills and two front legs, while amphiumas have minute front and back legs and lack external gills.

The family Ambystomatidae is entirely North American in its distribution. Most species are highly secretive and are only encountered under objects or intercepted as they migrate during spring rains to breeding ponds.

The family Hynobildae is exclusively Asian in its present distribution. Reproduction in this family is considered to be primitive, in that females lay eggs that are enclosed in a loose sac and are subsequently fertilized externally by the male.

The family Salamandridae is widely distributed in Europe, North Africa, Asia, and North America; the greatest diversity of salamandrids is found in the Eastern Hemisphere. Many species have developed highly toxic skin secretions to protect themselves from predators (human fatalities have been recorded from eating only one salamander). Many species advertise their toxicity by being very brightly and distinctly colored (this is known as aposematic coloration), and members of other, less-toxic families have also converged on these color patterns for protection from predators, a process called mimicry.

Members of the family Plethodontidae all share the unique feature of being lungless—respiration is accomplished by diffusion across their moist skins. Many species have abandoned laying eggs in water in favor of damp, terrestrial nests. Females guard the eggs until they hatch as miniatures of the adult, having completed their abbreviated metamorphosis while still in the egg.

The order Gymnophiona, on the other hand, consists of a highly specialized group of wormlike amphibians that are limbless. They inhabit tropical regions of North and South America, Asia, and Africa. Most are terrestrial burrowers and are rarely observed. Some primitive forms have dermal scales embedded in their skin. All caecilians possess a unique sensory organ called a tentacle. Fertilization is internal, and male caecilians possess a copulatory organ that is derived from the cloaca. The life history of most forms is incomplete, but in at least some, females retain eggs in the oviduct and give birth to fully developed young. Fossil caecilians are unknown.

Frogs

Finally, the order Anura is composed of tailless amphibians called frogs. Their hind legs are typically modified for jumping, their presacral vertebrae are usually eight in number, and their postsacral vertebrae are fused to form a coccyx. Frogs occur on all continents except Antarctica but reach their greatest diversity in the tropics of South America, Africa, and Asia. They have successfully invaded deserts, rivers, cold mountain streams, and arboreal vegetation. Several families have undergone tremendous adaptive radiation in the tropics, so that today almost 80 percent of the living amphibians are anurans.

Families that are widely distributed include the Bufonidae (toads), Hylidae (tree frogs), Microhylidae, and Ranidae (true frogs). These families are almost worldwide in their geographic distributions except for Australia (which lacks Bufonidae, Ranidae, and Microhylidae) and Africa (which lacks Hylidae). Toads often have dry, warty skins containing numerous glands that produce noxious, protective secretions. Tree frogs have expanded disks on the tips of their toes that have allowed them to occupy arboreal habitats unavailable to many other families.

The families Leptodactylidae, Brachycephalidae, Rhinodermatidae, Pseudidae, Centrolenidae, and Dendrobatidae reach their greatest abundance in Central and South America. The leptodactylids are a diverse assemblage that consists of nearly seven hundred species. Many of these lay eggs in specially constructed foam nests; other species have taken this a step further and deposit their eggs in damp, terrestrial situations, thereby avoiding aquatic predators almost completely. The dendrobatids are often small, brightly colored frogs that have been given the common name of poison arrow frogs because of their extremely toxic skin secretions. These secretions have been used by some Indian tribes to poison the tips of hunting arrows. Members of the family Pseudidae are unique in producing very large tadpoles that metamorphose into rather small frogs. The rhinodermatids consist of only two species, but one is unique in that the larvae do not feed and are carried in the mouth of the adult until they complete metamorphosis.

The Discoglossidae are European and Pelodytidae are Asian in their distribution patterns. The midwife toad (*Alytes obstetricians*) has an unusual reproductive mode, in that after fertilizing the eggs, the male cements them on his back and carries them to and from the water until they are ready to hatch.

The Rhacophoridae are a moderate-sized family (about 180 species), distributed over southern Africa and southeast Asia. Most members have expanded terminal digits, and some even have extensive webbing between their toes, which allows them to glide between arboreal perches. Diverse reproductive tactics also occur in this family. Several species use water-filled tree holes in which to deposit their eggs.

The family Myobatrachidae consists of a diverse group of about ninety-nine species that occur in Australia and New Zealand. One species (*Rheobatrachus silus*) is unique in its reproductive mode, which includes brooding eggs in the stomach of the female.

The family Leiopelmatidae is a small group of frogs that are disjunctly distributed in western North America and New Zealand. The tailed frog (*Ascaphus truei*) is the only frog to possess an intromittent organ that is used to transfer sperm to the female for internal fertilization. This organ has apparently evolved in response to the swift, cold streams in which the frog lives.

Bases of Characterization

As a group, amphibians are easier to characterize by the morphological features that they lack than by the unique characteristics that they possess. Missing are the scales that cover fish and reptiles (although these are not closely related structures), as are the hair and feathers associated with mammals and birds. Amphibians' skin is relatively thin, and it contains numerous glands. Large amounts of water can be lost or gained via the epidermis. In many forms, the skin serves as a major organ for respiration. Amphibians are ectothermic, which means that they do not have internal physiological mechanisms for maintaining a constant body temperature. The circulatory system is closed, and the heart is composed of three chambers (two atria and one ventricle).

The taxonomic relationships of salamanders are based primarily on the arrangement of bones of the skull, which of these bones possess teeth, and the shape of the centrum of the vertebrae. Living forms are further compared by the manner of reproduction. In general, salamanders have been relatively conservative, and characters such as the number of chromosomes have not proved especially useful in determining phylogenetic relationships. However, modern molecular techniques, such as electrophoresis, immunology, and the use of restriction enzymes, are adding to the understanding of selected groups. With these techniques, it has been possible to show that several forms (sibling species) that were indistinguishable based on morphological data are in fact genetically isolated from one another and are really distinct species.

The taxonomic relationships of frogs are also centered on differences in bony anatomy. Skull morphology, the shape of the vertebral centrum and its manner of development, and the arrangement of the bones that make up the pectoral girdle are important diagnostic characters. In living forms, molecular techniques are also shedding new light on relationships. The number of chromosomes is more variable and has more value as a diagnostic tool in frogs than it does in salamanders. The morphology of the larvae also is an important taxonomic tool.

The Importance of Amphibians

There are about three thousand recognized species of living amphibians. Yet, this number represents only a small fraction of the number of species that have been present on the earth over the past 350 million years. In many habitats, however, they still represent a major portion of the biomass, and, because ecologists often relate a group's "worth" to its biomass, amphibians can be considered major members of many terrestrial communities, often serving as keystone species for their ecological niches. Amphibians often exhibit traits such as low mobility, fidelity to breeding sites, and species-specific behaviors that are sought by ecologists and animal behaviorists for their studies. As a whole, salamanders and frogs represent some of the most thoroughly studied vertebrates.

Areas to which amphibians have contributed a significant portion of current knowledge include the evolution of mating systems, sexual selection, reproductive isolation mechanisms, niche partitioning, and community structure. Embryologists have long used amphibians to gain a basic understanding of complex development processes.

One area of extreme interest is the apparent decline of many populations of frogs and salamanders over large geographic areas, which is notably the case in western North America. The reasons for this decline are not yet known, but loss of breeding sites through habitat modification, acid rain, and competition from exotic species have all contributed to their demise.

—Robert E. Herrington

See also: Cold-blooded animals; Frogs and toads; Lakes and rivers; Metamorphosis; Pollution effects; Reptiles; Salamanders and newts; Systematics; Vertebrates.

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ANATOMY

Types of animal science: Anatomy, physiology

Fields of study: Anatomy, anthropology, developmental biology, embryology, entomology, evolutionary science, herpetology, human origins, invertebrate biology, marine biology, neurobiology, ornithology, paleontology, physiology, systematics (taxonomy), zoology

Anatomy is the branch of natural science that focuses on the structural organization of living organisms. Physiology, which is closely related to anatomy, is the study of function, activities, and processes of living organisms. It is concerned with such basic activities as reproduction, growth, metabolism, excitation, and contraction as they are carried out within structures such as the cells, tissues, organs, and organ systems of the body.

Principal Terms

COMPARATIVE ANATOMY: the study of relationships between the anatomies of different species

DEVELOPMENTAL ANATOMY: the study of the anatomical changes an animal undergoes in the process of growth

One common approach to the study of anatomy is from the viewpoint of a classification system that is based on the type of organisms studied, generally plant anatomy and animal anatomy. Animal anatomy can be further subdivided into human anatomy and comparative anatomy. Other anatomy subdivisions are developmental, pathological, and surgical anatomy and anatomical art. An example of developmental is the study of embryos, and an example of pathological is the study of diseased organs. Examples of applied anatomy are surgical anatomy and anatomical art. Anatomy encompasses the following systems: musculoskeletal, nervous, circulatory, immune, respiratory, digestive and excretory, endocrine, reproductive, and integumentary. These systems differ widely among animals, but most animals need to fulfill the functions of these anatomical structures in one way or another. For simplicity's sake, anatomy of warm-blooded vertebrate creatures will be discussed here.

Musculoskeletal System

A muscle is a tissue composed of fibers capable of contracting and relaxing to effect bodily movement. The skeleton is the internal supporting structure of a vertebrate, composed of bone and cartilage. Skeletons are bound together by tough and relatively inelastic connective tissues called ligaments. Ligaments allow the limbs, connected by joints, to move freely. Movements of the bones of the skeleton are effected by contractions of the skeletal muscles, to which tendons attach the bones. These muscular contractions are controlled by the nervous system.

Nervous System

The nervous system in vertebrates is a network of cells, tissues and organs that regulates the body's responses to internal and external stimuli. The nervous system has two divisions: the somatic, which allows voluntary control over skeletal muscle, and the autonomic, which is involuntary and controls cardiac and smooth muscle and glands. The autonomic nervous system has two divisions: the sympathetic and the parasympathetic. These divisions tend to have opposing effects. For example, the sympathetic system increases heartbeat, and the parasympathetic system decreases heartbeat. However, the two nervous systems are not always antagonistic. For example, both nerve supplies to the salivary glands excite the cells of secretion. Voluntary movement of head, limbs, and body is caused by nerve impulses arising in the motor area of the cortex of the brain and carried by cranial nerves or by nerves that emerge from the spinal cord to connect with skeletal muscles. Movement may occur also in direct response to an outside stimulus. These involuntary responses are called reflexes. Muscular contractions do not always cause actual movement. A small percentage of the total numbers of fibers in most muscles are usually contracting. This serves to maintain the posture of a limb. This slight continuous contraction is called muscle tone.

Circulatory System

The circulatory system is composed of the heart, blood vessels, and lymphatic system of the body. Blood is pumped by the heart through the right chambers of the heart, into the lungs, where it picks up oxygen, and back into the left chambers of the heart. From these, it is pumped into the main artery, the aorta, which branches into increasingly smaller arteries until it passes through the smallest, known as arterioles. Beyond the arterioles, the blood passes through a vast number of tiny, thin-walled structures called capillaries. Here, the blood gives up its oxygen and its nutrients to the tissues and absorbs from them carbon dioxide and other waste products of metabolism. The blood completes its circuit by passing through small veins that join to form increasingly larger vessels until it reaches the largest veins, the inferior and superior venae cavae, which return it to the right side of the heart. Contractions of the heart working with the contractions of the skeletal muscle propel the blood and contribute to circulation. Valves in the heart and in the veins ensure blood flow in one direction.

Immune System

The immune system is an integrated system of organs, tissues, cells, and cell by-products (such as antibodies) that differentiates self from non-self and neutralizes potentially pathogenic organisms or substances. The body defends itself against foreign proteins and infectious microorganisms by means of a complex dual system that depends on recognizing foreign patterns. The two parts of the system are termed cellular immunity, in which lymphocytes are the effective agent, and humoral immunity, based on the action of molecules.

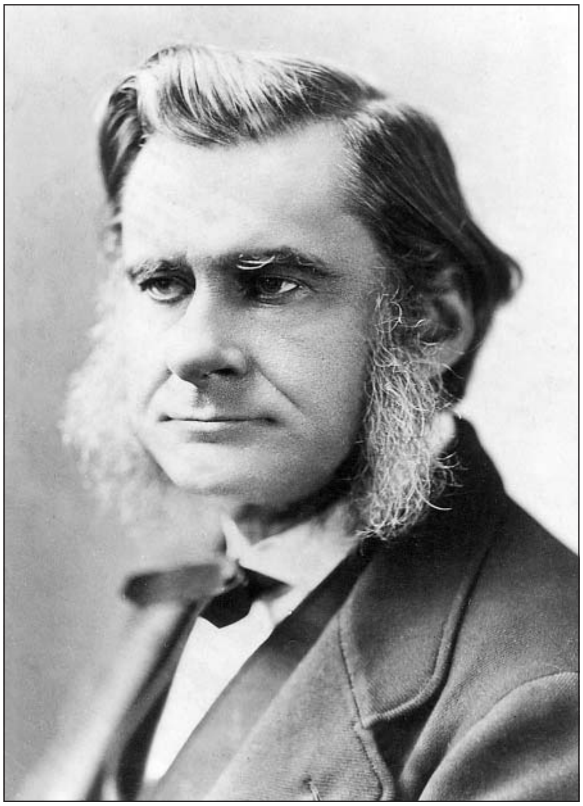
When particular lymphocytes recognize a foreign molecular pattern, termed an antigen, they release antibodies in great numbers; other lymphocytes store the memory of the pattern for future release of antibodies should the molecule reappear. Antibodies attach themselves to the antigen and mark it for destruction by other substances in the body's defense system, such as enzymes and phagocytes. The latter are cells that engulf and digest foreign matter.

Respiratory System

The respiratory system comprises the organs involved in the intake and exchange of oxygen and carbon dioxide between an organism and the environment. Respiration is carried on by the expansion and contraction of the lungs; the process and the rate at which it proceeds are controlled by a nervous center in the brain. In the lungs, oxygen enters tiny capillaries, where it combines with hemoglobin in the red blood cells and is carried to the tissues. Simultaneously, carbon dioxide, which entered the blood in its passages through the tissues, passes through capillaries into the air contained within the lungs. Inhaling draws into the lungs air that is higher in oxygen and lower in carbon dioxide; exhaling forces from the lungs air that is high in carbon dioxide and low in oxygen. Changes in the size and gross capacity of the chest are controlled by contractions of the diaphragm and of the muscles between the ribs.

Digestive System

The digestive system is composed of the alimentary canal, along with glands such as the liver, salivary glands, and pancreas that produce substances needed in digestion. Digestion starts with the ingestion and chewing of food mixed with saliva. The food passes down the esophagus into the stomach, where the gastric and intestinal juices continue the process. Thereafter, the mixture of food and secretions, called chyme, is pushed down the alimentary canal by peristalsis, rhythmic contractions of the smooth muscle of the gastrointestinal system. The contractions are initiated by the parasympathetic nervous system and can be inhibited by the sympathetic nervous system. In ruminants, the stomach has multiple sections, and chyme is passed back and forth several times between the stomach sections and the mouth for rechewing and redigestion. Absorption of nutrients from chyme occurs mainly in the small intestine; unabsorbed food and secretions and waste substances from the liver pass to the large intestines and are expelled as feces. Water and water-soluble substances travel via the bloodstream from the intestines to the kidneys, which absorb all the constituents of the blood plasma except its proteins. The kidneys return most of the water and salts to the body, while excreting other salts and waste products, along with excess water, as urine.



Thomas Henry Huxley's research in comparative anatomy helped establish the inductive method as the primary mode of scientific research. (Library of Congress)

Endocrine System

The endocrine system involves internal secretions related to the function of the endocrine glands such as the thyroid, adrenal, pituitary. Hormonal secretions from these glands pass directly into the blood stream. An important part of this system, the pituitary, lies at the base of the brain. This master gland secretes a variety of hormones, including hormones that stimulate the thyroid gland and control its secretion of thyroxine, which dictates the rate at which all cells utilize oxygen; control the secretion in the adrenal gland of hormones that influence the metabolism of carbohydrates, sodium, and potassium and control the rate at which substances are exchanged between blood and tissue fluid; control the secretion in the ovaries of estrogen and progesterone and the creation in the testicles of testosterone; control the rate of development of the skeleton and large interior organs through its effect on the metabolism of proteins and carbohydrates; and inhibit insulin—a lack of insulin causes diabetes mellitus.

The posterior lobe of the pituitary secretes vasopressin, which acts on the kidney to control the volume of urine; a lack of vasopressin causes diabetes insipidus, which results in the passing of large volumes of urine. The posterior lobe also elaborates oxytocin, which causes contraction of smooth muscle in the intestines and small arteries and is used to bring about contractions of the uterus in birth. Other glands in the endocrine system are the pancreas, which secretes insulin, and the parathyroid, which secretes a hormone that regulates the quantity of calcium and phosphorus in the blood.

Reproductive System

The union of male sperm and the female ovum accomplishes reproduction. In coitus, the male organ ejaculates millions of sperm into the vagina, with some making their way to the uterus. Ovulation is the release of an egg into the uterus; the uterus is prepared for the implantation of a fertilized ovum by the action of estrogens. In some primates, if a male cell fails to unite with a female cell, other hormones cause the uterine wall to slough off during menstruation. After childbirth, prolactin, a hormone secreted by the pituitary, activates the production of milk.

Integumentary System

Skin, the natural outer covering of the body, is an important part of the integumentary system. The skin is an organ of double-layered tissue stretched over the surface of the body and protecting it from drying or losing fluid, from harmful external substances, and from extremes of temperature. The inner layer, called the dermis, contains sweat glands, blood vessels, nerve endings (sense receptors), and the bases of hair and nails. The outer layer, the epidermis, is only a few cells thick and contains pigments, pores, and ducts, and its surface is made of dead cells that it sheds from the body. The sweat glands excrete waste and cool the body through evaporation of fluid droplets; the blood vessels of the dermis supplement temperature regulation by contracting to preserve body heat and expanding to dissipate it. Separate kinds of receptors convey pressure, temperature, and pain. Fat cells in the dermis insulate the body, and oil glands lubricate the epidermis.

—Mary E. Carey

See also: Antennae; Beaks and bills; Bone and cartilage; Brain; Cell types; Claws, nails, and hooves; Digestive tract; Ears; Endoskeletons; Exoskeletons; Eyes; Feathers; Fins and flippers; Fur and hair; Heart; Horns and antlers; Hydrostatic skeletons; Noses; Kidneys and other excretory structures; Lungs, gills, and tracheas; Muscles in invertebrates; Muscles in vertebrates; Scales; Sense organs; Shells; Skin; Tails; Teeth, fangs, and tusks; Tentacles; Wings.

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ANIMAL KINGDOM

Types of animal science: Classification, ecology, evolution, geography
Fields of study: Ecology, evolutionary science, genetics, population biology, systematics (taxonomy)

Among all the species that have been identified, about 75 percent are animals. Animals flourish on land, in the seas, and in the air. Today, twenty-seven distinct phyla of animals come in diverse forms and shapes, and live in almost every habitat. Together, these animals make up a crucial portion of all ecosystems.

Principal Terms

CLASS: the taxonomic category composed of related genera; closely related classes form a phylum or division

INVERTEBRATES: animals lacking a backbone

PHYLOGENY: the evolutionary history of a group of species

PHYLUM: the taxonomic category of animals and animal-like protists that is contained within a kingdom and consists of related classes

SPECIES: a group of animals capable of interbreeding under normal natural conditions; the smallest major taxonomic category

TAXONOMY: the science by which organisms are classified into hierarchically arranged categories that reflect their evolutionary relationship

VERTEBRATES: animals with a backbone or vertebral column

Human perception of the animal kingdom tends to focus on relatively large vertebrates. However, these large vertebrates are true minorities, accounting for just a tiny fraction of the animal world. Over 97 percent of animal species are invertebrates, the earliest animals to emerge. Insects and arthropods make up the vast majority of animal species and a huge percentage of the individual animals on earth. Most other animal phyla are also far more diverse and numerous than vertebrates. All vertebrates together constitute only part of a single phylum, Chordata. In simple terms, the small and boneless creatures called invertebrates dominate the animal kingdom. They live bountifully in diverse habitats: in pond muck, on ocean bottoms, in treetops, beneath leaf litters, and in many other environments.

Animals are easy to identify but difficult to define due to the diversity and complexity of all creatures in this kingdom. The best approach relies on a set of common characteristics that distinguish animals from individuals of other kingdoms, a field called systematics. First, animals are multicellular (made up of many cells). Second, animals are heterotrophic, obtaining nutrients and energy by consuming other organisms. Third, animals are usually capable of sexual reproduction, although other reproductive styles may exist. Fourth, animal cells contain no cell wall. Fifth, animals are mobile during at least some stage of their lives. Finally, animals are usually capable of rapidly responding to external stimuli through their nerve cells, muscle, or contractile tissue. These six characteristics taken together distinguish animals from other living creatures.

Based upon evolutionary theories, animal phyla show trends toward increasing cellular organization and complexity. In the most ancient phylum of animals, sponges, individual cells may have specialized functions but act independently, hence are not organized into tissues or organs. Cnidarians (jellyfish and their relatives), the phylum most closely related to sponges, have well-defined tissues that coordinate movement and sensory information. Flatworms, the next phylum to emerge, have organs and organ systems, such as a reproductive system. Organ systems are also found in all the remaining, more recently emerged animal phyla. The trend toward increasing complexity goes beyond the level of cellular organization and specialization. It includes the presence and type of symmetry in body plan, the degree of development in sensory organs and brain, the presence and type of body cavity, the presence of body segmentation, and the structure of the digestive system. The members of the latest phylum, including vertebrate animals such as seals, whales, horses, and humans, also exhibit a trend toward increasing size and sophistication of the brain.

Based upon these traits, animals can be grouped into twenty-seven phyla. The nine major phyla include, from simple to more complex, Porifera (sponges), Cnidaria (hydra, anemones, and jellyfish), Platyhelminthes (flatworms), Nematoda (roundworms), Annelida (segmented worms), Arthropoda (insects, arachnids, and crustaceans), Mollusca (snails, clams, and squid), Echinodermata (sea stars and sea urchins), and Chordata (primarily vertebrates).

The Sponges, Hydra, Anemones, and Jellyfish

Sponges (phylum Porifera) are the simplest multicellular animals that lack true tissues and organs. They resemble colonies in which single-celled organisms live together for mutual benefit. However, individual sponge cells are able to survive and function independently. All sponges, whether single-celled or colony-like, have a similar body plan. The body is perforated by numerous tiny pores, through which water enters, and by fewer large holes, through which water is expelled. Water travels within the sponge through canals where oxygen is extracted and microorganisms are filtered into cells for digestion. Some sponges can grow more than a meter in height. So far, more than five thousand species of sponges have been identified, all of which are aquatic and most of which are marine.

The phylum Cnidaria is composed of hydra, anemones, and jellyfish. Clearly more complex than sponges, cnidarians have distinct tissues, including contractile tissue that acts like muscle and nerve net that spreads through the body and controls movement and feeding behavior. However, they lack true organs and a brain. Their beautiful and diverse body shapes are variations of two basic body plans: tentacled and jellyfish-like. Tentacles attach to rocks and reach upward for grasping, stinging, and immobilizing prey. A jellyfish-like body can easily be carried by ocean currents. Cnidarians are radially symmetrical, with body parts arranged in a circle around the mouth and digestive cavity. All cnidarians are predators, but none hunt actively. They rely upon their tentacles to grasp small animals floundering by chance into contact with them. Once stimulated by contact, special cells called cnidocytes explosively inject poisonous or sticky darts into prey. The immobilized prey is forced through an elastic mouth into a digestive sac. The undigested food is expelled through the mouth. Cnidarians may reproduce sexually or asexually. Of the nine thousand or more species in this phylum, all are aquatic and most are marine. One of these, the corals, is of particular ecological importance.

Diverse Forms of Worms

Flatworms (phylum Platyhelminthes) are more complex than cnidarians, yet are the simplest organisms with well-developed organs. Their bilaterally symmetrical bodies are an adaptation to active movement, as found in other, more complex organisms. Their sense organs, consisting of light-detecting eyespots and cells responsive to chemical and tactile stimuli, inform their bodies whether to feed, forge onward, or retreat. When the flatworm encounters smaller animals, it sucks its prey through a muscular tube called the pharynx, located in the middle of the body. Compared with more complex organisms, however, flatworms lack both respiratory and circulatory systems. They can produce sexually or asexually. Most flatworms are hermaphroditic, possessing both male and female sex organs within one body. Examples of flatworms include parasitic tapeworms and flukes.

Roundworms (phylum Nematoda) reside in nearly every habitat on earth. Of an estimated 500,000 species, only 10,000 have been named. They are largely microscopic, although some may reach a meter in length. They have a rather simple body plan, with a tubular gut that runs from mouth to anus. A fluid-filled hydrostatic skeleton provides support and a framework against which muscles can act. They also have a tough but flexible cuticle on the outside of the body and a simple brain that processes and transmits information. They do not have circulatory or respiratory systems. Most nematodes reproduce sexually, with the male fertilizing the female by injecting sperm inside her body. Nematodes play a crucial role in breaking down organic matter in ecosystems. Some are also parasites to humans or other animals, such as hookworms that infect human feet, *Trichinella* worms that cause trichinosis, and heartworms that attack dogs' hearts.

The prominent feature of the phylum Annelida is segmentation of the body into a series of repeating units; hence they are called segmented worms. Each body compartment is controlled by separate muscles, collectively capable of far greater complexity of movement than in other worms. A well-developed closed circulatory system distributes gases and nutrients throughout the body. Primitive hearts, in essence short, expanded segments of specialized blood vessels, can contract rhythmically. A simple brain located in the head plus nerve cords along the length of the body and within each segment control movement and other activities. Among the nine thousand or so species identified, the best known examples are the earthworm and its relatives, and leeches. However, the largest annelids, the polychaetes, live primarily in the ocean.

The Arthropods, Molluscs, and Echinoderms

The phylum Arthropoda comprises insects, spiders, and crustaceans. By any standard, whether number of individuals or number of species, arthropods are the most dominant animals on earth. A mere 10 percent of animals described in this phylum constitutes one million species, including insects (class Insecta), spiders and their relatives (class Arachnida), and crabs, shrimp, and their relatives (class Crustacea). The enormous success of arthropods is due to several adaptational features. The exoskeleton allows precision movement; segmentation generates specialized and more effective organ systems; these, in turn, allow higher efficiency in gas exchange, circulation, and information processing. Most arthropods have well-developed sensory systems, including compound eyes and acute chemical and tactile senses. Of the three classes, insects are the most diverse and abundant, accounting for 850,000 species identified. Insects usually have three pairs of legs plus two pairs of wings. Their ability to fly helps them escape from predators and find widely dispersed food. Insects normally go through radical changes in body form through metamorphosis, from egg to larva to pupa and finally to winged adults that mate and lay eggs.

Spiders and scorpions are examples of the class Arachnida. They typically have eight walking legs and are mostly carnivores, living on either a liquid diet of blood (ticks and mosquitoes) or predigested prey (scorpions). Simple eyes equipped with a single lens are extremely sensitive to movement, which helps in catching prey or escaping from predators. There are about fifty thousand species of arachnids. Crab, shrimp, crayfish, and their relatives make up the class Crustacea, comprising roughly thirty thousand species. They are largely aquatic, with a wide variation in size. Except for two pairs of sensory antenna and mostly compound eyes, they are highly variable in body form.

As their name suggests, members of the phylum Mollusca—snails, clams, and squid—have a moist, muscular body supported by a hydrostatic skeleton. Some have a shell of calcium carbonate to protect their body; others escape predation by moving swiftly or by being distasteful if caught. They have an open circulatory system. Their nerve systems are more advanced than those of arthropods in that more nerves are concentrated in the brain. Reproduction is sexual; some species have separate sexes, and others are hermaphro-

Coral Reefs: Beautiful Undersea Gardens

Coral reefs are created by the concerted activities of corals and algae. Reef-building corals are involved in a mutualistic relationship with single-celled algae, which live embedded in the coral tissue. The algae benefit from the high mineral levels in the coral tissues. In return, algae provide food for the coral and also help produce calcium carbonate, the limestone that forms the coral skeleton. The limestone persists long after the coral's death, serving as a base to which many other algae may attach. The cycle continues for thousands of years until massive coral reefs are formed.

Corals require warm temperatures and clear water to thrive, and thus are most abundant in the tropical waters of the Pacific and Indian Oceans, the Caribbean, and the Gulf of Mexico, where the maximum water temperatures range between 72 degrees and 82 degrees Fahrenheit. Coral reefs form undersea habitats that become the basis of ecosystems with stunning diversity and breathtaking beauty. They are home to bottom-dwelling animals and provide shelter and food for the most diverse collection of invertebrates and fish in the ocean. A single reef may be home to three thousand species of fish, invertebrates, and algae.

Coral reefs are extremely sensitive to certain types of disturbance, including silt caused by soil erosion, sewage and runoff from agriculture on nearby land, and overfishing. On December 11, 2000, it was reported that more than 25 percent of the world's coral reefs have been lost to these disturbances. Approximately 70 percent of coral reefs could be gone within fifty years without effective remedy. This would prove devastating to marine ecosystems, as well as to the economies of many nations.

ditic. Together, there are five thousand species identified, among which clams, octopuses, oysters, scallops, snails, and squid are the most familiar.

Sea stars, sea urchins, and sea cucumbers compose the phylum Echinodermata. These animals are mostly marine, and adults have radial symmetry and lack a head and distinct brain. They have very simple nervous systems, and hence move very slowly on numerous, tiny, tube feet. They feed on algae or small particles sifted from sand or water. Most species reproduce by releasing sperm and eggs into the water, where larvae develop upon fertilization. Another distinct feature of echinoderms is their endoskeleton, a hard shell of calcium carbonate enclosed by an outer skin.

Phylum Chordata: The Tunicates, Lancelets, and Vertebrates

Animals of this phylum exhibit tremendous diversity in form and size. They include small sea squirts and lancelets (invertebrates), and birds, fish, amphibians, reptiles, and mammals (vertebrates). Members of this phylum possess four characteristics at some stage of their lives: a notochord—a stiff yet flexible rod that extends the length of the body and provides an attachment site for muscles; a dorsal, hollow nerve cord at the anterior end of the notochord that becomes a brain; specialized respiratory openings called pharyngeal gill slits; and a tail that extends past the anus. There are only two classes of invertebrates in Chordata, lancelets and tunicates, both of which are small marine animals. Lancelets reside mainly in the sandy sea bottom and live by filtering tiny food particles from the water. Sea squirts, a member of the tunicates, send out a forceful jet of water in response to touch or danger. Their filter-feeding, saclike bodies move slowly via contraction.

Vertebrates are the most conspicuous animals on earth. Their backbones and other adaptations have contributed to their success. There are seven major classes of vertebrates.

Jawless fishes (Agnatha) were the earliest vertebrates to arise in the sea. Two examples are hagfishes and lampreys. The colorful hagfishes are strictly marine, living in communal burrows in mud, feeding on polychaete worms. Lampreys live in both fresh and salt water. Some lampreys are parasitic, attaching to fish with suckerlike mouths lined with rasping teeth. They live on blood and body fluids sucked from their hosts. Cartilaginous fishes (Chondrichthyes) are skillful predators, and include sharks, skates, and rays. Their skeletons are made up exclusively of cartilage, void of bone. Many shark species have several rows of razor-sharp teeth, with back rows moving forward as front teeth are lost to action or aging. Most sharks, as most skates and rays, are shy and retiring creatures that do not attack humans. A few species, however, can be deadly when irritated. Bony fishes (Osteichthyes), spread over a wide range of aquatic habitats, are the most diverse and abundant vertebrates on earth. As suggested by their name, bones rather than cartilage make up their skeletons. Of seventeen thousand species identified, all bony fishes have bladders that help them float effortlessly. Some have lungs and modified fins that work as legs, which help them to survive periodic drying in freshwater habitats.

Amphibians (Amphibia) live a double life between aquatic and terrestrial habitats. They represent the transition of life from water to land. Some adaptations, such as lungs, a three-chambered heart, and moist skin, help them live a temporary land life. However, other traits, requiring water for fertilization and juvenile development, restrict the range of amphibian habitats on land. Their double life and permeable skin have made amphibians particularly vulnerable to pollutants and environmental fouling. About 2,500 species have been identified, including frogs, toads, and salamanders. The seven thousand species of reptiles (Reptilia) identified have bodies of diverse forms. Turtles, snakes, lizards, alligators, and crocodiles are all reptiles, as well as the huge and now-extinct dinosaurs. Reptiles have more efficient lungs than amphibians, a tough, scaly skin that resists water loss and protects the body, a mechanism of internal fertilization, and a shelled egg. The diversity of birds (Aves) is revealed through nine thousand species, including the delicate hummingbird, the endangered spotted owl, and the largest bird, the ostrich. Their ability to soar gracefully in the air depends on many anatomical and physiological traits. These features include a light body with hollow bones, light wings with feathers that also provide protection and insulation, reduced reproductive organs during nonbreeding periods, a single ovary in female birds, acute eyesight, and a delicate nervous system that facilitates the extraordinary coordination and balance needed for flight. Birds, which are warm-blooded, also have four-chambered hearts that help to maintain high body temperature and a high metabolic rate, crucial for flight. The last vertebrate class, mammals (Mammalia), is represented by some 4,500 species. In addition to being warm-blooded with high metabolic rates, mammals normally possess hair, produce milk for their offspring, assume a remarkable diversity in form, and possess more highly developed brains than any other class. The bat, cheetah, elephant, mole, monkey, seal, and whale exemplify the radiation of mammals into nearly all habitats, with their bodies finely adapted to their lifestyles.

—Ming Y. Zheng

See also: Arthropods; Birds; Cold-blooded animals; Deep-sea animals; Fish; Insects; Invertebrates; Mammals; Marine animals; Prehistoric animals; Reptiles; Systematics; Vertebrates; Warm-blooded animals.

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ANTELOPE

Type of animal science: Classification
Fields of study: Anatomy, ethology, genetics, physiology

More than seventy species of antelope exist, most in Africa but some also in Eurasia and North America.

Principal Terms

ASTRAGALUS: a pulley-shaped bone between the legs and ankles of antelope
BOVINE: relating to cows or oxen
BROWSER: an animal that feeds on leaves and twigs from trees
CUD: food regurgitated and chewed a second time after its initial ingestion
HERBIVORE: an animal that only eats vegetation
SAVANNA: a grassy expanse of land with few trees

Antelope are graceful animals that can run at speeds exceeding forty miles an hour and can sustain that pace longer than most of the predators pursuing them. With over seventy species of antelope observed and identified, there is a considerable range of characteristics among them. They range in size from the diminutive royal antelope (*Neotragus pygmaeus*) that stands about ten inches high and can weigh as little as four pounds, to the eland (*Tauratragus derbianus*) that, when fully grown, can stand six feet at the shoulders and weigh almost a ton.

Although most antelope live in grasslands, savannas, and forests, the tiny dik-dik (*Madoqua*) lives in semiarid regions. Whereas most antelope are gregarious animals that travel in herds for mutual protection, the bushback (*Tragelaphus scriptus*) is an elusive animal that travels alone and is active mostly at night. It avoids other antelope except for mating. The bongo (*Boocercus eurycerus*) travels in small groups, but often, particularly in old age, is solitary.

The names of various species of antelope reflect the colonial history of the parts of Africa in which they are prevalent. Settlers from the Netherlands named the dik-dik, the wildebeest (*Connochaetes*), the blesbok, and the duiker (*Sylvicapra grimmia*). The oryx and gazelle were named by French settlers. Impala (*Aepyseros melampus*) and kongoni are names drawn from the native Swahili language.

Physical Features of Antelope

Antelope of all species are generally slim, with long legs that can carry them at considerable speed when speed is necessary for survival. Antelope appear in a variety of colors—white, black, brown, gray, golden, orange, reddish, or a mixture of these colors. The red-orange bongo is particularly striking, sporting twelve thin white stripes down its side. Baby antelope frequently have white spots and stripes that disappear in adulthood.

Although they vary greatly in size, nearly all antelope, like all bovines and regardless of size, have two horns that are hollow inside and covered with a sheath, and that vary significantly from species to species. In the males of one species, the four-horned antelope (*Tetracerus quadricornis*), there are two sets of horns. One set, on the top of the head, is about five inches long, while a second set, on the forehead, is about two inches long.

Some antelope horns are quite long. The horns of the kudu (*Tragelaphus strepsiceros*) are shaped like corkscrews and can grow to five feet. In most species, both males and females have horns that, unlike the deer's, are not shed throughout the course of their lives. Usually the horns grow out of the top of the head and sweep backward. In the addax (*Addax nasomaculatus*), the horns have a spiral shape, while in the gemsbok (*Oryx gazella*), the horns are straight and swordlike.

Regardless of shape, horns are important to antelope. When they engage in mating competition, they use their horns extensively. Their chief defense mechanisms, however, are the protection gained from traveling in large herds and their ability to outrun most of their predators.

Because their diet consists of plants, which take longer to digest than meats, antelope have larger stomachs and longer intestines than carnivores. Like other bovines, an antelope has a rumen, a first stomach where food is stored when it is eaten and from which it is regurgitated for the animal to chew as cud.

Having lost their "thumbs" and "big toes" as they evolved, antelope developed split hooves from what are essentially overgrown toenails. They stand and run on the center hooves. They have a remarkable agility in running because they have a unique bone, the astragalus, located between the leg and the foot. It is pulley-shaped at both ends, giving antelope their speed and agility.

The History of Antelope

Some fossil remains of antelope date back to the end of the Cretaceous period, sixty-five million years ago. At that time some catastrophic event, not yet clearly identified, wiped out most complex life on earth, although the smaller species of antelope perhaps survived in limited numbers.

Early Bovidae were found in Eurasia and Africa, where antelope still live, although as northern Eurasia became cooler, antelope migrated gradually to more temperate climates, where the grasses and other plants they depended upon for food grew year around.

The American pronghorn (*Antilocapra americana*) roved the plains and grasslands as far north as Alberta, Canada, and as far south as northern Mexico, although its current range is much smaller. Fossil evidence suggests that the pronghorn lived alone or in small herds during the summer but that it became part of a large herd in winter, presumably to keep warm.

Migration and Eating Habits

All antelope are herbivores (vegetarians). They usually travel slowly within the security of their herds. Because of their numbers, they can anticipate danger as they travel and avoid it when it is imminent.

As they move through their habitats, some species, such as the wildebeest (also called the gnu), graze on the grass of the savannas in which they usually live. Species whose habitat is in forests tend to eat the leaves and slender branches of trees, often standing on their hind legs to reach these delicacies. Such antelope are called browsers.

Migrations are necessary for most antelope, as they exhaust the food supply in one area and are

Antelope, such as these springboks, usually live in herds for mutual protection against predators. (PhotoDisc) forced to move on to another. During dry periods, antelope usually move to wetter areas, where grass is more plentiful than in the arid regions. Such migrations are becoming increasingly difficult for these animals because of Africa's growing population. The development of large areas of land to accommodate the increasing human population is blocking the paths antelope once followed in their quest for food.

Having no permanent shelters, antelope follow cyclical routes that may cover more than two hundred square miles in any year. Their herds usually contain several hundred animals. Some antelope may be members of one herd in summer and of another herd in winter. Some, especially the old, the unattached, and the pregnant, may take time out from their herds for temporary solitude in marshes, along riverbanks, or in thick forests. Pregnant antelope who do this usually return to their herds as soon as their young are strong enough to follow them.

In order to assure the future of the antelope, reserves have been set up in some African countries. In these reserves, animals are protected from hunters and poachers. Attempts are made to guarantee that their food supply will not be compromised.

Antelope Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateral
Phylum: Craniata
Class: Mammalia
Subclass: Theria
Order: Artiodactyla
Family: Bovidae
Tribes: Reduncini (reedbucks, waterbucks, rheboks), Alecphalini (gnus, hertebeets, impalas), Hippotragini (horselike antelope)
Genus and species: Eleven genera and twenty-four species
Geographical location: Africa, North America, and parts of Asia
Habitat: Grasslands, savannas, and forests
Gestational period: Four to ten months, depending on the species
Life span: Between fifteen and twenty years
Special anatomy: Hooves, horns, slim legs

Mating and Reproduction

Within most antelope species there is no specific breeding season. Four to ten months following mating, the female antelope usually produces a single offspring, referred to in the larger species as a calf and in the smaller species as a fawn. Although single births are most common, the duiker frequently produces twins.

Once born, the offspring is usually hidden in grass or underbrush until it is strong enough to join the herd. This protective period lasts from four to eight weeks in most species, although among the reedbucks it lasts for four months. The young of some species, such as the wildebeest, are able to run within eight minutes of being born. Because of their vulnerability to predators, after the period of hiding young antelope are usually kept within the inner areas of the herd where their mothers can monitor them. Although infant mortality is high among antelope through both predation and disease, those that survive to adulthood can expect to live for up to twenty years. Human predators have been more threatening to antelope than such predators as tigers, lions, and cheetahs. As a result, some species, such as the bonetok (*Damaliscus pygarus*), currently exist only within the protection of animal reserves.

Farmers have indiscriminately shot many antelope because these animals eat the wild grasses that the farmers need to feed their livestock. As civilization has encroached upon areas once the sole domain of wild animals, domesticated animals have brought new diseases into those areas. Many antelope, especially calves and fawns, have succumbed to such diseases.

The Speed of Antelope

Although it is reasonably intelligent and has strong senses of sight and smell, the antelope's best defensive weapons are speed and agility. The impala has been known to jump nearly eight feet high and to bound as much as thirty-three feet in a

Antelope Relatives in North America

Some zoologists think that African and Eurasian antelope are misnamed. The pronghorn antelope (*Antilocapra americana*), the only species of antelope in North America, is, ironically, dismissed by many zoologists as not being a true antelope. It is the only living member of the family Antilocapridae and, as such, is not related to the Bovidae, unlike the species of antelope generally so designated.

African and Eurasian antelope are related most closely to bovines, as the name Bovidae suggests. Members of this group have three things in common: They are vegetarians; they eat their food, then regurgitate it and chew their cuds; and they have two horns, the only exception being the male four-horned antelope (*Tetracerus quadricornis*).

Bovines in North America include such animals as wild buffalo, American bison, cows, wild sheep, and mountain goats. Although antelope are smaller and sleeker than these animals, they are closely related to them.

Most zoologists agree that the closest relative of African and Asian antelope in North America is the Rocky Mountain goat (*Oreamnos americanus*), which is a bovid. Antelope are also remotely related to deer, giraffes, camels, and pigs.

single leap. The duiker, although it lacks the strength to jump as high and as far as the impala, can move very rapidly and, when it is being pursued, does so in a zig-zag pattern. It will finally elude its pursuers by diving into dense underbrush for protection.

What gives antelope their great propulsion in running is that they raise their two front legs, one after the other, and then their two hind legs. This gives them a forward thrust virtually unequaled in the animal world.

—R. Baird Shuman

See also: American pronghorns; Cattle, buffalo, and bison; Deer; Elk; Fauna: Africa; Fauna: Asia; Fauna: North America; Goats; Herbivores; Herds; Horns and antlers; Moose; Ruminants; Ungulates.

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ANTENNAE

Type of animal science: Anatomy
Fields of study: Anatomy, conservation biology, developmental biology, entomology, herpetology, invertebrate biology

Antennae serve as a means of feeling and communication through pheromones, and are a criterion to distinguish between families in insect taxonomy.

Principal Terms

LIPOPHILIC: fat soluble or water insoluble
MASTER CONTROL GENE: a gene that singlehandedly triggers the formation of an organ or structure
MAXILLARY: pertaining to the upper jawbone
OLFACTORY: pertaining to the sense of smell

Many animals, insects, and crustaceans have antennae, which serve as feelers or communication tools. Together with the morphologies of the eyes, head, wings, legs, and body, antennae also serve as a criterion to distinguish between families.

Antennae have many forms in different species. All flies have antennae, which can be of two types. The first, found in the members of the suborder Nematocera, such as crane flies, midges, and gnats, is whiplike, with two basal segments called the scape and the pedicel, as well as a flagellum of many similar segments. The second type, encountered in all members of the Brachycera group, has a flagellum contracted into a compound third segment. Crayfish tend to shed the oldest, most distal parts of their antennule once their carapace reaches about seven millimeters in length, and new growth occurs from the proximal end of the flagellum. The antennal flagellum also serves as the multimodal sensory organ that contains mechanoreceptors and chemoreceptors in crickets.

Cockroaches use their antennae to locate a wall and to retain a constant distance from it as they move along it. While running, they may make up to twenty-five body turns per second in order to avoid collisions with outward projections. It is believed that exceptionally efficient sensory input from the flagellum of the antenna reports the exact distance from the wall in order to evoke those turns.

The trap-jaw ant, found in the warmer parts of the western hemisphere, has a jaw that moves one thousand times faster than the human eye can blink. These ants use their hair antennae to detect prey; the touch of the antenna against the prey triggers the jaws to snap shut immediately. Antennal contact appears to be prevalent also in the organization of ant colonies, especially when ants from another colony are nearby. The contact increase is proportional to the numbers of ants present, in agreement with the increased density of nest mates.

Antennae, Pheromones, and Sexual Selection

Pheromones appear to play a vital role in insect survival and in communication between members of the same species. The selection and transportation of these lipophilic messengers are achieved by carrier proteins moving through the hydrophilic sensillum lymph in the antennae toward the membrane receptors. Wing fanning appears to enhance the air penetration of silkworm moth pheromones, as well as their interception by antennae. Odor recognition and resultant behavior are achieved among the members of the

Image Not Available

Drosophila genus through sensory neurons that exist in either the antennae or the maxillary palp. A study using locusts has indicated, however, that insects fed for the final two stadia (the period of time between molts) on nutritionally adequate synthetic foods have fewer sensilla on the maxillary palps and antennae than insects fed on the normal diet of seeding wheat.

Experiments on Drosophila species indicated that homothorax homeobox genes are antennal selector genes. Biological clocks that monitor daily cyclical activity appear to exist in fruit fly tissues of the antennae and other organs. These genes showed an increasing intensity of the reporter protein as a function of adult age.

The relationship between antenna morphology and sexual selection in the cerambycid beetle (*Stenurella melanura*) indicates that males with antennal symmetry appear to win more battles with other males for a female, while females with more symmetrical antennae were much more desirable to males. Researchers have also discovered that the mating behavior in a male sphinx moth is the result of the reaction of nerve cells in his antennae to a pheromone that is emitted by a female moth's abdomen. The same scientists found out that once female moths absorb male nerve cells through the implantation of the males' antennae in their heads, these female moths exhibit male mating habits. This shows that transsexually grafted antennae alter the pheromone-affected behavior in a moth.

The olfactory blocking ability of the honeybee is severely hampered when input from one antenna is removed, resulting in the bee's inability to neutralize one odor through the effect of another odor. This is an indication that, although antennae sensory neurons are important, more central processing regions of the brain must be involved in this blocking phenomenon. Recent studies have also proposed that the chemical L-glutamate activates antennular grooming behavior (AGB) in lobsters through a mechanistic pathway that is nonolfactory.

—Soraya Ghayourmanesh

See also: Anatomy; Ants; Arthropods; Bees; Beetles; Butterflies and moths; Cockroaches; Communication; Communities; Crabs and lobsters; Crustaceans; Flies; Grasshoppers; Insect societies; Insects; Mosquitoes; Pheromones; Praying mantis; Reproductive strategies; Sense organs; Termites; Wasps and hornets.

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ANTS

Type of animal science: Classification
Fields of study: Anatomy, ecology, entomology, invertebrate biology, physiology, reproductive science, systematics (taxonomy)

There are approximately 20,000 species of ants. Ants constitute almost 3 percent of the 700,000 insect species.

Principal Terms

caste: social division of an ant colony, including workers, soldiers, queens, and males
drone: a fertile male ant
myrmecology: the study of ants
soldiers: large workers who defend the colony and often raid other colonies
workers: sterile, wingless female worker ants

Ants are insects and like all insects have three body parts: head, thorax, and abdomen. Ants have six legs, which are covered with tiny hairs. These hairs are used to clean its two antennae. The antennae are used for touching and smelling. Ants' poorly developed eyes make these sensory organs all the more important. Myrmecologists contend that ants have a very elaborate communication system. For example, when ants locate food, they create a scent path with a chemical substance from the food to the nest, allowing other ants to travel from the nest and locate the food. Ants also touch each other's antennae to communicate.

Ants live in colonies. Each colony consists of a queen, workers, soldiers, and male ants. Ants build many different types of homes. Many ants build simple mounds of dirt or sand. Other ants use small sticks mixed with dirt and sand, which makes a stronger mound that offers protection from rain. Ant mounds consist of many chambers connected by tunnels. Different chambers are used for nurseries, food storage, and resting places for the worker ants.

Ants are found in almost all terrestrial habitats, with the exception of high altitudes and latitudes. Most ant species live in the soil, although some ants live in wood, like termites. Army ants do not make a home at all, but travel in large groups searching for food.

Image Not Available

Physical Characteristics of Ants

Ant coloration can be black, earth-tone reds, pale tans, and basic browns. Ant larvae are white and grublike. They have no legs and do not move about much on their own. Their large, dark stomachs can generally be seen through their cuticles. Ant pupae look like white adult ants, with their legs and antennae pressed close to their bodies. In some species, larvae spin silk, and the pupal stage is inside a cocoon. Newly emerged adult ants are often paler than older ones.

Without wings, a male can generally be distinguished from a worker by the larger size of his body, thorax, and abdomen. All workers are females.

Ants do not have lungs. Oxygen enters through tiny holes all over the body and carbon dioxide leaves through the same holes. There are no blood vessels. The heart is a long tube that pumps colorless blood from the anterior to the posterior then back up to the head again.

The Life Cycle of Ants

Ants go through four stages of metamorphosis—egg, larva, pupa, and adult—which can take from six weeks to six months to complete. Eggs are almost microscopic in size. After weeks of feeding and molting, larva enter the pupal stage. Pupae resemble adult ants but do not move around or feed and are often encased in a silky cocoon, which is protected fiercely by the soldier ants. Adults require several days to attain complete maturity after emergence from the pupal stage.

Male ants only serve one purpose, to mate with future queen ants. The queen grows to adulthood, mates, and then spends the rest of her life laying eggs. A variety of reptiles, amphibians, spiders, and other insects prey on ants. Bats and birds kill and eat the flying males and females.

Some ant species are considered pests because they inhabit human territory or consume resources that humans need. Many species of ants have poison sacs and/or stingers in the end of the metasoma for defense against predators. Worldwide, however, ants are one of the most important predators of small invertebrates, including other insects. Ants are important dispersers of the seeds that they harvest. Ants turn over and aerate the soil as much as or more than earthworms.

—*Jason A. Hubbart*

See also: Communication; Communities; Hierarchies; Home building; Insect societies; Insects; Reproductive strategies.

Ant Facts

Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Arthropoda
Subphylum: Uniramia
Class: Insecta
Subclass: Neoptera
Order: Hymenoptera (ants, bees, and wasps)
Suborder: Apocrita
Superfamily: Formicoidea
Family: Formicidae
Subfamilies: Myrmeciinae (bulldog ants), Ponerinae, Dorylinae (army ants), Cerapachinae, Leptanillinae, Myrmecinae, Pseudomyrmecinae, Dolichoderinae, Formicinae
Geographical location: All over the world
Habitat: All continents, but not at high altitudes and latitudes
Gestational period: Reproduction occurs during the summer
Life span: Queen ants live an average of three years, but some have lived as many as fifteen years; worker ants live an average of six months
Special anatomy: Complex eyes; many species have poison sacs and/or stingers in the end of the metasoma

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APATOSAURUS

Types of animal science: Classification, evolution
Fields of study: Anatomy, ecology, evolutionary science, paleontology, systematics (taxonomy)

Apatosaurus *was a quadrupedal, herbivorous dinosaur with short forelimbs and a long tail and neck. Although often depicted wading in deep water,* Apatosaurus *actually lived on dry land.*

Principal Terms

BRACHIOSAURIDS: long-necked, herbivorous dinosaurs, whose forelimbs were longer than their hind limbs

GASTROLITHS: stones found in the gut region, that aided in the digestion of coarse plant food

NEURAL SPINE: a projection extending off the upper side of a vertebra

ORNITHOPODS: bipedal, herbivorous dinosaurs

STEGOSAURS: herbivorous dinosaurs with vertical bony plates arranged along their backbones

In 1877, Othniel C. Marsh named a headless juvenile dinosaur skeleton collected near Morrison, Colorado, *Apatosaurus* and published a complete description of the material in 1878. *Brontosaurus* was named by Marsh in 1879 based on an adult skeleton collected at Como Bluff, Wyoming. Because *Brontosaurus* had no head, Marsh added one from a nearby site in 1883. Because the skeleton of *Brontosaurus* was more complete than that of *Apatosaurus*, its skeleton was mounted at a number of museums around the United States. In 1903, Elmer Riggs concluded that the specimens of *Apatosaurus* and *Brontosaurus* belonged to the same species and, using the rule of priority by which the first name assigned is the one used, combined them under the name *Apatosaurus*. In addition, he noted that the head that had been attached to *Brontosaurus* had a short snout and spoon-shaped teeth, and belonged to another sauropod, *Camarasaurus*. Many people still recognize this dinosaur as *Brontosaurus*, while *Apatosaurus* is the name accepted by most professionals.

Characteristics

Apatosaurus was confined to the Late Jurassic era (156 to 145 million years ago) of the western United States and, perhaps, adjacent Mexico. Adults were about 21 meters (70 feet) long and 4.5 meters (14.5 feet) tall, weighing 20 tons. The long, whiplike tail was lashed about in defense. Their maximum land speed is estimated to have been from twenty to thirty kilometers per hour. Since dry habitats predominated at this time in the western United States, *Apatosaurus* had to migrate long distances to find food. Its long, straight legs were highly suitable for walking. *Apatosaurus* was gregarious and traveled in herds.

Their heads were quite small relative to their large bodies. Only one partial skull of *Apatosaurus* has been found. Because the joint connecting the skull to the spine was very weak, the skulls were often lost before burial. The eyes were located at the back of the skull, as were the nostrils. The teeth were peglike and confined to the front of an elongate snout. Because the small head lacked both the teeth and the musculature for effective chewing, *Apatosaurus* nipped off leaves that were swallowed nearly whole. *Apatosaurus* probably held its head horizontally while feeding on shrubs and other low-growth vegetation. Contemporary stegosaurs and ornithopods ate the vegetation up to a height of about three meters. *Apatosaurus* foraged at heights above three meters. The tallest trees

Apatosaurus Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Reptilia
Subclass: Dinosauria
Order: Saurischia (lizard-hipped dinosaurs)
Suborder: Sauropoda (long-necked herbivores)
Family: Diplodocidae (quadrupeds whose forelimbs were shorter than their hind limbs)
Genus and species: Apatosaurus ajax, *A. excelsus*, *A. louisae*
Note: A number of competing classification schemes exist and will probably continue to do so in the future.
Geographical location: Western United States, including Colorado, Utah, and Wyoming
Habitat: The dry habitats that predominated in the western United States during the Late Jurassic
Gestational period: Although no eggs have been found, *Apatosaurus* was undoubtedly an egg layer; the frequency at which the eggs were laid, the time it took for them to hatch, and the reproductive life span of the adults are unknown
Life span: Based on mammalian models, sexual maturity would be reached after ten years, and the life span was probably in excess of one hundred years
Special anatomy: All the diplodocids, including *Apatosaurus*, had V-shaped neural spines on the upper side of the cervical (neck) vertebrae; a taut ligament running between the arms of the V held the neck rigid so that constant muscular exertion was not necessary to hold the head up against the pull of gravity

were eaten by brachiosaurids. Gastroliths helped grind up coarse plant parts prior to their being passed on to the stomach. Bacteria were present in the digestive tract to aid in breaking down food. Ferns, the chief herbaceous plants of the Late Jurassic, would have comprised the major part of their diet, although conifers, ginkgoes, and cycads were also eaten. Flowering plants, which made up a large part of the diet of Cretaceous herbivores, such as *Triceratops*, had not yet evolved. Although *Apatosaurus* browsed on low-growing vegetation, it could also rear up on its hind legs and tail to feed in the trees, engage in combat with other members of its species, defend its young, and, at least in the males, mate.

—Gary E. Dolph

See also: Dinosaurs; Fossils; Herbivores; Paleoecology; Paleontology; Prehistoric animals; Reptiles.

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APES TO HOMINIDS

Type of animal science: Evolution
Fields of study: Anthropology, evolutionary science, genetics, systematics (taxonomy), zoology

Although the study of fossil apes has taught scientists much regarding certain aspects of primate evolutionary development, they cannot yet trace more than a general connection between the apes and hominids such as man.

Principal Terms

APES: large, tailless, semierect anthropoid primates, including chimpanzees, gorillas, gibbons, orangutans, and their direct ancestors—but excluding man and his direct ancestors

AUSTRALOPITHECINES: nonhuman hominids, commonly regarded as ancestral to man

DRYOPITHECINES: extinct Miocene-Pliocene apes; their evolutionary significance is unclear

HOMINID: an anthropoid primate of the family Hominidae, including the genera *Homo* and *Australopithecus*

HUMAN: a hominid of the genus *Homo*, whether *Homo sapiens sapiens* (to which all varieties of modern man belong), earlier forms of *Homo sapiens*, or such presumably related types as *Homo erectus*

PRIMATES: placental mammals, primarily arboreal, whether anthropoid (humans, apes, and monkeys) or prosimian (lemurs, lorises, and tarsiers)

STRATIGRAPHY: in geology, a sequence of sedimentary or volcanic layers, or the study of them—indispensable for dating specimens

Primates are an order of the class Mammalia. The Primate order is divided into two suborders. Suborder Prosimii (lower primates) includes lemurs, lorises, and tarsiers. Suborder Anthropoidea (higher primates), to which monkeys, apes, and humans all belong, is divided further into infraorders: Platyrrhini (flat-nosed New World monkeys, definitely not ancestral to man) and Catarrhini (down-nosed Old World monkeys, apes, and man). The infraorder Catarrhini includes two superfamilies: Cercopithecoidea (Old World monkeys) and Hominoidea (apes and man). Within the Hominoidea, finally, are three families: Hylobatidae (lesser apes), Pongidae (great apes), and Hominidae (man). As this classification suggests, it is now taken for granted that human ancestry—if it could be traced satisfactorily—would include forms that, on other genealogies, gave rise to lower and higher primates, Old World monkeys, and a series of now-extinct creatures that were ancestral to certain of the apes as well.

The lower primates (prosimians) first appeared about seventy million years ago. They still exist (as lemurs, lorises, and tarsiers) but have been declining for the last thirty million years, probably because of unsuccessful competition with their own descendants, the monkeys. Prosimians have five digits on each limb, but the digits have claws rather than nails, and the limbs are entirely quadrupedal. Prosimians also lack binocular vision, but they do have dentition anticipating the molar development of the higher primates.

The Higher Primate Fossil Record

The earliest evidence of any kind of higher primate—some tiny pieces of jaw found in Burma—dates from the Eocene epoch, about forty million years ago. Two creatures named *Amphipithecus* ("near ape") and *Pondaungia* ("found in the Pondaung Hills") have been proposed, each being a very primitive monkey or ape, but the evidence thus far is too sparse to ally these forms with any possible descendants. Some two million years later, in the Fayum Depression of Egypt (then a lush forest), *Apidium* and *Parapithecus* ("past ape") existed. Known only from jaws and teeth, they are the oldest known Old World monkeys presently recognized. Their dental pattern (arrangement of teeth), however, is the same as that of *Amphipithecus*. Other teeth from the Fayum, perhaps thirty-five to thirty million years old, have a different cusp pattern, more like an ape's (and a human's) than a monkey's. Possibly, then, *Propliopithecus* ("before more recent ape") is the earliest evidence of an ape line distinct from the monkey line.

The oldest apelike animal about which scientists know enough to regard it as a probable human ancestor is *Aegyptopithecus* ("Egyptian ape"), also found in the Fayum, in Oligocene deposits about thirty-two million years old. In addition to jaws and teeth, an almost complete skull and some postcranial bones (meaning those below the skull) have been recovered. Since the Fayum at that time consisted of dense tropical rain forest with little open space, *Aegyptopithecus* is assumed to have been an arboreal quadruped. (In 1871, before *Aegyptopithecus* was known, Charles Darwin had predicted that such a human ancestor existed.) It is the most primitive ape yet discovered.

Proconsul ("before Consul," Consul being a chimpanzee in the London Zoo in 1933) and *Dryopithecus* ("forest ape") were either closely related to each other or identical. *Proconsul* appeared in Africa at the start of the Middle Miocene (about twenty million years ago) and was contemporary with *Dryopithecus* in Europe and Asia about fourteen million years ago. The relatively abundant fossils of these forms have been classified by some researchers into three species, together forming an extinct subfamily, the Dryopithecinae. One species in particular, *Dryopithecus major*, regularly left its remains on what were then the forested slopes of volcanoes; males grew significantly larger than females (a situation known as sexual dimorphism). In both of these respects, Dryopithecus resembled the modern gorilla, to which it may be ancestral. Like the gorilla, *Dryopithecus major* probably walked on its knuckles. In size, it was somewhat larger than a chimpanzee. The other two species, *Dryopithecus nyanzae* and *Dryopithecus africanus*, were smaller than *Dryopithecus major* and more like the chimpanzee. Outside Africa, *Dryopithecus* has been found from Spain to China.

The Ancestors of Modern Apes and Humans

Limnopithecus ("lake ape"), found in deposits in Kenya and Uganda of about twenty-three to fourteen million years ago, is thought to be an earlier form of *Pliopithecus* ("more recent ape"). Its gibbonlike skulls, jaws, and teeth are plentiful in European sediments of Middle Miocene to Early Pliocene age—sixteen to ten million years ago. For some researchers, these two forms constitute a separate subfamily, the Pliopithecinae, which they consider to be part of the family Hylobatidae (lesser apes). In some respects, they resembled the modern gibbon, but other aspects of their anatomy were quite different. For example, *Pliopithecus* possessed seven lumbar vertebrae, whereas gibbons (and humans) have only five. It seems to have been primarily arboreal, swinging from branch to branch. *Pliopithecus* has been known since 1837 (in France), and since then some almost-complete skeletons have been recovered. *Sivapithecus* ("Siva's ape," Siva being a Hindu deity), found in India and later in Africa, is a closely related form, Miocene in age. Both the dryopithecines and the pliopithecines are often regarded as the ancestors of modern apes.

Ramapithecus ("Rama's ape," Rama being another Hindu deity), found originally as a jaw fragment in India, is remarkable for its human-looking teeth. Some researchers regard it as the earliest member of the hominid line and therefore ancestral to humans. Others, however, relate *Ramapithecus* and *Sivapithecus* to modern orangutans, seeing no direct connection to man. Though *Ramapithecus* has been recovered from Late Miocene deposits in Africa and Indian and Early Pliocene ones in India (about fourteen to ten million years ago), only teeth and jaws have been found. As a result, many opinions regarding *Ramapithecus* are highly conjectural. The most striking feature of this genus, for example, is the greatly reduced size of its canine teeth, as compared with those of earlier (as well as modern) apes. Presumably, this indicates a changed diet of some sort. However, primates also use their teeth for nondietary purposes, including weaponry and display. It has therefore been suggested that the reduced tooth size of *Ramapithecus* might indicate its having begun to use other tools or weapons; if so, none has ever been found. Another conjecture has been that climatic change brought the primates down from the trees. Once on the ground, *Ramapithecus* then developed a hunter-gatherer style of sustenance that eventually included the formation of family units (male-female bonds), tool making, and a rudimentary form of language—the beginnings of culture. Unfortunately, all that is really known about *Ramapithecus* is what can be observed from a smattering of its bones.

Finally, there was *Gigantopithecus* ("giant ape"), a huge simian with protohuman teeth (clearly not ancestral to man, however) that outlasted *Dryopithecus*, *Ramapithecus*, and *Sivapithecus* to survive in Asia for almost nine million years. The largest primate that ever evolved (exactly how large is not known), it was alive in China as recently as a million years ago. Known for its immense molars, *Gigantopithecus* was apparently the only successful ground-living savanna ape. It probably competed with early hominid forms and may have been exterminated by them.

In broad outline, then, these are the fossil apes. Since much of the evidence (all of it, in several cases) consists of teeth and jawbones, it is not surprising that conjecture has played a very active part in attempts to associate this evidence with the evolution of the hominids. Before 1980, there was widespread consensus among experts with regard to an evolutionary main line extending at least from *Aegyptopithecus* through *Dryopithecus* (or *Proconsul*) and *Sivapithecus* to *Ramapithecus*, the latter being regarded as the first hominid. However, portions of two *Sivapithecus* faces, recovered from Turkey in 1980 and Pakistan in 1982, impressed researchers with their orangutan-like characteristics. Since firm ties between *Sivapithecus* and *Ramapithecus* had already been established, it began to seem that the entire lineage pointed toward the orangs rather than toward man. Another problem is that formerly accepted dating has come into question for such important branchings of the lineage as those which separated monkeys from apes and apes from man. New genetic studies having nothing to do with either fossils or stratigraphy have presented compelling (but controversial) arguments to the effect that these branchings occurred much later than hitherto believed. A third, even more serious problem is that there is virtually no pertinent fossil evidence regarding the development of simian primates into humans for a period beginning about fourteen million years ago and lasting until the appearance of the australopithecines about four million years ago. While anthropologists and biologists continue to learn more about the ancestry of modern simians, therefore, it is certainly not the case that a reliable lineage (or even a timetable) leading from other primates to humankind has been established.

The Problems of Theorizing from Fossils

The study of fossil apes is a specialization within the broader field of vertebrate paleontology, or the study of fossil bones. Like all paleontologists, therefore, paleoprimatologists are necessarily concerned with fossils and their stratigraphic occurrence. Because primates still exist, however, it is also important to study the behavior of living examples. Since behavior reflects environmental conditions, it is further necessary to reconstruct the climate, flora, and fauna of the region and time in which the fossils were found.

No complete fossil ape has ever been found. Any understanding of what they may have looked like is therefore conjectural—an extrapolation from what has been recovered to what has not. Skulls are undoubtedly the most desirable evidence, but they are not the most durable of fossils. Teeth, which constitute the hardest parts of the primate body, are preserved more often than any other part. Some kinds of fossil ape are known either exclusively or primarily from their teeth and jaws. Ape teeth differ from human teeth in two significant respects: They are generally larger (the canines especially), and the cusp patterns on their molars differ. The arrangement of teeth in an ape's jaw, moreover, is angular, like a V; in a human, the arrangement is rounder, like a U. Inevitably, whenever jawbones or molar teeth are found, an attempt is made to place them somewhere on a continuum that runs between the purely simian (ape) and the purely human. This procedure not only distinguishes primitive apes from primitive humans, and one kind of fossil ape from another, but also gives rise to inevitable conjecture as to possible anticipations of the human line.

A major difficulty with evolutionary sequences based solely upon dental evidence is that the head and body of a given species have not necessarily evolved at the same rate. One may be surprisingly apelike, the other somewhat human. Even more specifically, the fact that jaws are changing does not necessarily mean that crania (or any other specific body parts) are changing also. On the whole, scientists do not yet understand the evolution of primate anatomy well enough to interpret present evidence or reconstruct missing parts with much reliability. In the absence of factual evidence, the form taken by prevailing reconstructions at any given time may owe as much to professional politics as to objective knowledge. The controversy regarding *Ramapithecus*, which (on the basis of facial bones) moved that genus from a central position at the base of the human lineage to a similar position on a separate orangutan genealogy, has been

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a valuable lesson in the folly of premature commitment.

Ancient Fossils and Modern Primates

Most paleoprimatologists are to some extent modern-day primatologists also, necessarily expert in the comparative anatomy of all members of the higher primates and as knowledgeable as possible regarding their behaviors and environments. It is assumed that a changing environment (one becoming increasingly arid, for example) requires behavioral modifications and that these modifications will then create selection pressures favoring some types of anatomical variation over others; thus, one species will eventually change into (or be replaced by) another. The process is not well understood, but the primates—being so intensely studied—are often regarded as test cases for competing evolutionary theories. Some researchers stress evidence to the effect that species are always changing; others believe that species are created precipitously and then tend to endure relatively unchanged until they are abruptly superseded. All that is really known at present is that the ancient apes generally conform to a partially ascertainable progression from hypothetical earlier forms to modern-day primates—with a ten-million-year gap in between.

The Importance of Fossil Apes

The fossil apes are important for four reasons: They are an important group in their own right; they are important to the development of the mammals; they are important to the development of the primates; and, they are thought to be ancestral to humankind and therefore uniquely important among all nonhuman fossil genera.

One of the unique characteristics of humans is the ability to create, preserve, and transmit knowledge. *Homo sapiens* has learned to value learning, to hoard and increase knowledge in the realization that it fortifies and enhances his existence. Humans attempt to know and understand all present-day forms of life; in order to do so, however, it must also be known how these forms came into being through time. Biology, then, is inherently evolutionary and does not sharply distinguish between plants and animals of the past and those of the present.

Insofar as an understanding of life itself is the goal of biological studies, no single form of life is inherently more important than any other. From this point of view, one would say that fossil and living apes are studied for the same reason that algae, sponges, or nematodes are. A number of biologists would maintain this view. Many others, however, believe mammals—and especially primates—to be a "higher" form of life, anatomically more complex than sponges (though not necessarily more nearly perfect) and certainly capable of more complex behaviors. No mere study of anatomy, this viewpoint suggests, can sufficiently explain a primate.

The outstanding characteristic of all primates is their intelligence. One can find surprising levels of intelligence in other animals, however: Among invertebrates, such cephalopods as the squid and the octopus have the highly developed nervous systems, senses, and brains that are normally associated with mammals. Together with some birds and social insects, all the mammals are capable of surprisingly complex behavior. Nevertheless, the higher primates constitute an intellectual elite even among the mammals. Impressive as gorillas and chimpanzees can be in this respect, it is apparent that the human mind has a capacity well beyond theirs. The brains of extinct apes are seen as having been ancestral not only to those of modern apes but also to the brain of man.

Scientists are fortunate in the number of fossil ape skulls that have been found, for they make the increasing mental capacity of the higher primates easy to establish. Limb bones and other less durable parts of the skeleton are much rarer. When available, they indicate the relative lengths of arms and legs; the nature of the shoulder (a key to arboreal existence); the relation of pelvis and femur (a key to posture); and the shapes, capabilities, and functions of hands and feet. Without such evidence, scientists have only conjectures based upon the presumed place of the genus in question within a supposed evolutionary sequence. When proposed sequences differ, though they are derived from the same sparse evidence, conflicting suppositions about the evolutionary sequence are at work.

—Dennis R. Dean

See also: Convergent and divergent evolution; Evolution: Historical perspective; Extinction; Gene flow; Genetics; Hominids; *Homo sapiens* and human diversification; Human evolution analysis; Language; Learning; Mammalian social systems; Monkeys; Neanderthals; Paleontology; Primates; Punctuated equilibrium and continuous evolution.

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ARACHNIDS

Types of animal science: Anatomy, behavior, classification, ecology
Fields of study: Anatomy, ecology, ethology, invertebrate biology, systematics (taxonomy), zoology

Arachnids are ancient members of the phylum Arthropoda and represent some of the first terrestrial animals. Arachnids are mainly beneficial to humans in that they prey upon insects.

Principal Terms

ARTHROPODA: animals having jointed legs, an exoskeleton, and a ventral nerve cord

BOOK LUNGS: a system of blood-filled diverticula that are surrounded by air pockets located in a chamber called the atrium

CHELICERAE: pincerlike mouthparts used in macerating food

PEDIPALPS: modified walking legs; these may be clawlike, as in scorpions, or have a modified structure, a palpal organ for sperm transfer, as in male spiders

PODITES: the parts of the jointed appendages of arachnids

SENSILLA: hairlike structures associated with nerves that act as mechanoreceptors and chemoreceptors

TRACHEAS: a system of branched tubes that, in some arachnids, deliver oxygen to the blood

Arachnids belong to the phylum Arthropoda, and as such have the basic characteristics of this assemblage. These characteristics include having jointed appendages, an exoskeleton, an open circulatory system, and a ventral nerve cord. The Arachnida are a subgroup within the subphylum Cheliceriformes, those arthropods with a pair of primitively pincerlike chelicerae mouthparts. Arachnids are considered to have an aquatic origin, but most present-day forms are terrestrial in nature.

Arachnids all have the following characteristics: a body that is divided primitively into a prosoma and an opisthosoma; a pair of chelicerae used as mouth parts, a pair of pedipalps that often end in pincerlike claws and are modified for prey manipulation and sperm transfer; four pairs of walking legs in the adult (juveniles may have three pairs) originating from the prosoma; absence of antennae; simple eyes in most; coxial glands at base of the legs and malpighian tubules extending between the hemocoels and gut tube used for excretion and osmoregulation; gut tube with diverticula; breathing accomplished by book gills (aquatic forms), book lungs, or tracheal tubes; and a dorsal heart.

The following orders comprise the Arachnida: Scorpiones (scorpions), Uropygi (whip-tailed scorpions), Schizomida (schizomids), Amblypygi (whip spiders), Palpigradi, Araneae (spiders), Ricinuleids, Pseudoscorpionida (false scorpions), Solpugida (wind scorpions), Opiliones (daddy longlegs), and Acari (ticks and mites).

Scorpions

The scorpions are considered to be among the earliest land animals. They are considered to be derived from water scorpions known as Eurypterids. Scorpions were established in the terrestrial environment by the Carboniferous era, but are thought to have invaded the land in the Devonian. Scorpions are mainly nocturnal and are common in desert and tropical regions. Northern climates are free of scorpions due to the extreme cold. Their bodies are segmented but are divided into three portions: an anterior prosoma (carapace) and an opisthosoma divided into mesosoma and a metasoma. The prosoma bears the mouth parts which are pincerlike chelicerae used to chew the prey and allow copious amounts of digestive juice to be poured externally over the prey. The next pair of appendages are the clawlike pedipalps that act to catch and hold prey. Scorpions have four pairs of walking legs, each usually with eight segments. The mesosoma bears the genital pores and a pair of comblike structures, the pectines, which are chemosensors for tracking prey as well as for digging burrows, along with the legs. Scorpions breathe through ventrally placed book lungs and thus avoid traveling in water. The tail segment or telson bears at least one stinging spine. A number of species are highly poisonous and their sting may be fatal.

Uropygi, Schizomida, Amblypygi, and Palpigradi

Uropygi, whip-tailed scorpions, look like scorpions, having chelicerae mouthparts and large pedipalps for capturing prey. Some species attain lengths of up to eight centimeters. Like scorpions, these forms are mainly nocturnal. Uropygans earn their name by elongating the telson into a whiplike structure, the flagellum. At the end of this organ are pair of glands that can spay acetic and caprylic acids at would-be predators. They range from arid climates to the tropics and subtropics of South America and southern United States. Some species have been introduced into Africa.

The Schizomida are small, under a centimeter in size. Like uropygans, they possess glands that spray acid, although the telson in these forms is short. The first pair of walking legs is sensory in nature. Schizomids are common in Asia, Africa, and the Americas, inhabiting leaf litter and secreting themselves under rocks and fallen trees. They are tropical and subtropical.

Amblypygi resemble whip-tailed scorpions in body form, although they lack the elongated telson. Internally they resemble spiders, but do not have fangs and use their chelicerae for tearing apart prey. The first pair of legs is sensory in nature and may be quite long in some species (up to twenty-five centimeters in length.) These whip spiders are found in tropical areas under tree bark, leaf litter, and in caves.

Palpigradi are small arachnids under three millimeters in length. About fifty-five species have been described since their discovery in 1885. Not only have they have undergone a reduction in size, but their exoskeletons are thin and colorless, facilitating the loss of respiratory organs. They have a whiplike flagellum similar to that of the Uropygi.

Arachnids have eight legs, as opposed to insects, which have six. (Corbis)

The Aranae

Spiders comprise a large arachnid group, with at least 35,000 known species. They inhabit all terrestrial environments, and some species have adapted to freshwater and estuarine areas. The body is normally in two parts, a prosoma and an opisthosoma. Spiders are organized into three subgroups: those with a persistent segmented opisthosoma, the Liphistiidae, and two groups included in the Opisthothelae, the mygalomorph or tarantula-like spiders, and the araneomorph spiders that are more familiar to most people. Spiders have fanglike chelicerae that inject venom and digestive enzymes into the prey that liquefy the internal organs in order that the spider may pump out the contents. Although all spiders are venomous, only a few species are dangerous to humans. Among these are the black widow and brown recluse spiders. Black widows, belonging to the Theridiidae or cobweb spiders, are capable of inflicting a fatal bite, owing to the neurologic aspects of their venom. Males, who are multicolored and small, are also venomous. The brown recluse spiders are fairly common throughout the southern United States. Their venom is mainly hemolytic; that is, it dissolves tissues and may create large lesions as the result of digestion of tissue. Their bite is rarely fatal. Other lethal spiders occur in Australia (the funnel web spiders) and in South America (the ctenid hunting spiders). Another major characteristic of spiders is their ability to spin silk through organs called spinnerets. The spinnerets are connected to silk glands. Silk is used for webs, cocoons for eggs and over-wintering, wrapping prey, and draglines.

Arachnid Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Arthropoda
Subphylum: Cheliceriformes
Class: Chelicerata
Subclass: Arachnida
Geographical location: All continents
Habitat: Mainly terrestrial, with some few freshwater forms found among spiders
Gestational period: Extremely variable depending upon group or individual species
Life span: Variable, but some members may live up to twenty-five years
Special anatomy: All have eight legs as adults; pincerlike mouthparts that may be modified into fangs in some groups; most members are free-living but parasites are found among the *Acarina*; includes some of the most venomous animals of the world, such as the African fat-tailed scorpion, the American black widow spider, and the Australian red back and funnel web spiders

Spiders have many sense organs that include hairs that sense vibration and touch. Other hairlike structures are hollow and are chemoreceptors. Slit organs that include the lyriform organs are slits in the cuticle that lead to sensory neurons. They are considered to be mechanoreceptors. Vision is variable in spiders depending upon the life habits of the spider, ranging from eight eyes arranged in two rows on the prosoma to a complete lack of eyes. The jumping and hunting spiders have the largest eyes capable of forming an image.

Spiders have interesting reproductive behaviors that range from rhythmic web tapping to flashing iridescent pedipalps. A male will pick up sperm deposited in a sperm web with a specialized structure on one of the pedipalps. If he is successful in approaching a female, he will mate with her by inserting the pedipalp tip into her seminal receptacle and beat a hasty retreat; otherwise the female may recycle him. The female will lay up to three thousand eggs sometime after the mating.

Opiliones

Harvestmen are found throughout the world. The carapace is broadly joined with the segmented abdomen without the usual constriction seen in spiders. The legs of most are long and spindly, hence their common name of "daddy longlegs." They are most abundant in the tropics. They have pincerlike but small pedipalps that are used to feed on small invertebrates and insect eggs. They also are scavengers. For defense, they have two repugnatorial glands that give off noxious chemicals to ward off would-be predators. Unlike other arachnids, these male spiders have a penis for sperm transfer and females have an ovipositor with which they deposit their eggs in the soil.

Acarina

Both the mites and ticks are included in this group and have the largest number of species—possibly over a million—of any arachnid taxon. They may not be a monophyletic group but one that has more than one ancestor. These forms are cosmopolitan in distribution and are either free-living or parasitic on both plants and animals. Mites are the most diverse members of this assemblage. They have opted for small size with a trend toward fusing the prosoma and opisthosoma together. Mites are predatory on other arthropods, including other mites. Many others are parasitic on plants and vertebrates. Some have become aquatic and can be found in many freshwater and ocean environments where they may parasitize mollusks, crustaceans, and aquatic insects; some are suspension feeders. Mites cause various aliments that include skin mange and other irritations, feather loss in birds, as well as subcutaneous tumors. Mites can also act as vectors in disease distribution, including wheat and rye mosaic viruses. Other mites may destroy stored grain products and thus have negative economic impacts. The ticks are parasitic, blood-sucking parasites on vertebrates, although one beetle is also parasitized by this taxon. The chelicerae are modified with teeth for anchoring the tick in the skin of the host, which makes it difficult to remove. Ticks are vectors for many diseases, including protozoan, bacterial, fungal, and viral agents. Ticks transfer Rocky Mountain spotted fever as well as Lyme disease.

Ricinulei

These secretive arachnids are small, ranging from five to ten millimeters in length. There are only about thirty-five species, found in Africa, the southern United States, and Brazil. They have pincerlike pedipalps, and their third legs are modified for sperm transfer in males. There is a hood structure in front of the prosoma where brooding of the single egg of one species occurs. The reproductive habits are largely unknown. These are secretive animals living under leaf litter and in caves. They are predatory on smaller arthropods.

—Samuel F. Tarsitano

See also: Arthropods; Circulatory systems of invertebrates; Crustaceans; Exoskeletons; Insects; Poisonous animals; Reproductive strategies; Scorpions; Spiders.

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ARCHAEOPTERYX

Types of animal science: Classification, evolution
Fields of study: Anatomy, evolutionary science, ornithology, paleontology

The oldest known bird is the Late Jurassic Archaeopteryx*, which is important as evidence for the generally accepted view that birds evolved from small carnivorous dinosaurs through the development of feathers into flight structures.*

Principal Terms

Archaeopteryx: the oldest known bird, from the Upper Jurassic Solnhofen Limestone of Bavaria

archosaurs: major subdivision of reptiles, which includes the crocodiles, birds, and dinosaurs

cladistics: a method of analyzing biological relationships in which advanced characters of organisms are used to indicate closeness of origin

Cretaceous: a period of time that lasted from about 146 to 65 million years ago, the end of which was marked by the extinction of the dinosaurs

furcula: fused clavicles, the wishbone of birds

Jurassic: a period of geological time that lasted from about 208 to 146 million years ago, during which the birds originated

theropods: carnivorous dinosaurs, and the group from which birds developed

The first *Archaeopteryx* ("ancient wing") fossil to be discovered was a single feather found in the Solnhofen Limestone Formation of Bavaria in 1860, during quarrying operations. Since then seven skeletons have been found, the most complete of which are the British Museum specimen (discovered in 1862) and the Berlin specimen (discovered in 1877). Although most of the specimens seem to belong to the same species, *Archaeopteryx lithographica*, a case has been made that the seventh specimen represents a different and smaller species, *Archaeopteryx bavarica*. The Solnhofen Limestone was deposited in hypersaline lagoons that formed along the northern margin of the Tethys Sea during the Late Jurassic, and the fine-grained limestones that formed in the lagoons contributed to the exceptional preservation of soft-tissue structures, including feathers. *Archaeopteryx* may have lived around the lagoons in bushes and shrubs, as there is no evidence of trees, and occasionally may have been blown out into the lagoons during storms, becoming waterlogged and sinking into the fine carbonate sediment.

Archaeopteryx was a small animal, about the size of a pigeon, and is considered to be a bird, as it has feathers, with those on the wings specialized for flight. However, many of its skeletal characteristics are dinosaurian, and if the feather impressions had not been preserved it would undoubtedly have been identified as a small theropod or carnivorous dinosaur. In particular, the skull has openings characteristic of dinosaurs, and toothed jaws are present rather than a beak. The arms still terminate in separate clawed fingers, unlike the fused wing of a bird, and its pelvis and long bony tail are similar to those of a theropod. All modern birds have a fused mass of vertebrae called the pygostyle rather than a long bony tail. However, *Archaeopteryx* does have a furcula, the wishbone of birds, which acts as a spring during flight; a broad platelike sternum for the attachment of the flight muscles; and feathers, which probably developed initially from epidermal scales as insulation and were only later adapted for flight.

Archaeopteryx Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Aves
Subclass: Archaeornithes
Geographical location: Southern Germany
Habitat: Probably low bushes and shrubs around marine lagoons
Gestational period: Unknown
Life span: Unknown
Special anatomy: Dinosaurian features, including teeth, forelimbs with separate clawed digits, saurischian pelvis, long bony tail; body covered by feathers, including asymmetric flight feathers

Significance of *Archaeopteryx*

The status of *Archaeopteryx* as the oldest known bird has made it extremely significant in ongoing discussions about the origin of birds and the origin of flight. At the time of its discovery, shortly after the publication of Charles Darwin's *On the Origin of Species* (1859), it seemed to be a perfect "missing link" between birds and reptiles, and was proposed as such by Thomas Henry Huxley. However, the apparent lack of a furcula was used to discredit this view, and rival views suggesting that birds were most closely related to crocodiles, basal archosaurs (dinosaur ancestors), and even mammals became more popular. This changed in the 1970's when John Ostrom cataloged numerous similarities between *Archaeopteryx* and theropod dinosaurs, particularly the advanced dromaeosaur *Deinonychus*. Subsequent analyses using cladistics, a method in which the distribution of advanced characteristics in related species can be assessed by computer, have fully supported this view.

Analyses of the wings of *Archaeopteryx* have shown that the feathers are adapted for flight and that the animal was probably capable of fast cruising flight, although it would not have been very manouverable. Specimens of feathered dinosaurs and early birds from the Lower Cretaceous of China have shown that feathers probably originated as insulating structures that were subsequently adapted for flight in animals such as *Archaeopteryx*. How that happened is still a matter for debate, but the two main possibilities are the arboreal hypothesis, which suggests that flight originated in gliders that started to flap, and the cursorial hypothesis, which suggests that flight developed in animals that were running and jumping after prey.

—David K. Elliott

See also: Birds; Dinosaurs; Feathers; Flight; Fossils; Paleoecology; Paleontology; Prehistoric animals; Wings.

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ARMADILLOS, ANTEATERS, AND SLOTHS

Type of animal science: Classification
Fields of study: Anatomy, physiology, zoology

Anteaters, armadillos, and sloths belong to the order Edentata ("without teeth"). The order includes the giant anteater and three smaller anteaters, two genera of sloths, and eight genera consisting of twenty species of armadillos.

Principal Terms

ARBOREAL: living in trees
HERBIVOROUS: plant-eating
NOCTURNAL: active only at night

Anteaters, armadillos, sloths, and several extinct species make up an order of mammals called Edentata ("without teeth"), now found only in the Western Hemisphere and chiefly in South America. Only one species of the order, the long-nosed armadillo, is found in the United States, chiefly in Texas. Although the name of the order means "toothless," armadillos and sloths do have a single set of teeth, which look like wooden pegs, lack enamel, and are constantly growing. Only the anteaters do not have teeth.

Edentates live in a number of habitats, including subtropical and tropical environments. Giant anteaters live in grasslands but also can be found in western South American forests. They feed on termites and ants, either at night or during the day. Lesser anteaters live mostly in tropical rain forests and are nocturnal in their habits, preferring to hunt at night. Tree sloths live in trees in humid tropical forests, where they feed exclusively on leaves and plants. Armadillos are found in grasslands and forests and live in burrows. They feed mainly on insects and worms.

Physical Characteristics of Edentates

The four genera of anteaters share several characteristics: They have long heads, long, tube-shaped mouths with long tongues, but no teeth. They are mammals and belong to the family Myrmecophagidae. The giant anteater, *Myrmecophaga tridactyla*, is sometimes called the ant bear. It can reach six feet in length and weigh up to eighty-six pounds and lives in swampy areas and open grasslands in South America. It is gray in color with a white-bordered black stripe on each shoulder. It has a long, bushy tail and sharp front claws used to tear open termite nests. The claws are so long that, in order to move, the ant bear must tuck its claws under its front feet and walk on its knuckles. The long, narrow tongue has a sticky surface; it flicks rapidly out of a small mouth and is perfectly suited for licking up termites and ants that adhere to its surface.

The pygmy anteater, *Cyclopes didactylus*, also called the two-toed anteater, is the smallest of the anteaters. It reaches about fifteen inches in length, but half of that is tail. The pygmy anteater weighs only four pounds on average. It has a small nose and silky golden fur that make it look like the seedpods of the main tree it inhabits, the silk cotton tree. It lives high up in the tree, where it feasts on termites and seldom comes to the ground. It uses its tail to help it jump from tree to tree.

There are two species of Tamandua, or lesser anteaters, *Tamanda tetradactyla* and *T. mexicana*. Both species have three toes, no teeth, and very sharp claws. They are about four feet long, shortsighted, and very hard of hearing. Their noses are much shorter than those of the giant anteaters. Both species are shorthaired and brownish, with a black area that looks like a vest on the front side. They live in trees and use their long, prehensile tails to help them hold onto branches. They sometimes come to the ground, where they walk extremely slowly. They do most of their feeding at night, eating ants, termites, and other small insects.

The armadillo, Spanish for "little armored thing," originated in South America more than sixty million years ago. It is found as far south as Argentinean Patagonia, where the pichi, *Zaedyus pichi*, is very common. One species of armadillo, *Dasypus novemcinctus* (the nine-banded armadillo), is found as far north as northern Texas. The armadillo is not toothless, but its teeth are simple, rootless pegs at the back of its mouth. The shell covering most of the animal is made up of hundreds of bony plates that are fused together. Across the middle of its back, the armadillo has a hinge that joins together its front and rear sections, which allows the animal freedom of movement. Armadillos can contract and curl up into a ball to cover their unprotected underbellies. A full-sized adult weighs between eight and fifteen pounds. There are nine genera and twenty species of armadillos. The three-, six-, and nine-banded armadillos (the genera *Tolypeutes*, *Euphractus*, and *Dasypus*) get their names from the number of bands in their armor. The armor protects the animal from flesh-eating predators.

Sloths are arboreal (living in trees), with six species found in the rain forests of Central and South America. They are herbivorous, meaning they only eat plants. There are two main kinds of sloths: the three-toed sloth, called an ai, and the two-toed sloth, known as the unau. The ai, or *Bradypus grisues*, got its common name from its cry of distress, "ai-ai." It is about two feet long, slender, and has long legs. Its feet are armed with three long, hooklike claws, from which it hangs from branches. It has small ears, a tail, and a bullet-shaped head. One unusual feature is its long neck, which contains nine vertebrae, two more than is usual in mammals. Its coat of hair is dull gray and in another peculiar feature, an algae grows in the sloth's hair that gives it a greenish color, making the animal difficult to see among the green leaves. Three-toed sloths eat only the leaves of the cecropia tree.

The two-toed unau, *Choloepus hoffmanni*, is larger than the ai. Its neck has only seven vertebrae, and the animal has no tail. It has two claws on its front feet but three claws on its hind feet. Unlike the three-toed sloth, the unau can come down a tree headfirst and stand upright on all four feet. Its diet consists mainly of leaves, stems, and fruits. The eyesight and hearing of all sloths are not very well developed, and they usually find their way mainly by touch.

The Life Cycle and Habitat of Edentata

Solitary habits and a low reproductive rate characterize all three species of anteaters. The young

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are born one at a time with a gestation period of approximately 190 days. A mother carries a single offspring on her back for most of its growth period, which can last up to a year in the case of the giant anteater. The giant anteater lives in the grassland and forest of South America; it is the only anteater that lives on the ground. It is an excellent swimmer, however, and is frequently seen in the Amazon River. When it lives near human populations, it is active only at night, but in the forest it can be found hunting ants and termites during the day. Its home is an old burrow abandoned by another animal, or a hollow log. The giant anteater is becoming rare due to the trade in exotic pets and through the destruction of its habitats.

The pygmy anteater rarely comes down from the tall trees it lives in, and is active only at night. It lives high up in trees in the rain forest and feeds on termites. Its breeding habits are not known. The lesser anteater lives in trees, hanging on to branches with its tail. It emerges at night to eat insects, ants, and termites. Its breeding habits also remain unknown. Lesser anteaters are hunted for their tails, which are used to make rope, and native Brazilians sometimes bring them into their homes to rid them of termites.

The armadillo lives alone, in pairs, or in small groups. It is primarily active at night, and lives in burrows. It is a strong digger, and also a good swimmer despite its heavy shell. If the animal encounters a small stream or water-filled ditch, it usually just walks right across the bottom, under the water. If an armadillo comes to a larger body of water, however, it will swallow enough air to double the size of its stomach. This increased buoyancy then allows the armadillo to swim across. Once across, it takes several hours for the animal to release all the extra air from its body.

In some species of armadillo, the mother bears one to twelve identical young, all of which develop from a single egg. The gestation period for armadillos varies from sixty-five days to four months, depending on the species. Armadillos are found in tropical and subtropical regions, primarily in South America. Most species live in open areas, but some live in forests. They have a very good sense of smell that enables them to detect insects up to five inches below the surface of the earth. Armadillos are easily frightened and are very quick to run away from danger. The arma-

Edentata Facts

Classification:
Kingdom: Animalia
Subkingdom: Eumetazoa
Phylum: Craniata
Subphylum: Vertebrate
Class: Mammalia
Subclass: Theria
Order: Edentata
Family: Myrmecophaga (anteaters), Dasypodidae (armadillos), Bradypodidae (three-toed sloths), Megalonychidae (two-toed sloths)
Genus and species: Anteaters—three genera and four species; armadillos—eight genera and twenty species; sloths—two genera and five species

Geographical location: South and Central America, with only one species of Edentata in North America

Habitat: Anteaters—savanna, parkland, thorn scrub, and forest; armadillos—savanna, pampas, arid desert, thorn scrub, and deciduous, cloud, and rain forests; sloths—lowland and upland tropical forest

Gestational period: Anteaters—190 days; armadillos—60 to 120 days; sloths—6 to 11.5 months

Life span: Anteaters—unknown in the wild, twenty-six years in captivity; armadillos—twelve to fifteen years in the wild, nineteen in captivity; sloths—twelve years in the wild, thirty-one in captivity

Special anatomy: Anteaters have long sticky tongues and long tails; armadillos have shells surrounding most of their bodies; sloths have long tails and claws that enable them to hang from trees dillo is the only animal, besides humans, known to carry leprosy. For that reason it is illegal to sell a live armadillo in Texas.

The tree sloth usually lives alone and spends most of its time sleeping. The brief time that remains, it spends eating leaves and moving about. It sleeps hanging by its tail from a branch, with its feet bunched together and head tucked into its chest. Its greenish color makes it look like a bunch of dead leaves, making it almost invisible to other animals. Even at night it moves slowly, so as not to attract the attention of its enemies.

Sloths do not make nests, and sleep wherever they happen to be. They are not aggressive, but if two males come together in the same area during mating season, they will fight until one is killed. Mothers give birth to single young during the summer. The baby lives with its mother, clinging tightly to her breasts for five weeks, and then begins to eat by itself.

Extinct Edentata

The evolution of the anteater is not clear, but its oldest ancestor is believed to be some unknown form of insect. The three suborders of anteaters were separate for much of their history because they emerged long before North and South America were joined by the Isthmus of Panama, about 3.5 million years ago. All of the North American species died out before that contact was made.

The fossil record of armadillos includes groups that were about the same size as contemporary species, as well as a South American species, *Macroeuphractus*, that was at least 6.5 feet long. The skeleton of another ancestor, *Pampatherium*, found in a deposit in Texas, was as big as a rhinoceros. All of the ancestors of armadillos appear to have been plant eaters.

In the past, many varieties of sloths roamed the Americas from New Mexico to the southern tip of South America. They ranged in size from small animals the size of a fox to a giant ground sloth, *Megatherium*, which was larger than a full-grown elephant. A bear sloth, *Nothrotherium*, and other extinct members of the sloth family lived in South America about one million years ago.

—Leslie V. Tischauser

See also: Ants; Deserts; Fauna: South America; Rain forests; Teeth, fangs, and tusks.

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ARTHROPODS

Types of animal science: Anatomy, classification
Fields of study: Invertebrate biology, systematics (taxonomy)

Arthropods are the most numerous of all animal species, representing between 75 and 85 percent of all identified species. They are remarkably successful in all types of habitats and environmental realms.

Principal Terms

BIRAMOUS: having two rami; antennae are bifurcated

CUTICLE: a noncellular, secreted body covering

ECDYSIS: molting; the process of removing (escaping from) the old exoskeleton

EXOSKELETON: a protective system of external layers and joints that allows for antagonistic action of muscles

RAMI: the branches of an arthropod limb or appendage

SETAE: hairlike organs, typically sensory in nature, arising from the cuticle

TAGMATIZATION: functional specialization of groups of segments

UNIRAMOUS: having only one rami; antennae appear as a single, nonbifurcated structure

The phylum Arthropoda is the largest phylum in the animal kingdom and consists of myriad animals belonging to the subphyla Trilobita (extinct trilobites with biramous antennae, probably all marine), Chelicerata (horseshoe crabs, scorpions and pseudoscorpions, spiders, harvestmen, mites, ticks, and marine pycnogonids; all lacking antennae), Crustacea (all with biramous antennae), and Uniramia (insects, centipedes, millipedes; all with uniramous antennae). All of these subphyla are united by a common body plan similar to that of the annelids, in which the body is made up of a series of repeating segments, each bearing a pair of appendages. In contrast to annelids, however, arthropods have fused and modified segments for specialization. This fusion of groups of segments is known as tagmatization. The names for specific tagmata vary from subphylum to subphylum, but are most commonly recognized as the head, the thorax, and the abdomen. Appendages consist of articulated joints, moveable by muscles that insert onto specialized structures called apodemes that are attached to the cuticle.

Arthropods are found in all terrestrial and freshwater habitats and on all continents. They are also located in all marine realms, including in the abyssal depths and at hydrothermal vents, and are the only invertebrates to have conquered the aerial realm. Because of their widespread occurrence and their ability to occupy all niches on earth, they are considered the most successful animal phylum that has ever existed.

External Structure and Function

The first and last segments of the arthropod body differ in embryological origin from all of the rest and are considered as special segments. The first is called the acron and is preoral (lies before the mouth). The last is the telson and is postanal (occurs after the anus). Increase in segment numbers takes place in a growth zone immediately in front of (anterior to) the telson. Thus, the oldest segments are toward the head, while the youngest are toward the telson. The exoskeleton of each segment consists of two thickened plates, which are connected by a membranous cuticle. The cuticle is a nonliving, secreted material consisting of three layers: an inner endocuticle, an exocuticle, and an

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outer epicuticle, which is usually waxy. Despite this, the cuticle has many living structures that penetrate it and project beyond its surface. Chemical and mechanical sensory organs (setae) emerge generally as hollow projections from the cuticle and are typically hairlike in structure. Gland pores also penetrate the cuticle.

The cuticle is secreted by the epidermis and becomes hardened during a process of protein tanning and can be further strengthened by depositing calcium carbonate in the endocuticle (in Crustacea and Diplopoda). However, this hardened structure restricts growth and must be shed in a process called ecdysis (commonly called molting) in order for the animal to grow larger. Ecdysis is under neural and hormonal control. In preparation for ecdysis, the old cuticle is partially digested, particularly at joint locations and along specific lines of weakness. A flexible, untanned new cuticle is laid down under the old cuticle, and then the old cuticle cracks along the weak points so that the animal can emerge. The period between successive molts is known as intermolt, and the animal in each of these periods is called an instar; during this time cellular growth within the confines of the exoskeleton occurs. Some species of arthropods have terminal molts; that is, they molt a specific number of times and then cease all molting and growth. Other species retain the ability to molt and grow throughout their entire lives.

Internal Body Plan

The major, tubular blood vessel (heart) is dorsal, with blood flowing toward the head rather than toward the body. The circulatory system is greatly enlarged and occupies the space of the coelomic cavity, which is vestigial. In most arthropods, the circulatory system is open, so that all internal organs are bathed directly in blood rather than fed by smaller vessels (as is common in closed systems). The heart is pierced by a series of holes (ostia) which close when the heart muscle contracts so that blood can be propelled forward. Upon relaxation of the heart muscle, the ostia open and blood reenters the heart from the sinuses that feed into the sac surrounding the heart. The blood contains clotting agents, amoeba-like cells that act as phagocytic cells to attack pathogens, and oxygenating pigments.

Aquatic arthropods possess gills through which blood is circulated for gas exchange. Terrestrial forms have either book lungs or a series of cuticle-lined tubes called tracheas, which branch into smaller and smaller tubes to reach nearly all cells of the body. The tracheas open to the outside of the body via spiracles, which possess valves so that their opening and closing can be controlled to avoid water loss.

The arthropod gut has three divisions: a cuticle-lined foregut, a midgut, and a cuticle-lined hindgut. The foregut often is specialized for food storage and grinding and is separated from the midgut by a complex valve. The midgut has a large absorptive surface, which is called either the hepatopancreas or the digestive caecae. The hindgut serves as the area for water resorption and the formation of feces. Food and wastes are moved through the digestive system via muscular action due to the cuticular lining of the foregut and hindgut.

Osmoregulation and excretion of nitrogenous wastes are accomplished via one of two kinds of organs: the Malphigian tubules, or the nephridial coxal, antennae, or maxillary glands, all of which filter the blood for wastes. Marine forms excrete ammonia, while terrestrial forms conserve water through the excretion of uric acid.

The nervous system is of a ladderlike chain form, highly segmental, and ventrally located. Two longitudinal ganglia run along the midline of the animal. Paired ganglia arise in each segment and these are connected via lateral cords. The brain, composed of three pairs of ganglia, is found anteriorly above the esophagus; these ganglia then connect to the fourth set immediately below the esophagus. Sensory systems are highly evolved and include chemoreception (taste and smell), mechanoreception (vibration, touch, and deformation), and vision. Vision is accomplished via simple eyes (ocelli) and/or compound eyes, made up of a series of subunits called ommatidia. Compound eyes break up the image before it reaches the retina, and each ommatidium samples only a small part of the complete image.

Reproductive systems and strategies are highly variable. Sexes are usually separate, although hermaphroditism and parthenogenesis are known in some crustaceans and a few insects. Some arthropods display elaborate mating rituals; others do not. Some use direct copulation; others use indirect methods. Many arthropods pass through juvenile stages that are highly vulnerable to predators; hence the reproductive output of most arthropods is great. A few species, however, display direct development, where miniature adults are produced from eggs.

Phylogeny

Arthropods and annelids share a common ancestor, but it is unclear whether arthropods arose from an annelid ancestor or both shared an ancestor from another phylum. Some argue, based on molecular evidence, that annelids and crustaceans are not closely related at all. Traditionally, arthropods have been treated as a monophyletic group—all arose from a common arthropod ancestor. However, this idea is the subject of debate, with some arguing for a polyphyletic ancestry where each subphylum arose from a nonarthropod ancestor and then formed similar body structures via convergent evolutionary forces. Unfortunately, the fossil record does little to illuminate the phylogeny of arthropods, and current molecular evidence is contradictory.

—*Kari L. Lavalli*

See also: Arachnids; Centipedes and millipedes; Crabs and lobsters; Crustaceans; Exoskeletons; Horseshoe crabs; Scorpions; Spiders.

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ASEXUAL REPRODUCTION

Types of animal science: Development, reproduction
Fields of study: Cell biology, developmental biology, reproduction science

Asexual reproduction is any form of reproduction in which the fusion of haploid gametes is not the first step. There are many examples, such as the budding of a new hydra from the stalk of an existing one or the development of diploid eggs into larvae and, eventually, adults in aphids. The new organism formed is a clone of the original.

Principal Terms

CLONE: an organism that is genetically identical to the original organism from which it was derived

DIPLOID: having two of each chromosome; a normal state for most animals

HAPLOID: having one of each chromosome; a normal state for animal gametes

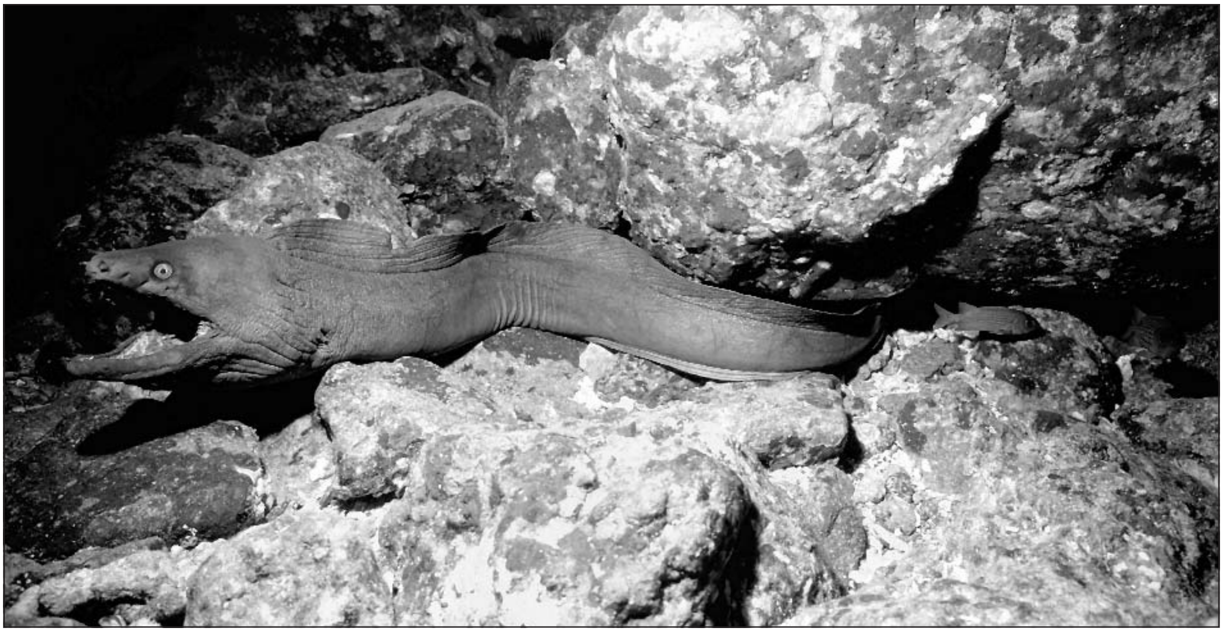
PARTHENOGENESIS: a form of asexual reproduction where the young are derived from diploid or triploid eggs produced by the mother without any genetic input from a male

TRIPLOID: having three of each chromosome; an abnormal state which is unable to produce normal haploid gametes

Although asexual reproduction is very common in organisms such as bacteria, protists, fungi, and plants, it is rarer among animals, especially among the more complex animals. In simple animals, such as sponges (phylum Porifera), the polyps of hydra, jellyfish, corals, and sea anemones (phylum Cnidaria), and many flatworms (phylum Platyhelminthes), asexual reproduction is common. Sponges can reproduce asexually when fragments break off and become established as new individuals or when mature sponges produce gemules, overwintering buds, that are produced and released by many freshwater and a few marine sponges. Cnidarian polyps frequently reproduce by budding. The buds start as small regions of less-differentiated tissue that differentiates into a new polyp. These new polyps can separate from the original to form new individuals or can remain attached and form colonies. The largest colonies to be produced asexually by budding are those produced by the reef-building corals. In some Cnidaria, the polyps release free-floating forms of the organism called medusae (jellyfish). The medusa form of the life cycle, which was formed asexually, reproduces sexually when it matures. Many species of flatworms reproduce asexually by fragmentation. When these worms are cut into fragments, most fragments can regenerate their missing parts, and thus form several organisms from the original one. Others, like many trematode flukes, asexually reproduce by polyembryony. In this mode of reproduction, larval flukes form many juveniles of the next larval stage internally, from the mature larva's own cells. The immature larvae that are produced, which are all genetic clones of the original larva, will be released to continue the life cycle.

Parthenogenesis

In higher organisms, asexual reproduction is much less frequent and far more complex. Rotifers (phylum Rotifera) are small aquatic organisms with rows of cilia around their mouths that seem to rotate as they beat. Rotifer populations are usually either mostly or entirely female. This happens because rotifers usually reproduce asexually by parthenogenesis. In this type of reproduction, the females produce diploid eggs instead of the haploid eggs that are needed for sexual reproduction.



Corals are among the many primitive species that reproduce asexually. (Digital Stock)

The diploid eggs have the same genes as the mother and are thus clones and mature into adults identical to their mother. In some rotifers, asexual reproduction is the only form of reproduction, and thus all of the organisms in these species are female. In other species, males are only produced during times of environmental stress, and sexual reproduction only occurs then.

Like rotifers, many populations of aphids (phylum Arthropoda), a common plant pest, are entirely or mostly female during parts of the breeding season. In spring and early summer, aphids reproduce parthenogenetically, with females producing diploid eggs that develop into adult female aphids. These eggs and the adults formed from them are clones of the original aphid. In late summer and early fall, the aphids reproduce sexually, producing haploid eggs that can be fertilized by haploid sperm from males.

Even among the very complex vertebrates, a few organisms can be found that reproduce asexually. The two most studied are the whiptail lizard, native to the deserts of the American Southwest and the northwestern part of Mexico, and the gecko, found on some tropical islands of the Pacific. These lizards exist in both sexually reproducing and parthenogenetic forms. Genetic study of their chromosomes has shown that the parthenogenetic species were first formed as diploid or sometimes triploid hybrids of two sexually reproducing forms. The hybrids could not undergo normal meiosis because different chromosomes inherited from each parent could not align properly. Thus, these lizards cannot reproduce sexually. They do, however, produce diploid or triploid eggs that can be triggered to start reproduction. The progeny that are produced are exact genetic duplicates of their mothers—clones.

With asexual reproduction, organisms do not have to waste energy in sexual activity. However, the energy savings is not without a price. With the exception of the rotifers, no populations of asexually reproducing organisms have very long histories, evolutionarily speaking. Unlike most sexually reproducing populations with varying degrees of diversity, all members of an asexually reproducing population are identical, except for mutations that arose after the population's inception. This lowered diversity makes the population much less likely to be able to adapt to change.

More or less water, higher or lower temperatures, introduction of parasites, or disease could more easily wipe out the entire population.

—Richard W. Cheney, Jr.

See also: Copulation; Gametogenesis; Hermaphrodites; Mating; Parthenogenesis; Reproduction; Reproductive strategies; Sex differences: Evolutionary origin; Sexual development.

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BABOONS

Types of animal science: Anatomy, behavior, classification, ecology, evolution
Fields of study: Anthropology, ecology, ethology, evolutionary science, human origins, systematics (taxonomy), wildlife ecology, zoology

Baboons are among the most widespread and adaptable of monkeys. Their behavior, ecology, and evolutionary history may shed light on human origins.

Principal Terms

COALITIONS: short-term alliances designed to gain access to a contested resource, often by fighting

MATRILINES: several generations of adult females all related by common descent from one foundress (female ancestor)

SEXUAL SWELLING: an estrogen-induced water retention that causes reddening and swelling in the perineal region and around the buttocks

Baboons are found as far north as the semidesert of Saudi Arabia (*Papio hamadryas*) and as far south as Cape Town in South Africa (*P. cynocephalus ursinus*). The regional variants of the cynocephalus (dog-headed) baboon (chacma in the south, Guinea in the west, olive in the north east, and yellow baboon in the southeast) are considered to be the same species by most experts. The northeastern variant, the hamadryas, is generally considered to be a separate species but can interbreed with the olive baboon of Ethiopia.

Baboons and Their Environment

Baboons are very numerous in Africa, and are among the most adaptable of all mammals. This adaptability also allows baboons to survive in wet forest and the driest semidesert regions. They eat almost any plant material or small animal they encounter. Baboons often survive quite well in and around human settlements. They sometimes cause severe crop damage when they visit farmers' fields, since they are capable of eating even the toughest roots, such as cassava and sweet potato,

Image Not Available

but they also forage on farmers' bananas and maize. Baboons can survive on garbage at tourist lodges, or find food in near deserts in Namibia, Ethiopia, and Saudi Arabia. Baboons sleep in trees or caves and cliff ledges, for protection from nocturnal predators.

Baboon Society

Except in the driest and coldest habitats, baboons form large groups and travel widely in the course of a day. Groups often exceed one hundred animals and contain scores of juveniles and females, plus a few adult males. These large social groups are composed of matrilines—a kin-group of sisters and their daughters who all descend from one female, plus their infant and juvenile male offspring—and unrelated adult males, who compete for mating access to females with sexual swellings. A large group can contain several matrilines, which may compete with each other over access to food, shelter, and male protection. The adult males in the group often fight fiercely among themselves, using coalitions to overcome single competitors. The typically calm life of moving in search of food is regularly interrupted by squabbles and mild competition over resources. More rarely, large fights break out within groups, and injuries follow. The most severe aggression is seen when a new adult male immigrates into a group, fights the other males to obtain high rank, and even harasses females and their young. Some cases of infanticide have been reported in such circumstances. The hamadryas baboons differ most in social organization. They do not build matrilines based on female kinship, but rather a female leaves the group in which she was born and bonds to a particular male as her future mate. This male plays an important social role as protector of a small group of one to three females. These small, one-male units travel and forage independently most of the time, but reunite with other units at night to form large herds often numbering in the hundreds.

Baboons have been studied extensively by biomedical researchers because of their physiological similarities to humans and because they are common animals in Africa. Baboons have also been studied intensively by anthropologists and evolutionary biologists interested in human origins. That is because the baboon evolved from an arboreal monkey that first exploited dry, open habitats some ten to twenty-five million years ago. In the past, anthropological theory suggested that our own ancestors followed a similar evolutionary pathway. Thus, baboons were seen for some time as a useful model for human evolution. This idea has changed somewhat over time as scientists have found that the group sizes, social organizations, and dietary habits of baboons probably do not mirror those of our ancestors. A more recent

Baboon Facts

Classification:
Kingdom: Animalia
Phylum: Vertebrates
Class: Mammalia
Order: Primates
Superfamily: Cercopithecoidea
Family: Cercopithecidae
Subfamily: Cercopthecinae
Tribe: Papionini
Genus and species: Papio cynocephalus (savanna baboon), *P. hamadryas* (hamadryas baboon), *P. leucophaeus* (drill), *P. sphinx* (mandrill)

Geographical location: Sub-Saharan Africa and parts of the Arabian Peninsula

Habitat: Mostly arid, tropical savanna-woodlands, but also temperate areas and rain forests

Gestational period: Six to seven months

Life span: In the wild, baboons older than fifteen years are rare, but in captivity adults may live to twenty-five or thirty years

Special anatomy: Reproductive females display a sexual swelling in the perineal region and around the buttocks that, at the time of ovulation, may contain several liters of fluid and turn bright red; adult males have extremely long canines which they use to threaten rivals, display their fighting ability to receptive females, or inflict wounds view holds that we can learn about antipredator behavior and habitat selection of our ancestors by observing baboons in similar habitats today.

—*Adrian Treves*

See also: Chimpanzees; Fauna: Africa; Fauna: Asia; Gorillas; Human evolution analysis; Lemurs; Monkeys; Orangutans; Primates.

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BATS

Type of animal science: Classification
Fields of study: Anatomy, ecology, physiology, wildlife ecology, zoology

Over nine hundred species of bats have been identified, classified in the general order Chiroptera, the second largest order of mammals.

Principal Terms

INSECTIVOROUS: depending on insects as food
MAMMARY GLANDS: glands that, in the female, secrete milk
MARSUPIAL: an animal whose young shelter in the mother's abdominal pouch
NOCTURNAL: occurring in the night
PLACENTAL: an animal where the young are enclosed in a membrane inside the mother's body during pregnancy
TERRESTRIAL: relating to the earth
VERTEBRATE: having a spinal column

Bats are somewhat difficult to study because of their secretive, nocturnal habits and their flight capabilities. Although well over nine hundred species have been identified and catalogued, additional species have since been discovered, primarily from the South American rain forests. New ones remain to be discovered, and the classification of bats continues to be improved.

Bats are the most widely distributed kind of terrestrial mammal. They are found from Alaska to the tip of Argentina and from near the Arctic Circle to South Africa. They occur widely through the tropical regions and in the temperate zones.

Physical Characteristics of Bats

Although bats range in size from tiny hog-nosed bats that weigh less than a penny to flying foxes whose wing spans exceed five feet, the majority of bats tend to be small. Despite variation in size, all species of bat share the same body form, with certain similarities in fur and skin, wings, teeth, reproductive system and patterns, and visual and hearing systems.

The bat's skin is black or dark grayish brown in color, with tiny transparent hairs on the membrane surface. While most bats have small eyes, perhaps encouraging the misconception that bats are blind, their auditory system is developed to an extraordinary degree.

Of the bats who feed on animals, some feed on insects and whole animals; vampire bats, which occur from Mexico to Argentina, feed only on the blood. Plant-eating bats feed on fruit and flowers.

Female bats give birth at the roost site, frequently while hanging upside down. Bat young are born in a breech presentation and are helpless until they are large enough to fly. Brown bats reach adult size and begin to fly at three to four weeks of age.

The Behavior of Bats

The major behavioral pattern of bats is nocturnal activity. During nocturnal flight, bats are protected from being visually spotted by predators and from exposure to the sun and to high temperatures, which promote heat absorption and the loss of body water necessary for temperature regulation.

Bats routinely seek shelter during the daylight hours. Caves provide protection from the sun and predators and allow bats to conserve energy under consistent temperature and moisture conditions. Bats also shelter in tree cavities, crevices, buildings, and trees.

While tropical bats are active all year round, bats in temperate regions hibernate during the winter in order to accommodate the diminished food supply. Most hibernating bats spend the summer feeding heavily on insects, building up enough fat to provide energy during hibernation. During hibernation, the bat allows its body temperature to fall to that of the surrounding air, and as its pulse and breathing rates slow down, it essentially enters a state of suspended animation.

The sole characteristic that sets bats apart from other mammals is flight. Some bats fly high, fast, and far, while others fly more slowly, maneuvering around obstacles, catching their prey on the wing, or plucking it from the ground. Soaring is uncommon in bats, as is swift flight in comparison with birds. Bats fly in flocks sometimes numbering in the thousands, a precaution against predators.

Microchiropteran bats use echolocation, a pulse system of high-frequency sounds and their echoes, to navigate and to locate food. Bats emit sound, then receive and analyze the data from the returning echoes which provide information on direction and distance to the target. Best suited to short distances, echolocation is so accurate that some bats appear able to distinguish among individual species of insects.

Bats are allies of human beings in controlling the insect population. Most species of bats found in the United States feed on beetles, moths, and crickets, many of which destroy vegetation and are damaging to agricultural interests. Recent studies also suggest important uses for anticoagulent compounds, found in vampire bats' saliva, that hinder the clotting of blood.

—Mary Hurd

See also: Ears; Flight; Hearing; Mammals; Nocturnal animals; Wings.

Bat Facts

Classification:
Kingdom: Animalia
Subkingdom: Metazoa
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Subclass: Theria
Order: Chiroptera (bats)
Suborders: Megachiroptera (flying foxes), Microchiroptera (bats)
Families: Pteropopidae (flying foxes, forty-four genera, 173 species); Rhinopomatidae (mouse-tailed bats, one genus, three species); Emballonuridae (sheath-tailed bats, thirteen genera, fifty species); Craseonycteridae (hog-nosed bats); Nycteridae (slit-faced bats, one genus, eleven species); Megadermatidae (false vampire bats, four genera, five species); Rhinolophidae(horseshoe bats, one genus, sixty-nine species); Hipposideridae (leaf-nosed bats, nine genera, sixty-one species); Mormoopidae (leaf-chinned bats, two genera, eight species); Noctilionidae (bulldog bats, one genus, two species); Mystacinidae (short-tailed bats, one genus, two species); Phyllostomidae (spear-nosed bats, forty-seven genera, 140 species); Desmodontinae (vampire bats, three genera, three species); Natalidae (funnel-eared bats, one genus, eight species); Furipteridae (thumbless bats, two genera, two species; Thyropteridae (disk-winged bats, one genus, two species); Myzopodidae (sucker-footed bats); Vespertilonidae (common or vesper bats, forty-two genera, 319 species); Molossidae (free-tailed bats, twelve genera, ninety-one species)
Geographical location: Every continent except Antarctica
Habitat: Mostly forests and deserts; some grasslands
Gestational period: Three to ten months, with delayed implantation
Life span: Generally three to five years; up to thirty years in captivity
Special anatomy: Head, body, tail, two wings, each supported by upper arm, forearm, hand; knee joints bend backward enabling the bat to hang upside down and still be ready to take flight easily

During the day, bats seek shelter in dark, enclosed spaces such as caves, tree crevices, and buildings, where they hang upside down until twilight. (PhotoDisc)

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BEAKS AND BILLS

Type of animal science: Anatomy
Fields of study: Anatomy, ornithology

Ornithologists tend to use the terms "beaks" and "bills" interchangeably in referring to the horny part at the end of a bird's head. The terms also may be used to refer to a horny head part in other animals such as turtles or the duck-billed platypus. However, the vast array of sizes, shapes, and structures adapted for a multitude of functions is only seen among birds.

Principal Terms

ADAPTIVE RADIATION: the process by which many species evolve from a single ancestral species in adapting to new habitats

DISPLAY: usually a visible movement or behavior used as a social signal in the context of aggression, courting, etc.

EGG TOOTH: a hard, calcified structure on the tip of the bill of a bird embryo that is used to help the bird break its shell during hatching

POLYMORPHISM: the occurrence of two or more structurally or behaviorally different individuals within a species

SEX HORMONES: hormones—androgens in males, estrogens in females—which are associated with sex characteristics and sexual behavior

SEXUAL DIMORPHISM: a difference in structure or behavior between males and females

All birds have bills (or beaks), and these exhibit so much variation in their structure that they are useful as one of the distinguishing characteristics among species. Bills are toothless, except in embryos, and are covered with a horny sheath. Many of the variations in bill form are associated with specialized adaptations to different feeding habits. In addition to their obvious role in feeding behavior, bills have a function in a number of other behaviors. Some birds use their bills in different ritualized displays, including threat displays and appeasement displays. Some bills are used for digging, for nest-building, for "sewing," for drilling, and for many other activities.

Structure of the Bill

Anatomically, bills are a compact, modified layer of epidermal cells formed around the bony core of the upper and lower jaws, or mandibles. The bill is normally hard and thick, but it is not rigid, and different bills can be bent and twisted in different ways and to different degrees. For their size, bills actually are relatively light, one of the many adaptations in birds for flight. Although bills do not have teeth, adaptations in some forms have functions similar to those of teeth. Some bills have sharp edges, and these may function in cutting food, for example. There also are different specializations in the bony and muscular elements that operate in conjunction with bills to compensate for the different physical stresses imposed by feeding. It is interesting to consider where birds' nostrils are located. In most species, they are found near the base of the upper mandible, but there are some notable exceptions. In that unusual bird, the kiwi, perhaps the only species of bird with a well-developed sense of smell, the nostrils are located at the tip of the bill.

Some species of birds, including puffins and pelicans, have structures or projections on the bill that are present only around the breeding season and are then shed after reproduction. The brightly colored, triangle-shaped bill of the puffin has scales on both the upper and lower mandible, which seem to serve a role during courtship.

The bill of the developing embryo possesses an interesting structure: the egg tooth. The egg tooth is a hard, calcified structure on the tip of the bill of a bird embryo that is used to help the bird to crack and weaken the shell so that hatching can take place. The embryo also possesses a special muscle, the "hatching muscle" which provides the force behind the egg tooth. After hatching, the egg tooth either drops off or is absorbed.

Variations in Bill Structure

Given the variety of foods eaten by different bird species, it is not surprising that there are so many differences in the form and size of bills. What may seem surprising, however, is the observation that closely related species may have quite different types of bills. Two good examples of this phenomenon are seen in the finches of the Galápagos Islands and in the Hawaiian honeycreepers. Both of these examples illustrate nicely the process of adaptive radiation, by which many species evolve from a single ancestral species in adapting to new habitats. Similar to the Galápagos Islands, the islands of the Hawaiian chain are of volcanic origin and, moreover, they are even farther removed from any major landmass than are the Galápagos. It is thought that the ancestral form of the modern Hawaiian honeycreeper was a nectar-feeding honeycreeper type of bird that migrated to Hawaii from South America. The birds underwent a remarkable evolution, with new species formed as a result of adaptation to new feeding opportunities. Species became different not only in the shape of their bills but also in their coloration. Species were produced that were red, black, gray, yellow, and green. Beaks varied from those that were large and heavy for crushing seeds to long, thin beaks suitable for collecting nectar from flowers.

As remarkable as are differences in beaks among closely related species, even stranger are differences in bills among individuals of the same

Birds use their beaks much as other animals use their paws: to catch prey as this kingfisher has done, to preen themselves, and to build their nests. (Digital Stock)

Darwin: Beaks and Evolution

During its voyage around the world, the HMS *Beagle* visited the Galápagos Islands in 1835. It was there that Charles Darwin was able to observe the interesting variety of plants and animals. The Galápagos are removed from any large land mass, being situated about six hundred miles west of the coast of Ecuador. Darwin's observations of the islands' fauna contributed to the development of his ideas about evolution and the origin of species. The different animal species living in the islands were quite different from species anywhere else in the world. Of particular interest to him were the thirteen species of finches that he collected. Finches are small, sparrow-sized birds, and the thirteen species were similar to one another except for features related to their feeding habits, especially their beaks. Darwin noted striking differences in the size and shape of the beaks and observed that their structure was related to the type of food the birds ate. Short, thick beaks were suitable for crushing seeds. Long, thin beaks were useful for feeding on insects. Large beaks were effective in opening hard fruits. Each species appeared to be adapted to its own local food supply. Darwin reasoned that the finches in the Galápagos had descended from a single ancestral species that had come to the island from South America. The adaptive radiation of the finches was one of the cornerstones of his reasoning that adaptation to the local food supply was related to the origin of new species by the process of natural selection.

species. Bills of three different sizes are found in a finch from Africa, the black-bellied seedcracker. The bills occur in three discrete sizes, ranging from relatively small to relatively large, and the sizes appear related to the type of seeds eaten, with large bills being better suited for dealing with hard seeds and small bills being better adapted for soft seeds. Bills of intermediate size do not fare very well with either type of seed in comparison with either the small or large bills. However, the intermediates are necessary in order to have available the genetic capabilities for the other two sizes of bills. This type of selection is an example of disruptive selection, which in this case tends to produce individuals of the two extreme bill sizes.

Differences in bill structure between males and females of the same species are also known. The huia (probably extinct) is a bird in New Zealand with several unusual characteristics, the least of which is the structure of the bills in the two sexes. As is true of bills in general, the form of the bill appears related to its function. Males have a relatively straight and sharp bill, whereas females have a thin, downward curving bill which is much longer than that of the male. Males use their bills to dig open the burrows of grubs living in dead wood. After the tunnels are open, females use their bills to pull out the grubs. The different structures of the bills in males and females appear related to an interesting division of labor during feeding.

A final example of interesting variation in bills is a case in which the color of the bill changes seasonally within the same individual. The sex hormones, testosterone and estrogen, are responsible for the development of secondary sex characteristics and behavior in males and females, respectively. There are striking changes in behavior during the breeding season. The bills of male and female starlings change color, to yellow in the males and to red in the females, due to the action of these hormones during the breeding season.

Modifications of Bills for Feeding

As different species of birds are observed feeding, one has a sense of awe at the great diversity of dietary items and the variety of bills that are specialized to eat them. Foot items include nuts, hard seeds, soft seeds, insects, larvae, roots, flowers, sap, fungi, nectar, carrion, and other types of organic matter. The specializations observed in bills are adaptations for specific types of food. In a brief discussion, it is not possible to describe the many variations seen in the size and shape of bills, but even descriptions of a few representative examples provide the basis for appreciation of the exquisite designs and functions of bills.

In carnivorous birds of prey, such as falcons and owls, the beak is used as a meat hook. The birds typically seize their prey with their feet and disarticulate the cervical vertebrae by biting into the neck. The bill has a so-called tomial tooth on each side of the upper bill just behind the curved end of the beak. There is a notch or groove on the lower mandible that fits with the tomial tooth.

Birds that catch insects in flight, such as flycatchers, have beaks that are broad and slightly hooked. Frequently, there are long bristles or feathers at the base of the bill which facilitate the catching of the moving prey.

The bill of the crossbill shows some unusual features. The tips of the beak do not meet when they are closed. The tips are displaced to the side and move past one another as the mouth is closed. The end of the lower mandible may cross to the left or to the right of the upper mandible. This type of bill appears adapted for serving as a wedge to pry open the scales of pine cones, enabling the bird to insert its tongue and to remove the seeds from inside.

An interesting specialization is seen in the beaks of tropical fruit pigeons. These birds feed on large fruits, and their bills can open not only in the vertical plane but also in a horizontal plane, like the jaws of a snake when swallowing large prey.

It is evident from these examples that bills of birds have become adapted for their feeding. There are even some examples of species whose bills have become so specialized for their specific food that the number of birds is completely dependent on the availability of that food source.

—*Donald J. Nash*

See also: Anatomy; Birds; Chickens, turkeys, pheasant, and quail; Cranes; Displays; Ducks; Eagles; Flamingos; Geese; Hawks; Hummingbirds; Ingestion; Nesting; Ostriches and related birds; Owls; Parrots; Pelicans; Penguins; Platypuses; Sparrows and finches; Storks; Swans; Vultures; Woodpeckers.

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BEARS

Type of animal science: Classification
Fields of study: Anatomy, conservation biology, evolutionary science, wildlife ecology, zoology

Bears are large mammals making up the family Ursidae, that have adapted to habitats as diverse as the sea ice of the Arctic and the bamboo forests of China.

Principal Terms

CANID: a member of the dog family (Canidae)
CARNIVOROUS: eating meat
CARRION: the meat of dead animals
HERBIVOROUS: eating plants
OMNIVOROUS: eating both meat and plants
PLANTIGRADE: walking on the entire foot, not just the toes
TAXONOMIST: a scientist who classifies and gives technical names to plants and animals
UNGULATE: a hoofed mammal
URSID: a member of the bear family (Ursidae)

Bears are large mammals, and comprise eight species in Europe, Asia, North and South America, and the circumpolar Arctic. The earliest bears lived in North America and Europe during the late Eocene epoch, approximately thirty-seven million years ago. Bears are classified as carnivores, having evolved from small generalized predators. Functionally, however, bears range from the almost completely carnivorous polar bear to the almost completely herbivorous giant panda. The remaining six bear species are omnivorous, opportunistically feeding on a wide range of plants as well as mammals, fish, insects, and mollusks. A brown bear in Alaska, for example, emerging from its winter den in April or May, may feed on carrion (winter-killed moose or caribou), switch to grasses, sedges, and roots as spring progresses, and then eat mostly salmon as the summer salmon runs begin.

The Classification Controversy

While most taxonomists today recognize eight species of living bears, there has long been disagreement over whether to consider the giant panda (*Ailuropoda melanoleuca*) a true bear. The issue is complicated by the existence of the red (or lesser) panda (*Ailurus fulgens*). The red panda is raccoonlike in appearance, while the giant panda looks like a bear, yet the two pandas share some anatomical and behavioral features. The fossil record on pandas is scant. Recent molecular studies have shed new light on the issue but are not conclusive.

Anatomical, biochemical, paleontological, behavioral, and reproductive evidence is all relevant to this issue but is subject to differing interpretations by different authorities. Some place both pandas in the bear family (Ursidae); some put both in the raccoon family (Procyonidae); some consider the giant panda a bear and the red panda a raccoon; some put the two pandas in their own family, naming it either Ailuridae or Ailuropodidae; and some put the red panda in Ailuridae and the giant panda in Ailuropodidae. Clearly there is no simple answer to the question of how to classify the pandas. However, in general usage among both biologists and lay persons at the beginning of the twenty-first century, the giant panda is considered a bear, and the red panda is not.

Physical Characteristics of Bears

Bears are heavy-bodied, stout-legged, short-tailed mammals with long skulls and short snouts. Most bears have thick fur. All have five toes with nonretractile claws on each foot. Some have claws modified for climbing and some for digging. Bears are plantigrade, walking on the entire sole of the foot. Even lacking some of the modifications for speed possessed by canids and ungulates, some bears can run forty miles per hour. Bears have good, but not exceptional, eyesight and hearing. Their sense of smell, however, is excellent and greatly aids them in finding food.

Bears range in size from the sun bear, which weighs 60 to 145 pounds as an adult, to the male polar bear, which weighs up to 1,770 pounds. Large Kodiak bears (a type of brown bear) are almost as large as the largest polar bears. The extinct bear *Arctodus*, which lived during the Pleistocene epoch, was the largest bear ever, and may have reached fourteen feet tall when standing on its hind legs.

All living ursids have forty-two teeth. They have large canine and incisor teeth, the premolars are often reduced, and the molars in all except the polar bear form crushing platforms for grinding plant material.

Bear Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Subclass: Eutheria
Order: Carnivora
Suborder: Fissipedia
Family: Ursidae (bears)
Subfamilies: Ursinae, Tremarctinae, Ailuropodinae
Genus and species: Ursus arctos (grizzly or brown bear), *U. maritimus* (polar bear), *U. americanus* (American black bear); *Selenarctos thibetanus* (Asian black bear); *Helarctos malayanus* (sun bear); *Melursus ursinus* (sloth bear); *Tremarctos ornatus* (spectacled bear); *Ailuropoda melanoleuca* (giant panda)

Geographical location: Europe, Asia, North and South America, and marine areas of the Arctic

Habitat: Varies by species; temperate forests, subalpine mountains, tundra, grasslands, tropical rain forests, deserts, and sea ice

Gestational period: Seven to eight months for the American black, spectacled, brown, and polar bears; four to seven months for the Asiatic black bear, giant panda, and sun bear; unknown for the sloth bear

Life span: Wild bears typically live fifteen to twenty-five years; rarely, wild bears live past thirty, and captive bears have exceeded forty years

Special anatomy: All living bears except the polar bear have flat molars, which are adapted for crushing plant material; some bears have claws adapted for climbing and some for digging; although most bears eat a considerable amount of plant material, they have retained the short, simple gut of their meat-eating ancestors

Hibernation

During winter, in areas where food supplies are scarce, many bears den up for a winter sleep. This hibernation differs from that of such deep hibernators as ground squirrels. A ground squirrel's body temperature may drop to the freezing point (32 degrees Fahrenheit) or slightly below. A bear's body temperature drops only 5 to 9 degrees Fahrenheit from its normal level of 99 degrees Fahrenheit. Its heart rate drops from forty to seventy beats per minute to eight to twelve, and its metabolism drops by about half. This slowing of the body's processes combined with the heat-conserving properties of the den allow a bear to go up to eight months without eating or drinking. Stored body fat is the bear's only source of energy. Hibernating bears do not defecate or urinate. Brown bears and American and Asiatic black bears hibernate, as do pregnant female polar bears.

Reproduction

A brief mating season of one to two weeks occurs in spring or summer. Females in heat are followed and courted by males. There is often fighting among males, with the strongest and most aggressive winning the right to breed.

In bears there is a delay in the implantation of the fertilized egg in the wall of the uterus. In the polar bear, for example, mating may take place in April, but the embryo will not implant and begin to grow until October. Because of this delay, the cubs, when born in December, are small and relatively undeveloped, weighing 1 to 1.5 pounds. The female is in her winter den at this time and is living off her fat, and the needs of her cubs do not overwhelm her capacity to produce milk.

Bear cubs generally leave their mothers at 1.5 or 2.5 years, at which time the female is ready to breed again. Therefore, most female bears give birth to cubs every second or third year.

Behavior

Bears are intelligent, single-trial learners. They can remember where and when they have found food in the past—a trait that is very useful to them in the wild, but is a problem if they gain access to human food or garbage. Bears conditioned in this way can quickly lose their fear of humans and are potentially dangerous.

Cubs learn how to find food and other life lessons by observing their mothers. Other than family groups of a mother and her cubs, bears are usually solitary. However, a rich, concentrated food source, such as runs of spawning salmon in a river, may cause bears to gather in one area. In this case, a dominance hierarchy is established and maintained. Bears posture and threaten one another, communicating with body language and, to a limited degree, facial expressions. Fighting occurs and sometimes results in injury but is rarely fatal. Through this dominance hierarchy, prime fishing spots are claimed by dominant bears, as are breeding rights. Conflict is minimized as the bears concentrate on what is most important: eating.

Conservation

In many areas of the world, humans have converted wildlands into farms, tree plantations, oil fields, mines, suburbs, and cities. Many species of bears have been greatly reduced as a result. The giant panda, an endangered species, numbers only about one thousand in the wild. The other Asian bears—the sun, sloth, and Asiatic black bears, as well as the spectacled bear from South America—are also severely threatened. The American black bear, however, is thriving, with an estimated population of 450,000. Polar bear populations have been stabilized by a treaty limiting hunting to native peoples, but may now be threatened by global climate change. Efforts are being made to restore the grizzly (a type of brown bear) in some western areas of the United States.

The conservation of bears worldwide requires the protection of wildlands such as na-

Bears, such as this brown bear, are extremely intelligent mammals, and they learn from only a single exposure to a situation. (Corbis)

The Eight Species of Bears

The Brown bear (*Ursus arctos*) was once widespread in Europe, Asia, and North America, but is now much reduced. It is a large animal (up to 1,500 pounds) that has a varied diet, including grasses, roots, berries, insects, fish, rodents, moose, elk, caribou, and deer.

The American black bear (*Ursus americanus*) lives in the forested areas of Canada, the United States, and Mexico. It is the most numerous bear in the world, with an estimated population of 450,000. It is an excellent climber and feeds on a wide range of plant and animal species.

The Asian black bear (*Selenarctos thibetanus*) inhabits the forests of much of southern Asia. It is very similar to the American black bear in looks and habits.

The Polar bear (*Ursus maritimus*) lives in the marine areas of the Arctic, where its main foods are ringed and bearded seals.

The Sloth bear (*Melursus ursinus*) of India, Sri Lanka, Nepal, Bhutan, and Bangladesh digs into termite mounds and then sucks up the angry termites as they swarm out.

The Sun bear or Malayan bear (*Helarctos malayanus*) of the tropical rain forests of Southeast Asia eats fruit, honey, snails, eggs, lizards, rodents, termites, and earthworms.

The Spectacled bear (*Tremarctos ornatus*) of the Andes Mountains is the only South American bear. It is largely a fruit eater.

The Giant panda (*Ailuropoda melanoleuca*) survives only in limited mountainous areas of west-central China and in zoos. Its main food is bamboo.

tional parks, forests, and wildlife refuges, and the animals that inhabit them. In multiuse areas, careful management of bear populations can assure their survival.

—Thomas Coffield

See also: Fauna: Arctic; Fauna: North America; Grizzly bears; Hibernation; Mammals; Omnivores; Pandas; Polar bears; Raccoons and related mammals; Salmon and trout.

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BEAVERS

Types of animal science: Classification, ecology
Fields of study: Ecology, systematics (taxonomy), wildlife ecology, zoology

Beavers were almost wiped out in North America by the fur trade in the nineteenth century. Now thriving in many areas, beavers are a keystone species in their ecosystem because their activities modify habitats dramatically.

Principal Terms:

castoreum: a secretion from the castor glands, used in scent marking

Castoridae: rodent family to which beavers belong

sexual dimorphism: a marked difference between males and females in some aspect of animal morphology, such as body size

Beavers are semiaquatic mammals who live on ponds, lakes, or streams. Most live in groups called colonies, which together erect a home, called a lodge, constructed of mud and sticks. So-called bank beavers inhabit cavities in the sides of stream banks rather than lodges.

A beaver colony consists of a family comprising the breeding pair and their offspring from the previous two years. Typical colonies consist of four to eight individual beavers. Beavers appear to be monogamous, and females are dominant over males and juveniles, at least during parts of the year. Members of the colony work together to maintain the lodge, build dams, and defend their territory against other beavers. Beaver colonies occur in typical densities of 0.4 to 0.8 colonies per square kilometer, though they can occur at higher densities when suitable habitat is plentiful.

The Beaver Life Cycle

Beavers have a single breeding season, in winter, during which mating takes place. Females experience a period of estrus that lasts for about two weeks, during which they are receptive for ten to twelve hours. Gestation lasts for about 110 days. Litter sizes range from zero to nine, with an average of two to four young born each year. Beavers are born in a relatively well-developed state; their eyes are open and they are fully furred. Young beavers nurse from their mother for two or three

Image Not Available

months, though beavers begin eating some solid food at only a few weeks of age. Beavers reach sexual maturity at 1.5 to 2 years, at which time they are forced by their parents to leave the colony.

Beavers are herbivorous and eat the woody parts of trees and shrubs. Favorite foods include aspen and alder trees. Beavers will chew down large trees, not to gain access to the large trunks, which are impossible for beavers to move, but rather to gain access to smaller branches growing at the top of the tree, which the beavers then eat.

Active year round, beavers must plan ahead to provide food for themselves during the winter. During the warmer months, the beavers will group branches together in the water near their lodges. During winter, when the pond or stream ices over, beavers swim under the ice to gain access to these stick piles as a source of food. A beaver lodge is constructed with an underwater entrance. Thus, during the winter, beavers can enter and exit the lodge without ever coming up above the ice.

Beavers are known as important habitat modifiers due to their dam construction behavior. Beavers chew down trees and use the tree trunks and their associated branches to build dams along streams. Dams cause water pooling and slow the water flow behind the dam, increasing water depth and creating suitable areas for building lodges. Furthermore, beaver dams cause localized flooding that can dramatically alter landscapes. Once beavers have used all of the surrounding vegetation, either in dam construction or as food, they will relocate to a new area. The abandoned beaver pond eventually fills in to become a “beaver meadow” which supports a variety of plants that would not otherwise occur in that location.

Beaver Facts

Classification:
Kingdom: Animalia (Metazoa)
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Subclass: Theria
Infraclass: Eutheria
Order: Rodentia (rodents)
Suborder: Sciurognathi (squirrel-like jaw musculature)
Family: Castoridae (beavers)
Genus and species: Castor canadensis (North American beaver), *C. fiber* (European beaver)

Geographical location: North America (*C. canadensis*), Europe and Asia (*C. fiber*)

Habitat: Ponds, lakes, and streams, except in southern Florida and the deserts of the southwestern United States

Gestational period: 100 to 110 days

Life span: Thirty-five to seventy years in captivity; ten to fifteen years in the wild

Special anatomy: Castor glands in both males and females are used for intraspecific communication; webbed hind feet and a broad flat tail allow for excellent swimming ability; dense, water-repellent fur

Physical Characteristics of Beavers

Beavers are one of the largest rodents, second in size only to the capybara. The two species in the family Castoridae are similar in many aspects. Both species show little sexual dimorphism and a normal range in body mass from twelve to twenty-five kilograms. Both male and female beavers have castor glands, which produce a substance called castoreum. Beavers deposit castoreum on piles of mud outlining the boundaries of their territories, in essence creating a message board for other beavers that pass by. Beavers also have broad, flat tails which are used not so much for packing mud, as is commonly believed, but instead as a means of communication. Beavers smack the water surface with their tails, producing a loud noise that can easily be heard by other animals. Beaver tails are also used for directional control while swimming.

Beavers are dark brown in color, and their thick fur coats contain a dense underfur that traps air and thus insulates the beaver. Long guard hairs provide a protective layer over the underfur. Their webbed hind feet function as excellent paddles when swimming. Forefeet are not webbed and thus are more capable of manipulating objects. Split claws on the first and second digit of the forefeet are used to groom the dense fur, thus maintaining its water repelling and insulating properties.

In North America, beavers have made a dramatic comeback in numbers after being hunted almost to extinction in the late nineteenth and early twentieth centuries. In Europe, beavers have fared less well and in some areas are listed as threatened or endangered, due mostly to destruction of suitable habitat.

—Erika L. Barthelmess

See also: Fauna: North America; Fur and hair; Home building; Lakes and rivers; Mammals; Otters; Rodents; Tails.

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BEES

Type of animal science: Classification
Fields of study: Anatomy, entomology, invertebrate biology

Over ten thousand species of bees form the order Hymenoptera. Honeybees, the best known, produce honey and beeswax.

Principal Terms

ABDOMEN: the hind part of a bee body, containing the stinger and most organs
PUPATION: the process whereby bee larvae metamorphose into bees
ROYAL JELLY: the protein- and hormone-rich food that workers feed queen larvae
THORAX: the midsection of the bee, from which legs and wings protrude

Over ten thousand bee species exist, classified in two groups. Social bees (for example, honeybees) live in groups of over ten thousand. Solitary bees (for example, carpenter and leaf cutter bees) live in smaller groups. Bees live from the tropics to the Arctic. Wild bees live in trees, bushes, and in the ground, building hives of beeswax, leaves, wood, or clay.

The best known and most plentiful bees are honeybees, imported to the United States during European colonization. Millions of U.S. honeybee hives produce hundreds of tons of honey yearly, one third of the honey made in the hives. The rest of the honey sustains the bees.

Honeybees—social bees—produce beeswax hives, each holding over ten thousand bees. Solitary carpenter bees tunnel into wood, such as trees or fence posts. Their colonies contain about one hundred bees. Another solitary bee class, the leafcutters, tunnel in wood and build from leaf bits joined by secreted glue. Miner bees live in sandy tunnels in groups of several thousands. Adult solitary bees are males or females.

Physical Characteristics of Bees

Bees are 0.1 inch to 3 inches long. There are three types of honeybees: workers, queens, and drones. In any given hive, 95 percent of the bees are immature female workers, 5 percent are males (drones), and one is a mature female (queen).

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The worker bee's main body parts are head, thorax, and abdomen. The head has five eyes, two antennae, and a mouth. Three small eyes sit atop the head, arranged triangularly. Two compound eyes at the front of the head contain many six-sided facets. Eye number, design, and arrangement give keen eyesight. Two antennae, organs of smell, protrude from the head. Their uses include finding food and recognizing bees that do not belong in a hive. The important mouth parts are the tongue and jaws. The tongue, a long, slender lower lip, is rolled in a tube used to sip flower nectar. Scissor-shaped jaws cut and shape things or bite defensively.

The thorax, behind the head, holds wings and legs. The four membranous wings beat over ten thousand times a minute. Front wings hook to rear ones to work as synchronized propellers. Wing speed and synchronization let bees fly precisely and carry loads of food outweighing the in-

René-Antoine Ferchault de Réaumur

Born: February 28, 1683; La Rochelle, France
Died: October 17, 1757; Saint-Julien-de-Terroux, France
Fields of study: Biology, entomology, chemistry, metallurgy
Contribution: Réaumur was the greatest entomologist of his time. He also made contributions to the biology of regeneration, metallurgy, chemistry and the early biochemistry of digestion.

René Antoine Ferchault de Réaumur was born in La Rochelle, France. Nothing is known about his early life. However, Réaumur became—among many other things—the foremost entomologist of his time. The fires that forged Réaumur began when he moved to Paris in 1703. In 1708, he was appointed to be a member of the highly prestigious French Academy of Sciences.

In 1710, King Louis XIV charged Réaumur with preparing a complete description of all the industries and natural resources of France. He was to prepare a document describing all the arts, industries, and professions present throughout the country. During this process, which concluded with his contributions to the Academie Royale des Sciences' publication of the *Description des Arts et Metiers* (1761-1798, 42 vols.; description of arts and handicrafts), Réaumur acquired a very wide knowledge of contemporary scientific and technological endeavors. This knowledge and the compilation of the huge report desired by Louis XIV were to stand him in good stead in many other scientific endeavors.

Among the wide-ranging scientific contributions arising from Réaumur's many activities in carrying out the king's charge were important contributions to metallurgy and to understanding the chemistry of iron and steel. He was the first scientist to recognize the importance of the carbon content of iron preparations that become steels of different types. In addition, in 1720 Réaumur invented the cupola furnace used for the melting of gray iron. Use of this furnace is still the most economical and widely utilized method for carrying out this process.

In 1734, Réaumur published the first volume of the work that was to make him the foremost entomologist of his time: *Mémoires pour servir à l'histoire des insectes* (1734-1742, 6 vols.; memoirs serving as a natural history of insects). The huge endeavor produced the first serious, complete, and comprehensive entomological work.

An overall naturalist, Réaumur's contributions to biology also included the discovery of the ability of crayfish to regenerate lost limbs. Furthermore, combining the known chemistry and biology of the day, Réaumur isolated gastric juice from animals and showed that its operation was chemical. He demonstrated the process in the laboratory in 1753.

In 1740, Réaumur's ability as a complete scientist led him to develop an opaque form of porcelain, still used, called Réaumur porcelain. He also invented, in 1731, a temperature scale or thermometer based upon the use of an alcohol-water mixture, in which water froze at 0 degrees and boiled at 80 degrees. This Réaumur temperature scale was widely used until the end of the twentieth century.

—Sanford S. Singer

dividual bee. The three legs on each side of the thorax end in claws and sticky pads, enabling bees to hang from flowers or walk upside down across hives. Bee legs and bodies are covered with fine hairs. They collect pollen (the second bee food after honey), which is transferred, via leg combs, to pollen baskets in the hindmost legs.

The abdomen, behind the thorax, contains the most organs. Beeswax, made in the abdomen, collects on abdomen wax plates harvested by mouth and used to build hives. At the rear of the abdomen is a stinger. It is 30 percent of the length of the bee's body. In worker bees the stinger is barbed, so that it remains in the animals it stings. This is fatal to the bee, because in freeing itself from its victim a bee rips away much of its abdomen. "Stingless" bees and drones lack functional stingers. Queens have barbless stingers.

Bee Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Arthropoda
Class: Insecta
Order: Hymenoptera (bees, ants, and wasps)
Suborder: Apocrita
Superfamily: Apoidea, with six families, four subfamilies, and tribes Bombini (bumblebees), Meliponini (stingless bees), Apini (honeybees)

Geographical location: Every continent except Antarctica

Habitat: All live on land in forests, plains, swamps, and deserts; colonies are in hives or tunnels, in trees, fallen logs, or sandbanks

Gestational period: Three to five weeks

Life span: Honeybee workers live six to eight months, queens live up to ten years, and drones live until winter; solitary bees do not live in hives kept warm year-round, so most die in winter

Special anatomy: Three legs on each side of the thorax; two pairs of synchronized, membranous wings; a poison stinger; a tongue for sipping nectar; pollen baskets

The Life Cycle of Bees

Every honeybee begins as an egg laid in a beeswax cell. In three days a grub hatches. Workers first feed all grubs royal jelly. Soon, worker grubs get a honey-pollen substitute. After several days, the queen grubs are sealed into cells and enter a third life stage, pupation, spinning cocoons and metamorphosing into queens. Drones, from unfertilized eggs, only fertilize queens leaving to begin new colonies. This kills the drones and gives each queen enough semen to fertilize all the eggs—often a million—she lays during her life.

Workers do all hive jobs except egg laying. They feed grubs, guard hives, keep air fresh by beating their wings to make air currents, gather pollen and nectar, seek bee glue (propolis) from trees, use propolis to mend hive-wall breaks, and build egg, honey, or nectar cells. They die six to eight months after birth.

Solitary bees differ from honeybees in several ways. First, all are functional males or females. Second, they make homes from leaves (leaf-cutter bees), wood (carpenter bees), or clay (mason bees). They lay eggs in cells holding pollen and honey, and larvae and pupae develop independently. Their colonies are smaller than honeybee hives because winter kills most inhabitants; colony continuation depends on female survivors. Finally, their jaws and stingers differ, enabling the use of different materials in building from their environment.

Destructive and Beneficial Bees

Bees pollinate most flowering plants, and thousands of plant species could not survive otherwise. In addition, the bee industry annually gleans hundreds of tons of honey and beeswax, earning sixty million dollars a year. Sweet, nutritional honey is used to flavor drinks, as a health food, and in salad dressings, is poured over pancakes, and is used in many other ways. Beeswax also has many uses, from candles to lipstick and eyebrow pencil components. Even "destructive" bee stings may have benefits; many people believe that stings cure arthritis and rheumatism.

—*Sanford S. Singer*

See also: Altruism; Antennae; Coevolution; Communication; Flight; Insect societies; Insects; Plant and animal interactions; Poisonous animals; Sex differences: Evolutionary origin; Wasps and hornets; Wings.

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BEETLES

Types of animal science: Anatomy, behavior, classification, ecology, geography, reproduction
Fields of study: Anatomy, ecology, entomology, reproduction science, zoology

Over 300,000 species of beetles have been identified, classified in the general order Coleoptera, the largest order of animals in the insect world. Beetles constitute more than 40 percent of the 700,000 known insect species.

Principal Terms

CUTICLE: outer nonliving layer of the beetle's body
ELYTRA: rigid front wings of beetles, that cover the second, functional pair of wings
EXOSKELETON: the external skeleton of beetles
MANDIBLES: insect jaws
MOLTING: the sloughing off of old body covering, which permits the beetle to grow
PARTHENOGENESIS: reproduction in which an unfertilized egg hatches
THORAX: the middle section of insects, from which the legs protrude

Beetles are the largest order of both the insect and the animal worlds. Approximately 300,000 species, some 26,000 of which exist in the United States, have been identified. Every year, however, thousands of new species are discovered and classified. Beetles are found on every continent except Antarctica. There is no reason to believe that some of these highly adaptable creatures do not exist on the somewhat temperate Antarctic Peninsula.

Although most beetles are land animals, some are aquatic, carrying air bubbles on their legs, which provide them with air when they are submerged. Most aquatic beetles live in freshwater, feeding on small fish and tadpoles, although a small number of beetles live in salt water. Other beetles live largely underground or beneath the bark of trees, while some species go through their life cycle in caves and are blind. The remarkable adaptability of beetles, which date to the Triassic period, has made them one of earth's most enduring species and accounts for their being found in a broad variety of geographical locations and climates.

Physical Characteristics of Beetles

With over 300,000 species of beetles cataloged and classified, the variations within each species are notable. These insects can range in size from very small to quite large. The fungus beetle is smaller than the period at the end of this sentence, never growing beyond one-fiftieth of an inch in length. The Hercules beetle, found in Central American rain forests, is typically six inches long and often exceeds that length.

Despite variations in size, each species of beetle shares anatomical characteristics with every other species. All beetles have three main body parts in common: the head, the thorax, and the abdomen. The head usually contains the mouth and the eyes, although some blind cave beetles have no eyes. All beetles have antennae that protrude from the front of the head and are vital to communication. Blind beetles have more fully developed antennae than sighted ones.

A beetle's mouth consists of three parts, the frontal mandibles, the maxillae or second jaw in four or five sections, which is jointed and has palpi (segmented appendages) on its outer side, and the labium or lower lip, which resembles the maxillae but has only three sections. In vegetarian beetles, the jaws point down, whereas in predatory beetles, they point forward.

The thorax is behind the head and consists of three segments. The first, the prothorax, larger in beetles than in other insects, has one pair of legs on its underside. The second segment has a second pair of legs and the elytra, the cutaneous wing covers found in all beetles. In some species of ground beetles that do not fly, the elytra may be joined as a single, hard piece of cuticle. The third segment bears the third pair of legs and the delicate hind wings used for flying by species that fly.

The abdomen, which contains most of the beetle's internal organs, is behind the thorax. It has nine segments, not all of which are visible. In most species the abdomen is covered almost entirely by the second pair of wings, although in a few species, up to half the abdomen is exposed. In most species, a straight line runs along the abdomen where the two elytra meet.

Regardless of size or species, all beetles share this basic anatomy. Individual differences, however, characterize various species. Ground beetles that tunnel into the earth have short, strong legs with projections that make them efficient diggers. Predatory beetles have long legs because they must move rapidly to trap their prey.

Image Not Available

The Life Cycle of Beetles

All beetles pass through four stages of development, called metamorphosis. Life begins within eggs laid by the female beetle, usually in a protected place such as beneath a rock, on the underside of a leaf, or inside the bark of a tree. The females in some species lay up to two thousand eggs at once, while in other species a single egg is laid.

When the eggs hatch, a small wormlike creature, called a larva or grub, emerges. The larvae of some species are mobile and have legs, while those of other species may be legless and can move about only by wiggling. Those with legs are predatory and move about easily in their quest for food. The legless larvae usually attach themselves to plants and survive by eating the leaves. Beetle larvae have huge appetites and frequently are destructive to crops. Their voracious eating causes them to grow rapidly, forcing them to shed their old skins, which they outgrow, in a process called molting.

When the larva reaches full size, it enters the next phase of its metamorphosis by becoming a pupa, sequestering itself in a safe place where it remains for about a month. Its body changes drastically as it evolves toward its adult stage. When the pupa cracks, the adult beetle emerges, its body soft and flexible. Within twenty-four hours, however, the body hardens and the metamorphosed beetle looks and acts like other adult beetles.

The integrity of the species is maintained in some types of beetles by the shape of the male sexual organs which allows them to enter only females of that species. Also, the white fringed weevils of Argentina and some other beetles are parthenogenetic, which means that their eggs are not fertilized by a male. This species is exclusively female.

Destructive and Beneficial Beetles

Many species of beetles are destructive, devouring everything in their paths, ruining crops, devastating forests by attacking the roots of trees, and wreaking general havoc wherever they exist. Japanese beetles were particularly destructive to farm crops in New Jersey during the 1930's. The boll weevil deposits its eggs in vegetables or in the blossoms of cotton plants. The resulting larvae quickly consume the plants in which they are hatched. Some types of beetles eat grain and flour, while the larvae of carpet beetles eat all kinds of fiber.

The predatory nature of some species of beetle can help solve ecological problems. St. John's wort, also called Klamath weed, is a rapidly growing plant that annihilates grasses that grow in the places where it takes hold. It also causes animals that eat it to have sore mouths and debilitating skin eruptions. When it was discovered that a leaf beetle the size of a pea would devour this intrusive plant, such beetles were introduced into the affected areas and within a few years had eradicated the plant.

Ladybugs contribute to agriculture by eating aphids and other pests from the leaves of plants. In many parts of the Third World, people depend upon the larvae of beetles to add protein to their diets. Many folk remedies, including aphrodisiacs and diuretics, are made from dried beetles. Scarabs and other beetles consume carrion and clear away dead material that is potentially infectious.

—*R. Baird Shuman*

See also: Antennae; Cockroaches; Exoskeletons; Insects; Metamorphosis; Parthenogenesis; Wings.

Beetle Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Arthropoda
Subphylum: Unirama
Class: Insecta
Subclass: Endopterygota
Order: Coleoptera (beetles)
Suborders: Polyphaga (rove beetles, scarabs, stag beetles, metallic wood boring beetles, click beetles, fireflies, blister beetles, mealworms, ladybugs, leaf beetles, longhorn beetles, weevils); Adephaga (ground beetles, tiger beetles, predacious diving beetles, whirligig beetles); Archostemata (small, rare group characterized by wings coiled in a spiral)
Geographical location: Every continent except Antarctica
Habitat: Mostly land (forests, deserts), although some live in freshwater and a rare few in salt water
Gestational period: Varies greatly among species
Life span: Many exist for four months to a year; several species of ground beetles in Alaska, protected from subzero temperatures by an ability to produce glycerol that creates an antifreeze in their bodily fluids, survive for up to eight years
Special anatomy: Six legs, three on each side of the thorax; two pairs of wings, two hard, cutaneous wings on top that serve as armor, two more membranous wings underneath used in flying

Some Types of Beetles

Blister beetles, which are usually brightly colored, emit a strong chemical that blisters the skin of predators intent on harming them.

Carpet beetles live and breed in houses, often laying their eggs in carpeting. Their larvae eat carpets and other items of cloth.

Click beetles can arch their backs so that a protrusion pops out, stinging the mouth of any predator. If it is dropped on its back, it can click again and land upright.

Japanese beetles, brought into the northeastern United States on produce from Asia, are extremely destructive to plants of every variety.

Metallic wood borers, living largely beneath the bark of trees, have mouths designed for drilling into wood both for food and to provide a safe place to lay eggs.

Rowing beetles live on the surfaces of freshwater lakes and ponds, using their well-developed middle and hind legs like oars to move across the water at the rate of sixty strokes a minute.

Scarab beetles, also called Dung beetles, roll animal waste such as horse manure into balls—sometimes as large as baseballs—and lay their eggs inside; these balls provide food for their larvae.

Tiger beetles, unlike most other beetles, can fly immediately without first warming up in the sun or climbing to the edge of a leaf or end of a stem to take off.

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BIODIVERSITY

Type of animal science: Ecology
Fields of study: Ecology, environmental science, population biology

Biodiversity refers to the total number of animals and other forms of life, including different species and genetic variants.

Principal Terms

AQUACULTURE: the artificial growth of animals or plants that live in the water; the culture of something living in water

BIODIVERSITY: the number and kinds of animals and plants and the variations in genetic material they possess

EXOTIC SPECIES: organisms that are not naturally found in a place but have been artificially introduced, whether by accident or intentionally

EXTINCT: no longer found anywhere on earth

EXTIRPATED: not found in an immediate local area but found elsewhere on earth

HABITAT: an assemblage of plants, animals, and the physical land, water, minerals, and other elements that support a life-form; usually refers to a single species

INVERTEBRATE: an animal without a backbone; for example, worms, clams, crabs, insects, and jellyfish

SPECIES: a group or groups of interbreeding natural populations of organisms that are reproductively isolated from other such groups

SUBSPECIES: a group or groups of interbreeding organisms that are distinct and separated from similar related groups but not fully reproductively isolated

THREATENED SPECIES: animals or plants so few in number that they may soon be endangered and then extinct

The study of biodiversity is relatively new. The word was coined by Edward O. Wilson in order to explain the biological living resources and wealth lost when whole areas of tropical rain forest were destroyed by clear-cutting and burning. Many, if not all, of these tropical rain forests were in remote areas, often in developing countries, untouched by modern civilization, and relatively unstudied by scientists. As a result, many of the plants and animals, especially insects, were unknown to scientists. Many of the species lived nowhere else on earth and, once destroyed, became extinct. Scientists realized that these tropical rain forests held a great wealth of species and that their destruction was removing large numbers, perhaps millions, of species, along with the DNA that made each species unique. Wilson referred to this loss of species as a loss of the forests' biological diversity, or biodiversity. The loss is not merely of the species that become extinct but also of the combination of highly specific genetic material in each species.

Because the study of biodiversity involves the study of individual species, their loss, and their habitat, the subject is closely tied to endangered species, ecology, and conservation biology. Endangered species are those plants and animals that are nearly extinct; threatened species are not yet at the point of being endangered but will be if measures are not taken soon. Both plants and animals, including insects, worms, clams, crayfish, and other creatures, may be considered either threatened or endangered. Specific habitats, especially those that are unique and found in only one location on earth, can also be considered threatened. Protecting individual species often means protecting the habitat the species needs for survival.

During the nineteenth century and the first part of the twentieth, some animals were hunted to extinction. Several other species were hunted to near extinction or were extirpated (removed) from large areas, largely by extensive changes to their habitats. As a result of the losses and near losses, some scientists, resource managers, and political leaders instituted programs and activities to prevent extinction and to restore species that were near extinction. Animals (and later plants) that were near extinction were officially designated as endangered and given legal protection to prevent their extinction. Eventually these efforts grew to encompass a much broader field of work by experts in many fields.

One of the more difficult aspects of protecting a single species is the importance of the habitat to the well-being of the species. This fact is one of the underlying principles driving the whole study of biodiversity. Scientists have learned that the habitat is critical for restoration of a species and that protecting the habitat is a powerful means of preventing species loss and protecting biodiversity. As a result, programs and individuals trying to protect or restore biodiversity or individual species have come into conflict with those who use or plan to use large areas of land and whole habitats for purposes such as housing or industrial development, harvesting, and aquaculture.

Threats to Biodiversity

Scientists generally believe that three major factors cause the loss of biodiversity: resource overharvesting, habitat loss, and introduction of exotic species. Overharvesting or excessive hunting and catching caused the loss of species such as the great auk, passenger pigeon, and Steller's sea cow. Some species of whales nearly suffered the same fate. However, for the vast majority of animals and plants, overharvesting is not a major cause of endangerment or extinction. Many animals that are commonly harvested have large and dispersed populations, so harvesting stops before it causes populations to decline to the point of endangerment and extinction. This does not mean that overharvesting is not a problem, but that it is seldom the sole cause of population declines and not the most frequent cause.

A number of international controls have been implemented to prevent, limit, or discourage the killing of some of the animals that are threatened by overharvesting in many countries around the world. Many such controls ban the import or shipping of either live animals (tropical birds such as parrots) or parts of them (elephant ivory and rhinoceros horn). The animals endangered by overharvesting—the rhinoceros, elephant, and parrot—tend to be long-lived and restricted in distribution. Their reproductive rates are low, and populations often require a large habitat. The habitats of many of these animals are threatened by human activities, which makes the effect of their being slaughtered for commercial reasons that much more pronounced. In 1997, one of the major international treaties governing commercial transactions in rare and endangered species was modified to permit some African nations to sell stocks of certain animal products that had been previously prohibited. Some experts worried that the change in the laws would again provoke illegal overharvesting.

Many animals are threatened in their native habitats by exotic species introduced into the area. These exotic species often cause biological pressures that the native species cannot handle. They may threaten native species directly by competing for food, living space, critical habitat (such as nesting space), or other necessary environmental resources. Some exotic animals are aggressive and drive away or attack the native ones. In the United States, sea lamprey were introduced into the Great Lakes and have driven populations of many native species to precipitously low levels or even extirpated them.

Exotic species may also present indirect threats by introducing diseases, parasites, or hitchhiker species that arrive with the exotic. In South Carolina and Texas, exotic shrimp are used in aquaculture, and they can carry a deadly virus that may threaten native shrimp if released into the wild by accident. Zebra mussels were carried into the Great Lakes water system in the ballast water of ocean tankers. With no natural controls, zebra mussels have multiplied to the point that they are not only a nuisance to human activities but also serious competition for native aquatic animals.

Habitat Loss and Degradation

The most significant threat to biodiversity, as occurs in tropical deforestation, is habitat loss or degradation, including poisoning. Habitat loss is the elimination of a habitat, often by cutting, plowing, filling, or other construction or harvesting methods. When all the trees in a forest area are felled for wood (a practice known as clear-cutting), the habitat is lost until the trees regrow, an event that may never take place. Degradation is the elimination or lessening of some characteristic of the habitat that is critical for one or more species. Changing the temperature or speed of the water flowing in a stream can render it no longer suitable for a particular fish or mussel. Filling or draining a wetland alters the moisture content of the soil and changes its suitability for plants or animals.

One of the earliest examples of habitat degradation was the poisoning of bald eagles and peregrine falcons in the United States by the pesticide dichloro-diphenyl-trichloroethane (DDT). DDT was widely used throughout the world (and still is in some countries), is highly persistent, and accumulates in animals at ever-increasing levels in a trophic system (a system in which one animal feeds on another that feeds on another, and so on). Falcons and eagles were some of the birds of prey that took in so much DDT that they were poisoned and their eggs became too thin-shelled to survive. Their populations began to decline from reproductive failure. Many species of freshwater mussels are highly sensitive to chemicals and do not survive even low levels in the water. Many of the mussel species have become rare and endangered as a result of this poisoning, and they are not the only species to suffer from environmental poisons.

Altering stream and river flow via dams, diversions, withdrawals, and dredging is another form of habitat degradation that can dramatically change the way animals and plants use the aquatic system. In river systems throughout the Pacific Northwest, salmon return from the ocean to spawn (lay eggs and reproduce) in the river where they grew from egg to fish before migrating to the open ocean. If a dam blocks the river or if the conditions in the river are no longer suitable, the salmon are not able to spawn. In salmon, the fish that spawn in a given river are distinct and genetically identifiable, almost forming a subspecies. Therefore, authorities in the Pacific Northwest have had to determine the relationship between individual spawning groups and the watershed habitat before altering streams and rivers.

The cutting of mature forests in the Pacific Northwest and in Alaska eliminated the habitat for the spotted owl. Great controversy resulted from limits, restrictions, or bans on logging in these forests, which were prized for the high quality lumber that could be made from the trees. These and similar conflicts formed the basis for many studies on scientific, legal, and policy matters concerning the Endangered Species Act in the United States.

Controversies have arisen over habitat protection programs and laws in the United States and other countries because of the restrictions and limitations imposed on development, logging, and other human activities. People on one side argue that the potential benefits from protecting a species are greater than any inconvenience or costs that might ensue, and those on the other side argue that the economic benefit from the activity that threatens the species outweighs any ecological concerns. However, in some cases, companies and governments have worked hard to preserve species believed to be of economic value.

Biodiversity Research

Biodiversity is studied at the level of populations, of individuals (including molecular biology), and in the interactions between organisms and their environment. Research on biodiversity includes genetic, ecological, and behavioral studies and investigations focusing on diseases and life histories.

Loss of habitat, often through clearcutting forests, is one of the greatest threats to biodiversity today. Many territorial animals require large ranges, and breaking up forest space (habitat fragmentation) is as destructive as cutting down the whole forest would be. (PhotoDisc)

Much of the work on any specific species, especially large vertebrates, is conducted in the field, using techniques for observing, counting, tracking, and monitoring the population. Most invertebrates cannot be studied other than by observation and counting. One of the goals of ecological research on biodiversity is to understand the life histories and ecology of individual species. Scientists seek to explain life span, reproductive patterns and strategies, food preferences, environmental requirements, and limits. Other major goals are to describe the habitat requirements and better understand the relationship between the species and the habitat.

The management and legal aspects of various programs are included in biodiversity studies. This research is closely related to the field of conservation biology. Such study entails examining areas such as how programs work; what money is spent, by whom, how, and for what use; whether habitats or species are protected, restored, or lost; and the time required for various activities. These considerations are generally part of program evaluation, a topic that can be more thoroughly researched in the field of management science. The legal aspects of preserving biodiversity and protecting endangered species have been studied by a number of legal and policy-making organizations, including the Environmental Law Institute and Environmental Defense Fund, both of Washington, D.C. The National Research Council, the operating arm of the National Academy of Sciences has published a number of reports on the Endangered Species Act, and these usually address legal, policy, and science issues.

Modern molecular genetic techniques are applied to the study of individual species of plants and animals and their restoration. Tissue, often a blood sample, taken from a single individual is analyzed to determine the genetic relations among members of a population. Scientists may then assess the potential of the remaining individuals to act as the beginning or nucleus for a new population. Modern techniques can determine the genetic makeup of animals and whether the individuals are distantly enough related to form a breeding pair without suffering the adverse consequences of inbreeding.

Artificial breeding and culture are techniques often employed with the few remaining members of a population. These animals may be brought in from the wild and confined, as were the last remaining California condors. The animals are kept in captivity so that artificial breeding and maintenance techniques can be used to raise additional members of the population. Once the population is large enough for release or other factors are favorable, reintroduction into the wild may be attempted.

Zoological parks and botanical gardens have been involved in maintaining the few remaining specimens of some species. With the help of such facilities, animal tissue has been stored in culture, and sperm have been frozen for later use in breeding. Parks and gardens now play an active role in species propagation and husbandry through breeding, nourishment programs, studying and preventing disease, and behavioral training to reintroduce zoo animals into the wild.

Increasing Awareness of Biodiversity's Importance

Human activities eliminated more than a few animals from the face of the earth before the second half of the twentieth century, when national and international laws were enacted to protect endangered species and the modern environmental movement began. Among the animals lost were the great auk in 1844 and the passenger pigeon in 1914. These animals were hunted to extinction under the mistaken belief that extinction could not happen, and because authorities lacked a way to limit the hunting of the animals. Despite international efforts to protect animals from extinction, in the latter part of the twentieth century many countries allowed or encouraged the wholesale destruction of tropical rain forests, along with the animals that lived there.

In 1973, amid growing awareness of the need to prevent further extinctions, the Endangered Species Act was passed by the Congress of the United States. The act gave the U.S. Fish and Wildlife Service the responsibility for enforcing the law and set procedures for determining which species should be listed as endangered. The act also established the category of threatened species to protect those that were close to becoming endangered. Subsequently, this protection was extended to the habitats on which the animals depend.

Studies by academic and government scientists revealed that most species are threatened by habitat loss or degradation, overharvesting, or exotic species. Most of the problems arise from habitat loss or degradation rather than overharvesting, which had been the cause in several of the cases that prompted passage of the Endangered Species Act. Scientifically, and eventually legally, one of the most difficult tasks is to determine habitat requirements and then ensure that the required habitat is protected. Identifying and protecting habitats became an important part of all programs aimed at protecting biodiversity. Loss or degradation of habitat became one of the criteria that federal agencies used to take legal action or make official decisions.

Many human activities such as logging, building, mining, and farming can destroy or degrade valuable habitats on which endangered species depend. As a result, endangered species protection programs and activities have been in conflict with some business interests seeking to carry out those activities that threaten species or their habitats.

Efforts, activities, and programs to protect biodiversity rely on the latest techniques and methods. These include electronic tracking of large animals, molecular analysis of genetic material, and cellular studies of tissues to help determine actual or potential threats to animals. Ecologists investigate life histories, including feeding habits, environmental requirements and limits, and migration patterns.

—Peter L. deFur

See also: Biogeography; Breeding programs; Clines, hybrid zones, and introgression; Cloning of extinct or endangered species; Coevolution; Demographics; Ecological niches; Ecology; Ecosystems; Endangered species; Extinction; Fauna: Africa; Fauna: Antarctica; Fauna: Arctic; Fauna: Asia; Fauna: Australia; Fauna: Caribbean; Fauna: Central America; Fauna: Europe; Fauna: Galápagos Islands; Fauna: Madagascar; Fauna: North America; Fauna: Pacific Islands; Fauna: South America; Gene flow; Genetics; Habitats and biomes; Plant and animal interactions; Population analysis; Population fluctuations; Population genetics; Population growth; Symbiosis; Urban and suburban wildlife; Wildlife management; Zoos.

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BIOGEOGRAPHY

Types of animal science: Ecology, evolution, geography
Fields of study: Ecology, evolutionary science, paleontology, population biology

To understand the underlying geography of plant and animal distributions, biogeographers must integrate considerations of historical and current events and conditions.

Principal Terms

BIODIVERSITY: all of the different kinds of organisms living on earth or in a given area

DISPERSAL: the movement of organisms from one geographic area to another; movements may be the result of an animal's own efforts or the consequence of being passively transported by natural or human-mediated means; dispersal is limited by barriers

PLATE TECTONICS: often referred to as continental drift, the modern theory assumes that the current position of continents and oceans is the consequence of dynamic forces that involve land masses "floating" on the earth's molten core

PLEISTOCENE GLACIATION: a period from about 1.8 million years ago to the last 100,000 years, characterized by alternating glacial and interglacial cycles; during the glacial periods ice sheets many miles deep covered as much as a third of the earth's surface

VICARIANCE: an event involving the erection of a barrier to dispersal that splits the distribution of an organism and facilitates the differential evolution of the geographically separated descendants

Biogeography is the science that seeks to understand spatial patterns of biodiversity. By examining past and present distributions, biogeographers attempt to explain why certain groups of organisms occur where they do, what enables them to live there, and what factors prevent them from moving or living elsewhere. To address these issues, biogeographic investigations must consider the effects of climate, topography, and other kinds of organisms, as well as historical events such as tectonic effects and glaciation. Because such historical considerations are frequently important and conditions are constantly changing, a group's closest relatives and their distribution must be taken into account in order to accommodate evolutionary events.

Because biogeography is such a broad discipline, individuals can rarely address an entire spectrum of relevant questions. Consequently, most biogeographers become specialists. For example, phytogeographers study plant distributions, and zoogeographers examine those of animals. Historical biogeographers reconstruct origins, dispersal events, and extinction through time. Ecological biogeographers concentrate on interactions between organisms and their environments to explain distribution patterns, and paleoecologists try to bridge the gap between historical and current conditions. Also related to the breadth of the discipline is the necessity for biogeographers to be conversant in one or more related fields. A broad knowledge of biology is obviously fundamental, as is an understanding of physical geography, but geology, paleontology, and climatology, among others, may be equally important.

Trends in Biogeography

Several consistent trends have emerged from biogeographic studies. Communities in isolated regions (especially large islands that have not been in contact with continents for long periods of time) tend to be unlike those found anywhere else. More types of organisms are found in tropical than in temperate or arctic regions. Fewer types of organisms are found on oceanic islands, although the organisms that are present may be found in phenomenal densities. On the other hand, some inconsistencies are striking. For example, some groups of related organisms are found throughout the world, whereas other groups have very restricted ranges.

Generally speaking, groups of organisms that are broadly distributed are either very old (their ancestors were in place before the continents drifted apart) or very mobile. Mobile organisms may be able to disperse actively, that is, on their own power (some species of birds and large marine mammals are good examples), whereas others are dispersed passively. Seeds of many plants, microscopic planktonic organisms, and insects are often transported by wind, currents, or other organisms. Limits to the dispersal of organisms are myriad. Size limits the ability to be blown by the wind; for example, dandelion thistles are more readily dispersed by even mild breezes than are walnuts. If water is a factor, buoyancy is critical. Coconuts are found on tropical shorelines around the world in large part because they do not sink, nor are their hard shells easily penetrated by salt water. Physical barriers often limit dispersal. Deserts effectively block organisms that require moisture, land halts movement of aquatic forms, and mountains prevent the passage of plants and animals that cannot tolerate the conditions associated with high elevations. Some barriers even appear to be "psychological;" birds that could easily fly cross a stream or lake, for example, often will not.

Island Biogeography

In 1967, Robert H. MacArthur and Edward O. Wilson published a classic volume entitled *The Theory of Island Biogeography*. Although islands have figured prominently in modern biology (Charles Darwin and Alfred Russel Wallace both relied heavily on evidence from islands when formulating their theories of natural selection), only during the last third of the twentieth century was island biogeography recognized as a distinct discipline. Many of the principles that form the foundation of biogeography emanated from studies of islands. Among these are relationships between biodiversity and island size, ecological heterogeneity, and proximity to continents; between isolation and endemism (species evolving in a given area and found nowhere else in the world); and between island size and location and rates of immigration, colonization, and extinction. In addition, island biogeographers frequently have been at the center of debates arguing the relevance of dispersal versus vicariance. Central to these disputes is whether disjunct distributions of organisms are attributable to movement over barriers (dispersal) or to the creation of a barrier that separated a previously contiguous range (vicariance). Although both have undoubtedly played important roles, the debate rages over which was primarily responsible for the current distributions of many faunas, both on islands surrounded by water and on terrestrial "islands" surrounded by other inhospitable habitats.

—Robert Powell

See also: Adaptations and their mechanisms; Biodiversity; Clines, hybrid zones, and introgression; Communities; Demographics; Ecological niches; Ecology; Endangered species; Fauna: Africa; Fauna: Antarctica; Fauna: Arctic; Fauna: Asia; Fauna: Australia; Fauna: Caribbean; Fauna: Central America; Fauna: Europe; Fauna: Galápagos Islands; Fauna: Madagascar; Fauna: North America; Fauna: Pacific Islands; Fauna: South America; Genetics; Habitats and biomes; Paleoecology; Paleontology; Population analysis; Population genetics; Wildlife management.

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BIOLOGY

Type of animal science: Fields of study
Fields of study: Cell biology, conservation biology, developmental biology, invertebrate biology, marine biology, neurobiology, population biology, zoology

Biology is the science that studies life and living organisms.

Principal Terms

BIODIVERSITY: the total of all living organisms in an environment

DEOXYRIBONUCLEIC ACID (DNA): the carrier of all an organism's genetic information

NATIONAL INSTITUTES OF HEALTH: the United States' governmental division that monitors and improves public health

XENOTRANSPLANTATION: the transplantation of organs from one species to another

Biology is an extensive field subdivided into categories based on the molecule, the cell, the organism, and the population. Molecular biology touches on biophysics and biochemistry. It is the branch of biology that deals with the structure and development of biological systems in terms of the physics and chemistry of their molecules. Cellular biology is closely related to molecular biology through understanding the functions and basic structure of the cell. The cell is the smallest structural unit of an organism that is capable of independent functioning, consisting of one or more nuclei, cytoplasm, and organelles, all surrounded by a semipermeable membrane. Botany is the science or study of plant life. Ecology, also referred to as bionomics, is the study of relationships between organisms and their environments.

Developmental biology encompasses a number of issues, including gene regulation, genetics, and evolution. These are concepts of importance to vertebrates, invertebrates, and plants. A gene is a hereditary unit that occupies a particular location on a chromosome, determines a particular characteristic of an organism, and can undergo mutation. Genetics is the branch of biology that deals with heredity, especially the hereditary transmission and variation of inherited characteristics. Evolution is the theory that groups of organisms change with the passage of time, mainly as a result of natural selection, so that descendants differ morphologically and physiologically from their ancestors. Population genetics, the study of gene changes in populations, and ecology have been established subject areas since the 1930's. These two fields were combined in the 1960's to form a new discipline called population biology, which became established as a major subdivision of biological studies in the 1970's. Central to this field is evolutionary biology, in which the contributions of Charles Darwin are noted.

Microbiology is the branch of biology that deals with microorganisms. The study of bacteria, including their classification and the prevention of diseases that arise from bacterial infection, is the primary focus of microbiology. This branch is of interest not only among bacteriologists but also among chemists, biochemists, geneticists, pathologists, immunologists, and public health professionals. Parasitology is the study of parasites, organisms that feed on or in different organisms while contributing nothing to the survival of their hosts. Ethology is the scientific study of animal behavior. Animal behavioral studies have developed along two lines. The first of these, animal psychology, is primarily concerned with physiological psychology, and has traditionally concentrated on laboratory techniques such as conditioning. The second, ethology, had its origins in observations of animals under natural conditions, concentrating on courtship, flocking, and other social contacts. One of the important recent developments in the field is the focus on sociobiology, which is concerned with the behavior, ecology, and evolution of social animals such as bees, ants, schooling fish, flocking birds, and humans.

Ethics is the study of the general nature of morals and of specific moral choices. Bioethics addresses such issues as animal experimentation, cloning, euthanasia, gene therapy, genetic engineering, genome projects, protection of human research subjects, organ transplants, and patients' rights.

Biotechnology is the industrial use of living organisms or biological techniques developed through basic research. Biotechnology products include antibiotics, insulin, interferon, and recombinant DNA, and techniques such as waste recycling. The Office of Biotechnology Activities of the National Institutes of Health monitors scientific progress in human genetics research in order to anticipate future developments, including ethical, legal, and social concerns, in basic and clinical research involving recombinant DNA, genetic testing, and xenotransplantation (the use of organs from other species of mammals for transplants). In addition to organs donated from humans, researchers are exploring the use of partially or wholly artificial organs manufactured in the laboratory.

Biodiversity focuses on such issues as conservation, extinction and depletion from overexploitation, habitat pollution, global patterns and values of biodiversity, and endangered species protection.

Well known pioneer biologists include naturalist and explorer Sir Joseph Banks (1743-1820), naturalist and explorer Charles William Beebe (1877-1962), biochemist Gunter Blobel (b. 1936), environmentalist Rachel Carson (1907-1964), biochemist Stanley Cohen (b. 1922), biophysicist and codiscoverer of DNA, Francis Crick (b. 1916), naturalist and father of evolutionary theory Charles Darwin (1809-1882), zoologist Richard Dawkins (b. 1941), marine biologist Sylvia Earle (b. 1935), bacteriologist Paul Ehrlich (b. 1932), bacteriologist and discoverer of penicillin Sir Alexander Fleming (1881-1955), microscopist Antonie van Leeuwenhoek (1632-1723), botanist and taxonomist Carolus Linnaeus (1707-1723), ethologist Konrad Lorenz (1903-1989), zoologist A. S. Loukashkin (1902-1988), botanist and geneticist Barbara McClintock (1902-1992) , botanist and genetic theorist Gregor Mendel (1822-1884), endocrinologist and inventor of the birth control pill Gregory Goodwin Pincus (1903-1967), naturalist Alfred Russel Wallace (1823-1913), biophysicist and codiscoverer of DNA James Watson (b. 1928), and sociobiologist Edward O. Wilson (b. 1929).

—Mary E. Carey

See also: Anatomy; Animal kingdom; Ecology; Embryology; Ethology; Genetics; Marine biology; Paleoecology; Paleontology; Physiology; Systematics; Veterinary medicine; Zoology.

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BIOLUMINESCENCE

Types of animal science: Behavior, physiology
Fields of study: Biochemistry, marine biology, physiology, systematics (taxonomy)

Bioluminescence is visible light emitted from living organisms. Half of the orders of animals include luminescent species. These organisms are widespread, occurring in marine, terrestrial, and freshwater habitats. Bioluminescence is used for defense, predation, and communication.

Principal Terms

LUCIFERASE: one of a group of enzymes that catalyzes the oxidation of a luciferin

LUCIFERIN: one of a group of organic compounds that emits visible light when oxidized

MELANOPHORE: a melanin-containing cell

PHOTOPHORE: a light-emitting organ consisting of a lens, reflector, and light-emitting photogenic cells

SYMBIOSIS: the intimate living together of two dissimilar organisms in a mutually beneficial relationship

Bioluminescence is the visible light produced by luminous animals, plants, fungi, protists, and bacteria, that results from a biochemical reaction with oxygen. Unlike incandescent light from electric light bulbs, bioluminescence is produced without accompanying heat. Bioluminescence was first described in 500 B.C.E., but the chemical mechanism of bioluminescence was not elucidated until the beginning of the twentieth century. The ability to luminesce appears to have arisen as many as thirty times during evolution. The chemical systems used by luminescent organisms are similar but not exactly the same. Most organisms use a luciferin/luciferase system. The luciferin molecules are oxidized through catalysis by an oxidase enzyme (luciferase). The oxidized form of luciferin is in an excited electronic state that relaxes to the ground state through light emission.

Animals may produce light in one of three ways. The bioluminescence may be intracellular: Chemical reactions within specialized cells result in the emission of visible light. These specialized cells are often found within photophores. These light-producing organs may be arranged in symmetrical rows along the animal's body, in a single unit overhanging the mouth, or in patches under the eyes, and are connected to the nervous system. Alternatively, the bioluminescence may be extracellular: The animals secrete chemicals that react in their surroundings to produce light. The third option involves a symbiotic relationship between an animal and bioluminescent bacteria. Several species of fish and squid harbor bioluminescent bacteria in specialized light organs. The symbiotic relationship is specific—each type of fish or squid associates with a certain type of bacteria. The bacteria-filled organ is continuously luminous. The animal regulates the emission of light either with melanophores scattered over the surface of the organ or with a black membrane that may be mechanically drawn over the organ.

Although bioluminescence is widespread in animals, its occurrence is sporadic. Most of the bioluminescent animal species are invertebrates. Among the vertebrates, only fish exhibit bioluminescence; there are no known luminous amphibians, reptiles, birds, or mammals. Although bioluminescence is found in terrestrial and freshwater environments, the majority of luminous organisms are marine. Scientists estimate that 96 percent of all creatures in the deep sea possess some form of light generation.

Image Not Available

Functions of Bioluminescence

There appear to be three main uses of bioluminescence: finding or attracting prey, defense against predators, and communication. Although visible light penetrates into the ocean to one thousand meters at most, most fish living below one thousand meters possess eyes or other photoreceptors. Many deep-sea fishes have dangling luminous light organs to attract prey. Terrestrial flies have also exploited bioluminescence for predation. The glow of glowworms (fly larvae) living in caves serves to attract insect prey, which get snared in the glowworms' sticky mucous threads. Fungus gnats (carnivorous flies) attract small arthropods through light emission and capture the prey in webs of mucous and silk.

Bioluminescence can serve as a decoy or camouflage. For example, jellyfish such as comb jellies produce bright flashes to startle a predator, while siphonophores can release thousands of glowing particles into the water as a mimic of small plankton to confuse the predator. Other jellyfish produce a glowing slime that can stick to a potential predator and make it vulnerable to its predators. Many squid and some fishes possess photophores that project light downward, regardless of the orientation of the squid's body. The emitted light matches that of ambient light when viewed from below, rendering the squid invisible to both predators and prey.

The best known example of bioluminescence used as communication is in fireflies, the common name for any of a large family of luminescent beetles. Luminescent glands are located on the undersides of the rear abdominal segments. There is an exchange of flashes between males and females. Females respond to the flashes of flying males, with the result that the male eventually approaches the female for the purpose of mating. To avoid confusion between members of different types of fireflies, the signals of each species are coded in a unique temporal sequence of flashing, the timing of which is controlled by the abundant nerves in the insect's light-making organ. Females of one genus of fireflies (*Photuris*) take advantage of this by mimicking the response of females of another genus (*Photinus*) to lure *Photinus* males that the *Photuris* females then kill and eat.

Some marine animals also utilize bioluminescence for communication. For example, lantern fishes and hatchetfishes (the most abundant vertebrates on earth) possess distinct arrangements of light organs on their bodies that can serve as species- and sex-recognition patterns; female fire worms release luminescent chemicals into the water during mating, beginning one hour after sundown on the three nights following the full moon; and deep-sea dragonfish emit red light that is undetectable except by other dragonfish.

—Lisa M. Sardinia

See also: Communication; Deep-sea animals; Displays; Fish; Insects; Marine animals; Marine biology; Mating; Octopuses and squid; Physiology; Predation.

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BIRDS

Type of animal science: Classification
Fields of study: Anatomy, evolutionary science, ornithology, physiology, systematics (taxonomy), zoology

There are about 8,600 hundred living species of birds, in about twenty-eight taxonomical orders. All birds have feathers, a feature unique to them; most birds also have other evolutionary adaptations that enable them to fly.

Principal Terms

Archaeopteryx: the earliest known bird, known only from the fossil record; it lived during the Jurassic period

Aves: the class within the phylum Chordata to which all birds, and only birds, belong

crop: a specialized part of a bird's digestive system that holds and softens food

endotherm: an animal that, by its own metabolism, maintains a constant body temperature (is "warm-blooded"); birds and mammals are endotherms

gizzard: a part of a bird's stomach that uses ingested pebbles to grind up food

ornithology: the branch of biology that deals with the study of birds

thecodonts: extinct reptiles that lived during the Permian period; they were the ancestors of both dinosaurs and birds

Within the animal kingdom is a class of animals that has 8,600 living species, with each species having a feature found in no other class of animals: feathers. These animals, the birds, also have horny beaks, two hind limbs that allow them to walk, swim, or perch, and two forelimbs called wings, which often help them to fly or swim. Birds have anatomical systems that are quite similar to those of mammals, and both of these classes of animals are warm-blooded, or endothermic. Along with other vertebrates, birds have skeletal, muscular, circulatory, digestive, respiratory, urinary, reproductive, and nervous systems. They have an outer covering of skin and a variety of sense organs. Each system, however, has unique adaptations designed to enable birds to fly.

Avian Physiology

Feathers, found on all birds, are a lightweight body covering that insulates and protects the birds. The large, vaned feathers on the wings and tails provide most birds with the aerodynamic lift and maneuverability needed for flight. The shape, color, and size of some feathers is also important for camouflage, recognition, or behavioral displays. The skeletal systems of birds have many bones that are homologous to reptilian or mammalian bones, yet unique modifications give birds the strength, flexibility, and lightness to fly. Most birds have bones that are pneumatized, or filled with air. The supporting bones, however, are highly mineralized and very strong. Some bones that are found in reptiles and mammals are missing in birds; other bones are fused. There are also more cervical vertebrae in birds' necks, and they are unusually flexible, allowing great movement of the head and neck.

The circulatory systems of birds are very similar to those of mammals, and they have a four-chambered heart. The oxygen-carrying erythrocytes of birds are larger than those of mammals and, unlike those of mammals, have a nucleus. Heartbeat rates are a function of activity, environmental temperature, and size. A hummingbird's heart often beats more than one thousand times per minute.

The beak of a bird may serve a number of functions that include probing for, catching, crushing, tearing, and swallowing food. The toothless beak does not grind or chew food but passes it to the pharynx, next to the esophagus, and then to a storage chamber, the crop. Food eventually is passed to a glandular stomach, where digestion begins, and then to a muscular gizzard that, with the aid of a horny lining and grit or sand, grinds and digests it further. The gizzard leads to the intestine, where digestion is aided by secretions from the liver and pancreas. The feces empty into a cloacal chamber. The cloacal chamber is also the terminus of the urinary and reproductive systems. The cloaca is the only posterior opening in birds; since all sex organs are internal, including the penis and testes, the sex of a bird cannot usually be determined by examining this area.

The visual and auditory sense organs of birds are usually acutely developed. Senses of smell, taste, and touch, on the other hand, are often poorly developed. Pigeons can discriminate motions that are up to three times faster than any humans can distinguish; some hummingbirds can see ultraviolet light, which is invisible to humans. Eagles, hawks, and vultures can detect objects at remarkable distances; they have a retinal cell density that is twice that of humans. Oilbirds and some owls can locate prey in total darkness.

These anatomical systems, and the varied external sizes, shapes, and colors, as well as behaviors that include courtship patterns, migration, and vocalization, evolved during millions of years of avian evolution. Birds are thought to have evolved from reptiles, probably thecodonts, more than 150 million years ago. Several fossils of the earliest known bird, *Archaeopteryx*, have been dated at 150 million years old. The fossils clearly show feathers and wings on a crow-sized bird body that has teeth and some reptilian skeletal features.

Types of Birds

More than nine hundred species of birds can be found only in the fossil record. Two extinct bird groups were especially common about ninety million years ago—the large, toothed, diving bird *hesperornis* and the gull-like *ichthyornis*. Two groups of huge flightless birds have become extinct within historical times: the giant moas of New Zealand (about 3 meters tall), and the elephant birds of Madagascar (about 2.7 meters tall).

Birds belong to the taxonomical class Aves. This class is divided further, first into orders—groups of birds that have broadly similar characteristics. Orders are divided into families, families into genera, and genera (sing. genus) into species.

Flightless and Perching Birds

There are several surviving orders of large, flightless, running birds. These include Struthioniformes, with a single living species that is the largest living bird: the 2.5-meter-tall ostrich of Africa. Somewhat similar in appearance, but with differences great enough for them to be placed in a different order, are the two species of rheas, belonging to the order Rheiformes. Some of these South American birds stand 1.5 meters tall. Australia has two superficially similar groups of birds in the order Casuariiformes: the three species of tropical forest-dwelling cassowaries, which are sometimes more than 1.5 meters tall, and the single species of the slightly taller emu, which roams the open plains.

Not far away, in New Zealand, are the kiwis. Their order, Apterygiformes, contains three species of the smallest of the primitive flightless birds. Some stand about thirty centimeters tall; they have no visible wings (only vestigial flaps), have feathers that look somewhat like hair, and may lay an egg that is one-quarter their body weight—proportionally the largest egg of any of the living birds.

The largest order of entirely flightless birds, with fifteen living species, is Sphenisciformes, the penguins. This order includes the emperor penguin of Antarctica, at 1.2 meters tall, and, along the equator, the most northern penguins, the Galápagos penguin, at a little less than 60 centimeters tall.

With rare exceptions, all other birds are capable of flight. The forty species of tinamou, however, of the order Tinamiformes, are weak fliers. They are

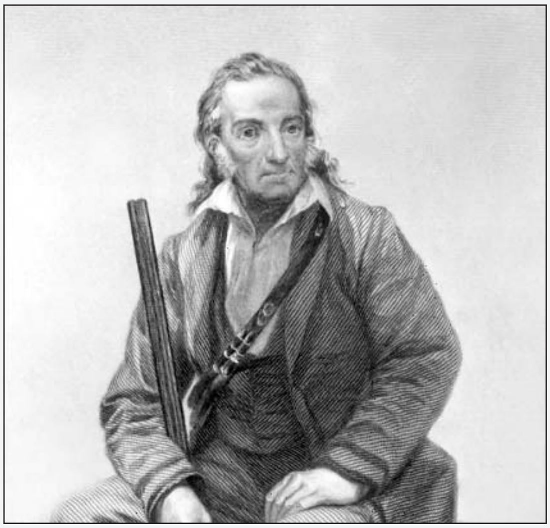
John James Audubon

Born: April 26, 1785; Les Cayes, Saint-Domingue (now Haiti)
Died: January 27, 1851; New York, New York
Field of study: Ornithology
Contribution: Audubon became famous for his beautiful, highly detailed paintings of North American birds and later through his naturalistic renderings of New World native animals.

Born the illegitimate offspring of a French merchant and planter and a Creole woman, Audubon was subsequently adopted by his father in 1794, after the elder Audubon took his young son to France. While growing up in the French countryside, Audubon developed a talent for drawing birds. At the age of eighteen, he was sent by his father to the United States to manage family business interests, thus avoiding conscription into the Napoleonic army. Audubon's commercial ventures did not prosper, and by 1820 he declared bankruptcy. Thereafter, Audubon supported himself through portrait painting and by teaching art, dancing, fencing, and French. He worked briefly as a taxidermist at the Western Museum Society of Cincinnati.

From the day he landed in the United States, Audubon found North American birds fascinating. He began drawing them during his wide-ranging travels whenever he could take time away from his business. Audubon explored the east coast from Labrador to Louisiana, visited the Mississippi Valley, and eventually ventured as far west as the Rocky Mountains. After 1820, Audubon decided to publish a portfolio depicting, in realistic color, the birds of his adopted land. A trip to Philadelphia in 1824 to investigate possible support for his projected publication proved a great disappointment; most of the city's naturalists and engravers refused to help. Audubon then realized he needed European backing to carry out his ambitious project of producing a series of full-color volumes, which he hoped to finance on a subscription basis.

Audubon found a warm welcome and indispensable subscribers in Edinburgh, Scotland, in 1826, and in London the following year. The London engraver Robert Havell, Jr., proved an effective collaborator during the eleven years (1827-1838) it took to produce the four-volume Elephant Folio edition of *The Birds of America*, with its 435 hand-colored plates displaying 1,065 life-size birds. The first volume received wide praise; thereafter, Audubon gained sufficient subscribers in Britain, France, and the United States to pay for the rest of the series. A young Scots naturalist, William MacGillivray, helped write the accompanying text, *Ornithological Biography* (5 vols., 1831-1839), describing the habits of the illustrated birds, and an index volume, *A Synopsis of the Birds of America* (1839).



John James Audubon was renowned for his detailed paintings of American birds. (Library of Congress)

Although his name is now associated with wildlife preservation, Audubon was an enthusiastic hunter. His usual practice was to shoot birds and either draw the fresh-killed specimen or stuff it for later use in the studio. Critics of Audubon have noted that some of his birds are posed in unlikely or fanciful positions, and the later plates in his series are crowded with dissimilar species as he strove to save costs and conclude the work. At their best, his bird portraits are both scientifically accurate depictions as well as carefully designed works of art. They won Audubon a reputation as the leading painter of American birds, gaining him wide popularity and his works enduring fame as valuable collector's items.

—*Milton Berman*

thought to be most like the ancestor of all living birds. Tinamous superficially look like quail, and they are found only in Central and South America.

The largest order of birds, with 5,200 species—60 percent of all living bird species—is Passeriformes. These birds are collectively called perching birds because of their grasping, unwebbed toes—three in front and one behind—all at the same level. Most Passeriformes have anatomical features that allow them to sing very well, and they are commonly referred to as songbirds. This diverse order includes finches, cardinals, grosbeaks, buntings, sparrows, orioles, blackbirds, tanagers, vireos, waxwings, thrushes, kinglets, mimids, warblers, wrens, shrikes, nuthatches, creepers, titmice, chickadees, swallows, crows, jays, larks, flycatchers, and starlings. Lesser-known Passeriformes include broadbills, ovenbirds, woodcreepers, antbirds, tapacolos, manakins, pittas, birds of paradise, bowerbirds, bubuls, babblers, honey eaters, white-eyes, sunbirds, honeycreepers, waxbills, cotingas, wagtails, and flower-peckers.

Aquatic Birds and Fowl

Two bird orders are most often associated with the open oceans or the marine coastlines of continents or islands. Procellariiformes, with ninety living species, contains albatrosses, shearwaters, and petrels. They all have webbed feet, long, narrow wings, and nostrils consisting of raised tubes. The fifty-two species of the order Pelecaniformes are the only birds with all four toes connected by webs; most also have an expandable throat patch. This order includes pelicans, tropic birds, boobies, gannets, cormorants, frigate birds, and anhingas.

Many types of birds generally inhabit areas that border bodies of water. The bays, estuaries, salt marshes, swamps, freshwater lakes, and rivers of the world teem with a multitude of birds. The largest of these orders, with 313 species, is Charadriiformes. This order contains three fairly common groups of birds. The shorebirds, often seen probing their long bills into sand or mud for food, include sandpipers, lapwings, plovers, avocets, stilts, phalaropes, oystercatchers, and jacanas. The gull-like group includes the web-footed gulls, terns, jaegers, skuas, and skimmers. Several of the forty-three species of gulls can be very cosmopolitan and are one of the most familiar sights at seaports and coastal resorts. The third group is the web-footed alcids—auks, murres, and puffins. They are northern oceanic birds that come ashore (mostly to rocky shores and cliffs) only to breed.

The eighteen species of grebes make up the order Policipediformes. These weak fliers are excellent divers and use their fleshy, lobed feet to dive for invertebrates or fish. The shallower waters of marshes and the edges of rivers and lakes are likely to have long-legged waders that belong to the order Ciconiiformes. These 110 species of herons, egrets, storks, ibises, bitterns, and spoonbills are usually fairly large birds with long necks and bills. They probe for mollusks, crustaceans, and fish, and sometimes for reptiles, amphibians, mammals, or birds.

The rails, gallinules, crakes, coots, and cranes are the aquatic groups of the 187 species in the order Gruiformes. Standing 1.5 meters tall, some of the cranes are among the tallest of the flying birds. The heaviest of all flying birds, the kori bustard, is also in this order. It weighs about twenty kilograms (approximately fifty pounds). The bustards, button quails, and several smaller families are terrestrial Gruiformes more often found in open plains or brushland.

The two smallest aquatic orders are Gaviiformes, the loons, and Phoenicopteriformes, the flamingos. The loons are excellent divers and breed only in or along cool northern waters. Flamingos, on the other hand, are found primarily in shallow, warmer, tropical, and temperate waters. With long legs and necks, these tall waders filter small aquatic organisms through their heavy, curved bill.

Anseriformes is an order of 151 species of semiaquatic birds that are hunted by people throughout the world. Several species have been successfully domesticated. This order includes a small family of stoutly built South American birds, the screamers, which resemble pheasant with wing spurs. The larger family of waterfowl includes ducks, swans, and geese, which are found worldwide except for Antarctica. They all have webbed feet and swim well; some are also excellent divers. Another order which has been hunted and domesticated for centuries is Columbiformes. The gentle doves of this order have long been symbols of peace and, along with pigeons and sandgrouse, give the three hundred species of this order worldwide distribution, except for polar regions. The pet bird trade has been especially interested in several of the 317 species of Psittaciformes. The birds of this order are primarily tropical or subtropical and include parrots, cockatoos, lories, parakeets, and macaws.

The bird order that has been the most exploited, however, both by hunting and domestication for food and eggs, is Galliformes, the fowl-like birds. The 253 species of this order include pheasant, grouse, quail, chickens, turkeys, guinea fowls, ptarmigans, megapodes, partridges, curassows, guans, chachalacas, and the hoatzin.

Predator Birds and Other Orders

Man is not the only efficient predator of birds: Many of the 271 species of the order Falconiformes are skilled at grasping a duck off a pond, a pigeon from the air, or a sparrow from a bird feeder. The order Falconiformes includes hawks, eagles, falcons, kites, kestrels, caracaras, vultures, condors, buzzards, and the osprey and secretary bird. All have strong, sharp claws and bills and are powerful fliers.

Another order of powerful predators of vertebrates is Strigiformes, the owls. The 131 species of owls are largely nocturnal, have large eyes with binocular vision, hear exceptionally well, and fly silently with unusually soft feathers. They do not tear mammals apart as the Falconiformes do, but usually swallow their prey whole and later regurgitate a pellet of hair and bones.

Some 1,200 more species are included within another 7 orders of birds. The order Cuculiformes, containing 143 species, includes the cuckoos, anis, roadrunners, and coucals. Most taxonomists also place the brightly colored touracos of Africa in this order. Most of the ninety-three species of the order Caprimulgiformes are either nocturnal or primarily active at twilight. This order includes night-hawks, nightjars, whippoorwills, frogmouths, potoos, and the oilbird.

Two small orders of medium-sized birds with long tails are Coliiformes (mousebirds) and Trogoniformes (trogons). While the six species of mousebirds are found only in Africa, the thirty-five species of trogons are distributed throughout tropical Africa, America, and Asia. Although the 191 species of the order Coraciiformes range from small to large in size, most are brightly colored and have a conspicuous bill. The kingfishers, todies, motmots, bee-eaters, rollers, hoopoes, and hornbills make up this order.

The order Apodiformes contains two superficially different groups of birds, the swifts and the hummingbirds. The 69 species of swifts are found in most areas of the world; the 319 species of hummingbirds live only in temperate and tropical America. Another large but more diverse order is Piciformes. These 374 species include woodpeckers, piculets, jacamars, puffbirds, barbets, honey guides, and toucans. Some woodpeckers are cosmopolitan and regularly frequent bird feeders.

Tracking and Studying Birds in the Field

Ornithologists, the scientists who study birds, have been assisted by millions of people throughout the world in their studies of bird populations and their movements. One of the largest bird projects is the Christmas bird count, sponsored by the National Audubon Society. This North American bird study has been done yearly since 1900 and involves more than forty thousand people each year. Field observers are given one day each winter to count all the birds they can find in a specified area. The information compiled about numbers of birds and species distributions is published in *American Birds*.

More than a million birds in North America are captured each year, fitted with a small aluminum band that has a unique number, and released unharmed. Some are recaptured later, sometimes years later, and perhaps hundreds or thousands of miles from the place they were banded. This technique gives information about the sizes of bird populations, mortality rates, longevity, migration routes and times, sex ratios, and age distributions. Some banders study avian parasites and sequences of feather molting. Hunters and the general public also contribute valuable information when they report dead banded birds.

Sophisticated electronic equipment has been used in many avian studies. Radio transmitters have been attached to some of the larger birds, and their individual movements have been recorded. Radar has been used to monitor both the movements of individual birds and the progress of flocks. Bird songs have been recorded and converted into graphic sonograms, which can show song differences between individuals of the same species.

Many museums have large collections of preserved or stuffed birds and bird skeletons, nests, and eggs. These may be used for anatomical or biochemical studies of birds. Taxonomists use these collections, along with studies of recently collected and live birds, to recognize species and arrange them into various classification groups.

Paleontologists studying the fossils of extinct birds have classified some nine hundred species of birds that are no longer alive. Fossils have given direct evidence about the relatedness of many bird groups; however, because they usually contain only information about bone structure, they provide limited data about species and must be interpreted carefully.

Studying Birds in the Lab

As well as considering the appearance and anatomical structures of birds, ornithologists now consult many areas of biology to put together the various taxonomic groups. Fieldwork has provided enormous amounts of information about the ecology, behavior, singing, breeding habits, and biogeography (location) of birds. In the nineteenth century, Charles Darwin used the structure, function, and biogeography of the finches on the Galápagos Islands to work out the species of these birds. These studies contributed significantly to the development of his theory of evolution by natural selection.

Birds come in all shapes, colors, sizes, and habits, but with very few exceptions, the one characteristic they all share is the ability to fly. (Corbis)

Fieldwork has also helped resolve many problems that have developed in the classification of birds. In 1910, bird books listed nineteen thousand species of birds. Several thousand new kinds have been discovered since then, yet now only 8,700 species are recognized. Many studies have shown that two groups of birds that look different and were at one time considered different species are in fact able to mate and produce offspring. These two groups are then reclassified as a single species. Each original group is considered a subspecies, race, or variety, depending on how similar they are to each other. In North America, for example, the Baltimore oriole and yellow-shafted flicker are common in eastern areas, and the Bullock's oriole and red-shafted flicker are common in the west. Each type of bird looks different and can easily be recognized, so they were initially classified as four species. As towns developed in mid-America, patterns of vegetation changed, and the orioles and flickers moved with the towns until the eastern and western populations finally met. Field studies in the twentieth century showed that the two flicker types were mating and producing offspring; the two orioles were, as well. The taxonomy was adjusted to reflect this new information, and now the two flickers are considered a single species, the northern flicker. Similarly, the two orioles were combined into one species, the northern oriole.

Avian biochemistry and genetics are also areas of intensive research. Studies of the size, shape, number, and staining patterns of chromosomes have been used to show the genetic relatedness of many bird species. Just as feathers, bones, and chromosomes have been shaped by the long evolutionary history leading up to each living bird, so have molecular structures been modified over time. Bird proteins have been analyzed and compared using a variety of techniques, including spectrophotometry, electrophoresis, antibody-antigen reactions, and amino acid sequencing. Studies of avian deoxyribonucleic acid (DNA) using electrophoresis, DNA hybridization, and recombinant DNA technology have also added new insights into the evolutionary relatedness of bird species. Because DNA controls the structure of all proteins and all physical structures in a bird (or in any animal), many researchers think the comparison of DNA structure provides the best overall view of species relatedness.

Popular Ornithology

There has probably been no other area of scientific inquiry that has attracted the interest of the public as much as has the study of birds. There has undoubtedly been no other area of science where the public has made such significant contributions. From the forty thousand Christmas bird count participants to the two thousand bird banders in North America, millions of interested nonscientists around the world have collected a wealth of information about birds.

Birds are often described as environmental indicators, and their population numbers and health are monitored to get an idea of overall environmental integrity. The decline in the number of migrant warblers in North America, for example, is described by some ornithologists as an indication of environmental changes in their wintering grounds in tropical America, whereas other ornithologists believe that it reflects deterioration of their breeding grounds in North America.

Conservation projects throughout the world have used bird studies as a means of focusing on when it has become necessary to fight for the protection of a particular species, subspecies, or race of birds. Major progress has been accomplished with ospreys, peregrine falcons, bald eagles, brown pelicans, trumpeter swans, whooping cranes, kirtland's warblers, and other birds. Yet each project is time-consuming and costly and must be carefully carried out. The governmental designations "endangered species" and "threatened species" cover only very narrow, clearly defined taxonomic groups.

Birds have fascinated people—scientifically, aesthetically, and emotionally—perhaps more than any other group of animals. The vast data collected and the complex taxonomical classification of birds is something that can be passed on to generations to come. It can be hoped that an environment where these creatures can prosper will be passed on as well.

—*David Thorndill*

See also: *Archaeopteryx*; Beaks and bills; Chickens, turkeys, pheasant, and quail; Courtship; Cranes; Displays; Ducks; Eagles; Feathers; Flamingos; Flight; Geese; Hawks; Hummingbirds; Migration; Nesting; Ostriches and related birds; Owls; Pair-bonding; Parrots; Pelicans; Penguins; Respiration in birds; Sparrows and finches; Storks; Swans; Tool use; Urban and suburban wildlife; Vision; Vultures; Warm-blooded animals; Wings; Woodpeckers.

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BIRTH

Type of animal science: Reproduction
Field of study: Reproduction science

Birth is often defined as the act of being born, via parturition, from a mammal or another vivaparous organism, after pregnancy. More broadly stated, it is the beginning of awareness in an animal.

Principal Terms

GESTATION: the term of pregnancy

HORMONE: a substance produced by one organ of a multicellular organism and carried to another organ by the blood, which helps the second organ to function

LARVA: a newly hatched form of an organism that looks very different from adults of the species and must undergo metamorphosis to the adult form

METAMORPHOSIS: the form changes in a larva that turn it into the adult form

MOTILE: able to move about spontaneously

OVIPAROUS: born from an externally incubated egg

PARTHENOGENESIS: a process whereby a female sex cell develops without fertilization, in an organism that reproduces sexually

UTERUS: the organ in which fertilized eggs develop during gestation

VIVIPAROUS: born alive after internal gestation

ZYGOTE: a fertilized egg

Animals are born in one of two ways. They may be born via parturition after an internal pregnancy (a gestation period). They may also be born from an egg that hatches externally. This includes eggs that are spawned and then fertilized externally by organisms such as fishes; those fertilized internally and laid in huge numbers to hatch on their own, as in snails and millipedes; or those laid in much smaller numbers and incubated by their parents, as in birds.

In all animals, male and female reproductive cells (gametes) unite to form a single cell, known as a zygote. The zygote then undergoes successive cellular divisions, as well as cellular differentiation, to form a new organism. In most higher animals, individuals of a species are male or female, according to the type of reproductive cells they produce. Male reproductive cells—the sperms—are motile cells, with heads containing nuclei and tails that allow them to move. Female reproductive cells—eggs or ova—are round cells many times larger than sperms. They also contain large amounts of cytoplasm located around the nucleus.

Viviparous Birth

In viviparous organisms, a fertilized egg will develop into an incompletely finished miniature or miniatures of an adult of the same species. After fertilization of an egg, the zygote enters the uterus, undergoes both cell division and differentiation, and forms an embryo within the mother. In due time parturition (birth) occurs. Most viviparous organisms are mammals. Early in gestation the implanted dividing egg and the uterine wall become interconnected by a placenta, composed of both maternal and embryonic tissue. The placenta brings oxygen and nutrients to the embryo and carries away wastes. The transfer of nutrients uses the circulatory systems of both the mother and the embryo.

At the time of birth, hormonal changes cause the mother's birth canal to enlarge, the muscles of the uterus to rhythmically contract, and the em-

Birth in Cattle

The birth of a calf, relatively representative of the births of artiodactyls, is simpler than that of primates. The first signal of readiness to calve is the passage of mucus and a bloody discharge. After this, the pregnant cow lays down on the ground. Within an hour or two, she gives birth to her calf or calves. In normal birth, each calf is delivered in either a front or a rear presentation. Most cows deliver their calves front end first (front presentation). Initially, a dark bulge, the amniotic sac (water bag), is seen in the birth canal. This is soon followed by the tips of the calf's hooves, toes down. These hooves are soft so that they do not injure the mother during the birthing process. However, they harden quickly.

A front presentation calf is born in the "diver position," with its front legs stretched out and its head between them. The legs protrude about a foot, and then the head comes out, nose first. The head is soon followed by the shoulders, and then the rest of the calf slides out. Usually, afterbirth (the placenta) comes out as well. However, it may take several hours after calving for this to happen. Within a few hours after birth, the calf is ready to nurse and grow.

bryo is expelled as a newborn. The overall process can be exemplified with the female gorilla. She menstruates monthly and can mate successfully at any time of year. Her gestation period is 9.5 months and yields one or two almost fully formed offspring. Gestation is much shorter in smaller primates and there are variations in the difficulty of parturition, related to the head-first entry of young into the world.

Some primates—including humans—must undergo major dilation of the uterine mouth (cervix) before parturition can begin. This allows the large head of the fetus to pass out of the body safely. In species such as monkeys, in which the head of the fetus is close to the size of the cervical opening, far less dilation is needed. In other placental mammals, the position of fetuses in the uterus and the fashion of birth differ.

Oviparous Birth

Many animals, including snails, insects, birds, lizards, and fish, lay eggs either before they are fertilized or before their young are completely developed. These organisms are termed oviparous. In the case of snails, most species are hermaphrodites. This means that each snail has both male and female sex organs. However, each individual snail usually mates with another snail of the same species, passing sperm to its partner and getting sperm from the partner. Fertilized eggs are then spawned into the water or laid on rocks or aquatic plants. The eggs hatch in two weeks to two months. Hatching is considered to be the time of birth of the young snails. In most cases, offspring hatch as miniature replicas of their parents.

In insects, eggs are laid in a wide variety of places. For example, grasshoppers lay eggs in the ground or on plants. When the offspring are born, they hatch as wingless grasshopper larvae, called nymphs. Over several months the nymphs undergo metamorphosis to adult locusts. In contrast, ants, wasps, and termites lay their eggs in special chambers in their nests (or colonies). Worker termites place eggs laid by a colony's queen into hatching chambers in "nurseries." Termites are born as wormlike larvae when eggs hatch. The larvae undergo metamorphosis into workers, soldiers, or reproductives (kings or queens) as a result of being fed varied amounts of hormones obtained from queens.

Birds lay eggs in nests, that are located in a wide variety of locales depending on species. Adults then incubate the eggs by sitting on them. Offspring are born when they use a specialized egg tooth to break open their egg shells. In the case of lizards, the eggs are laid after they are fertilized. However, they are not cared for by parents. Large lizards such as alligators, crocodiles, and caimans lay eggs covered with hard, calcium-containing shells like those of bird eggs—reptiles and birds are distant relatives—in holes in the ground, where they hatch into offspring that look like adults. Most fish lay fertilized eggs on plants or on the bottom of the sea, lakes, or rivers, and leave their offspring to hatch on their own. These offspring then develop into adults.

Ovoviviparous Birth

Ovoviviparous animals produce eggs in shells like those of the oviparous organisms but the eggs are hatched within the body of the mother, or by expulsion from her body. There are numerous examples of ovoviviparous organisms among animals. They include some oysters, snails, and other gastropods, as well as numerous species of sharks, and the live-bearing tropical fish such as the guppy or swordtail. The eggs of live-bearing guppies hatch internally, just before leaving the mother's body, and the young are born alive. These young fish usually leave the body of the mother head first.

In all cases, the development of the egg or eggs of ovoviviparous species begins with internal fertilization of the female of the species. Then, the zygotes formed pass through many cycles of internal cell division and differentiation. Ultimately, each egg yields a miniature of the adult organism involved. However, there is no placenta formed and the zygote becomes the complete organism in processes that depend on a yolk sac for food and energy. Often, upon birth, the newborn organism has part of its yolk sac left and can survive for one or several days without eating.

—Sanford S. Singer

Types of Shark Birth

Reproduction in sharks is very interesting. Most often it is ovoviviparous, with the eggs fertilized internally, hatching within the female, and being born as live young. Some sharks are oviparous, laying eggs externally. Often these eggs are encased in tough shells with filaments that anchor them to rocks or sea plants, while development occurs.

In still other sharks, the young develop in the uterus in a fashion very similar to that seen in mammals. In those cases, the yolk sac becomes a yolk placenta in the folds of the uterine wall. This yolk placenta brings nutrients to the embryo, as well as carrying wastes away. In such cases gestation lasts between six months and two years. In cases of live birth, the offspring of some sharks are up to three feet long, almost fully developed, and capable swimmers that eat the same prey as do the adults.

See also: Asexual reproduction; Breeding programs; Cleavage, gastrulation, and neurulation; Cloning of extinct or endangered species; Copulation; Determination and differentiation; Development: Evolutionary perspective; Estrus; Fertilization; Gametogenesis; Mating; Parthenogenesis; Pregnancy and prenatal development; Reproduction; Reproductive strategies; Reproductive system of female mammals; Reproductive system of male mammals; Sexual development.

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BONE AND CARTILAGE

Type of animal science: Anatomy
Fields of study: Anatomy, biochemistry, physiology

Bone is a connective tissue, much of which derives from cartilage. It forms vertebrate skeletons, which are body support networks, prevent organ damage, anchor muscles so that they can function, provide calcium to serve the body needs, and contain the sites of blood cell synthesis.

Principal Terms

ARTICULAR: pertaining to bone joints

BONE: the dense, semirigid, calcified connective tissue which is the main component of the skeletons of all adult vertebrates

CALCIFICATION: calcium deposition, mostly as calcium carbonate, into the cartilage and other bone-forming tissue, which facilitates its conversion into bone

CARTILAGE: elastic, fibrous connective tissue which is the main component of fetal vertebrate skeletons, turns mostly to bone, and remains attached to the articular bone surfaces

COLLAGEN: a fibrous protein very plentiful in bone, cartilage, and other connective tissue

CONNECTIVE TISSUE: any fibrous tissue that connects or supports body organs

OSTEOBLAST: a bone cell which makes collagen and causes calcium deposition

PERIOSTEUM: the fibrous membrane which covers all bones except at points of articulation, containing blood vessels and many connections to muscles

Bone is the hard substance that forms the supportive framework of the bodies of all of vertebrate organisms. This framework, the skeleton, is composed of hundreds of separate parts called bones. The bones support the bodies of vertebrates and protect their delicate internal organs, such as the brain, lungs, and liver, from injury. In addition, the muscles are attached to the bones, which act as levers to enable their function in actions as diverse as walking or swallowing. Furthermore, bone provides the calcium needs of the body, serves as the main repository for calcium storage, and contains the sites where the red blood cells are made.

Much of the bone in adult vertebrates derives from cartilage, elastic, fibrous connective tissue which is the main component of fetal vertebrate skeletons. Such bone, for example, that of the long bones, is called cartilage bone. Cartilage is an extracellular matrix made by body cells called chondrocytes. It is surrounded by a membrane, the periosteum, and much of its firmness and elasticity arises from plentiful fibrils of the protein collagen that it contains. These fibrils and their many interconnections provide mechanical stability and very high tensile strength, while allowing nutrients to diffuse into the chondrocytes to keep them alive. The blood vessels which surround the cartilage in the periosteum provide all of the needed nutrients and remove the cellular waste materials produced by life processes.

The cartilage-containing skeletons of newborn vertebrates become cartilage bone by ossification, a process which includes calcification, chondrocyte destruction, and replacement by bone cells, which lay down more bone. This cartilage, called hyaline cartilage, remains at the articular sites of bones. In young vertebrates, cartilage is the site for the con-

The bones of the vertebrate skull are designed to protect the brain; in fact, they do such a good job that skulls last far longer than the tissue they encase. (Digital Stock)

Physical Characteristics of Bone

To best serve their biofunctions, bones must be very hard, strong, and rigid, but remain supple enough to stay unbroken under normal conditions. These characteristics are provided by the collagen fibrils and insoluble calcium phosphate which make up the bones. The bones must also be light enough to allow vertebrates to move easily and remain erect.

Overly heavy bones are prevented by the occurrence of two general types of bone tissue. The first of these is compact bone, the portion most familiar because it makes up the hard exterior of many bones, except at their very ends. The second bone type, cancellous bone, which appears spongy, is found at the ends of long bones and inside them. It serves to lighten the bones, acting in the same fashion as the air-filled sinuses of the skull, which diminish the overall weight of the skull without weakening it. Bones are covered on their outsides by the important fibrous membrane called the periosteum, along with cartilage. Their insides are lined by an endosteum membrane, very similar to the inner layer of the periosteum.

It is also useful to think of bones in terms of woven, lamellar, and osteonic forms. These terms indicate the relative number of cells in a bone matrix region and the arrangement of collagen fibers in the region. Collagen fibers of woven bone crisscross within the bone matrix, and its bone cells are distributed randomly. In lamellar bone the collagen fibrils are more ordered and fewer bone cells are present. Osteonic bone is also well-organized. However, its cells are found in concentric rings, with narrow channels (Haversian canals) inside them. A blood vessel passes through each canal and feeds the concentric cell rings formed around it. The bone layers form from the outside in, within the internal bone cavity. This narrows its

tinued growth and calcification that produces the bone lengthening required for the attainment of adult size and stature. In addition to the cartilage bone, so-called membrane bone occurs exclusively in the top portion of the skull.

Bone is thought to have developed over a half billion years ago, as shown by its presence in the fossils of fishlike carnivores of that time period. In those creatures, it seems to have been formed into interconnected external plates covering their bodies as sheaths that strengthened and protected their bodies. The existence of bone only at the surfaces of these fossils has led many scientists to suppose that the first function of bone was protection, rather than body support. Be that as it may, bone has both functions in modern organisms. It is interesting to note that many of these early organisms lacked bone in their heads. It seems possible that this lack may have led to the development of the separate mechanisms for formation of membrane bone and cartilage bone, different means to the same end.

diameter more and more. A Haversian canal and its rings develop when cancellous bone is converted into compact bone.

Bones are either "long" or "short" bones. Most long bones are located in the arms and legs. They are divided into three parts: a shaft (the diapysis), the long central part of the bone; a flared portion at each bone end (the metaphysis); and a rounded bone end (the epiphysis). The short bones, designed for flexibility, include those in the skull, spine, hands, and feet. The centers of bones—medullary cavities—are most often filled with either red or yellow bone marrow. The yellow marrow is mostly fat. Red marrow is a network of blood vessels, connective tissue, and blood-cell-making tissue. Red blood cells (erythrocytes) are made in this red marrow. Each bone has nerves that stimulate it and blood vessels that supply nutrients and take away wastes.

Bone Composition, Development, and Remodeling

Between 66 and 70 percent of bone is an inorganic mineral composite made of calcium phosphate and calcium carbonate, which is mostly hydroxyapatite. Much of the remainder of bone is the fibrous protein collagen. This mineral and protein together are called the bone matrix. Within the bone matrix are the three types of specialized cells which ensure its formation, remodeling as is needed, and continuity throughout life. The first cell type, the osteoblast, produces the bone matrix and surrounds itself with it, synthesizing collagen and stimulating mineral deposition. The second cell type, the osteocyte, is a branched cell that becomes embedded in bone matrix, is interconnected, and acts in the control of the mineral balance of the body. Finally, the osteoclast cells destroy the bone matrix whenever it is remodeled during skeleton growth or the repair of bone breaks and bone fractures.

The stepwise conversion of cartilage into bone begins when the chondrocytes of hyaline cartilage enlarge and arrange themselves in rows. This is followed by the synthesis of collagen fibers, and mineral deposition around them. Just below the inner surface of the periosteum a vascular membrane—the perichondrium—forms and supplies the osteoblasts needed for bone formation. Simultaneously, osteoclasts excavate layers through the bone layer and set the stage for the formation of additional bone.

Membrane and Cartilage Bone

Membrane bone, such as that which makes up the upper portion of the skull, forms after cells of vertebrate embryo connective tissue gather together in the area where such bone is to form. This aggregation is followed by the development of small blood vessels in the area and the differentiation of the connective tissue cells into osteoblast cells, which make collagen, intracellular material, and cause the deposition of calcium.

In contrast, cartilage bone, in the long bones, for example, forms where cartilage was initially laid down in the vertebrate embryo. This kind of bone, also called the endochondrial bone, results via osteoblast formation from chondrocytes, followed by ossification. The differentiation between membrane bone and cartilage bone, which are indistinguishable after ossification, is made by the careful examination of appropriate tissue structures during the course of embryogenesis.

The conversion of cartilage into endochondrial bone is not complete until adulthood. At the ends of the immature cartilage bones, regions of actively growing cartilage (epiphysial plates) occur. In these regions, continued longitudinal cartilage growth followed by ossification leads to the lengthening of bones required for the development of newborn vertebrates into full-sized adults. At adulthood, the cells of the epiphysial plates stop reproducing. It is believed that imbalances between chondrocyte numbers and bone matrix material levels in articular cartilage probably play major roles in the genesis of arthritis.

All the bones in the bodies of the vertebrates change their sizes and shapes as these organisms pass through their lives. The processes involved are collectively called remodeling. An example of such change is the growth of the long bones in circumference as the limbs grow from puberty to adulthood. In the course of such bone growth the periosteum provides the osteoblasts required to deposit bone matrix around the bone exterior and to calcify it. At the same time the endosteum-derived osteoclasts often dissolve bone in the interior, thus enlarging the marrow cavity.

Remodeling in such cases occurs in response to biosignals including those caused by increases in the need for bone to bear additional weight or to anchor increased muscle mass. Conversely, inactivity and the lack of exercise can result in remodeling which produces diminished bone mass. The complex changes involved in bone remodeling are also controlled by vitamin D and hormones originating in the pituitary gland, the thyroid gland, and the parathyroid glands. Abnormalities in bone growth and remodeling are associated with a great many bone diseases, ranging from rickets to bone cancer.

—*Sanford S. Singer*

See also: Anatomy; Cell types; Endoskeletons; Exoskeletons; Growth; Horns and antlers; Hydrostatic skeletons; Locomotion; Muscles in vertebrates; Nutrient requirements; Vertebrates.

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BRACHIOSAURUS

Types of animal science: Classification, evolution
Fields of study: Anatomy, ecology, evolutionary science, paleontology, systematics (taxonomy)

Brachiosaurus *was a quadrupedal, herbivorous dinosaur whose role as a high browser in Late Jurassic ecosystems was similar to that of the giraffe today.*

Principal Terms

CENTRUM: the spool-shaped body of a vertebra

DIPLODOCIDS: quadrupedal, herbivorous dinosaurs whose hind limbs were longer than their forelimbs

PLEUROCOEL: chamber formed in the centrum of a vertebra to reduce its weight

STEGOSAURS: quadrupedal, herbivorous dinosaurs with vertical bony plates along their backbones

SYSTOLIC PRESSURE: the pressure in blood vessels when the ventricles of the heart contract

Brachiosaurus altithorax was described by Elmer Riggs in 1903 based on a specimen from the Late Jurassic (156 to 145 million years ago) of Colorado. However, the best skeletons are from the Tendaguru Hills of Tanzania, which, at the time the skeletons were collected, was known as German East Africa. Field work started in 1909 and continued until 1912. The dig was not a small affair. Almost $600,000 was raised to fund the dig. In 1909, 170 workers were employed, and their numbers swelled to 500 in 1911 and 1912. About 235 metric tons of fossil material was removed. No permits for further fieldwork have been issued for this area since the 1920's.

Characteristics

Brachiosaurus was a quadrupedal, herbivorous dinosaur whose forelimbs were longer than its hind limbs. This sauropod had a very long neck which it held erect and a short tail which was held out horizontally. Spoon-shaped teeth filled most of the jaws. The nostrils were positioned on a large, dome-shaped crown over the eyes. The enlarged nasal cavity may have been used to produce sounds. If not, the animal must have had a keen sense of smell. *Brachiosaurus* was between 22.5 and 25 meters (85 feet) long, 16 meters (52 feet) high, and weighed between fifty and eighty tons. The animals had a maximum speed of between twenty to thirty kilometers per hour. Unlike *Apatosaurus*, *Brachiosaurus* is a relatively rare sauropod in the western United States, hinting that it may have lived a solitary existence there rather than being part of a herd.

With its long, erect neck and long forelimbs, *Brachiosaurus* could feed on the cones and leaves of the tallest trees (conifers, cycads, and gingkoes). By feeding in the treetops, *Brachiosaurus* did not compete with other sauropods, such as *Apatosaurus*, or stegosaurs, such as *Kentrosaurus*, which fed at lower levels. To supply the brain with blood, *Brachiosaurus*'s heart would have to pump at a systolic pressure of more than 630, have had four chambers, and weighed about 400 kilograms (about 882 pounds). In comparison, humans' normal systolic pressure is somewhere between 120 and 130, with a heart that weighs about 300 grams (10.5 ounces). To help move the blood along, the artery walls may have been heavily muscularized, and a reservoir of oxygenated blood may have existed in the head for emergencies, when the animal was forced to change the level of its head rapidly.

—*Gary E. Dolph*

Image Not Available

See also: *Apatosaurus*; Dinosaurs; Fossils; Herbivores; Paleoecology; Paleontology; Prehistoric animals; Sauropods.

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Brachiosaurus Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Reptilia
Subclass: Dinosauria
Order: Saurischia (lizard-hipped dinosaurs)
Suborder: Sauropoda (long-necked herbivores)
Family: Brachiosauridae (quadrupedal herbivores whose forelimbs were longer than their hind limbs)
Genus and species: Brachiosaurua altithorax, *B. atalaiensis*, *B. brancai*, and *B. nougaredi*
Note: A number of competing classification schemes exist and will probably continue to do so in the future.

Geographical location: Late Jurassic of Algeria (*B. nougaredi*), Colorado and Utah (*B. altithorax*), Portugal (*B. atalaiensis*), and Tanzania (*B. brancai*)

Habitat: In the United States, *Brachiosaurus* is a relatively rare sauropod in the dry habitats represented by the Morrison Formation; in Tanzania, *Brachiosaurus* was far more numerous in the mesic (moist) habitats characteristic of the Tendaguru Formation

Gestational period: Although no eggs have been found, *Brachiosaurus* was undoubtedly an egg layer; the frequency at which eggs were laid, the time it took for the eggs to hatch, and the reproductive life span of the adults are unknown

Life span: Based on mammalian models, sexual maturity would be reached after ten years and the life span was probably in excess of one hundred years

Special anatomy: The neural spines on the cervical vertebrae of the brachiosaurids were not V-shaped as they were in the diplodocids; instead, the neural spines on the vertebrae at the junction of the neck and back were highly elongate for attachment of the muscles that held the neck and head erect, resulting in a pronounced hump over the shoulders; the centrum of each vertebra contained several pleurocoels

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BRAIN

Types of animal science: Anatomy, physiology
Fields of study: Biochemistry, cell biology, histology, neurobiology

The brain is the center of the body's information integration and storage, and the site that determines how an animal will react to changes in its environment. Both the brain and spinal cord receive information from sensory receptors and send messages to the muscles and glands, telling them how to respond to internal or external changes.

Principal Terms

BRAINSTEM: lowest or most posterior portion of the vertebrate brain, including midbrain, pons, and medulla oblongata; controls "housekeeping" functions such as breathing and heartbeat

CELL BODY: the central portion of a neuron, containing the nucleus, where most processing and integration of information occur

CEREBELLUM: second largest part of the brain, manages fine muscle control and muscle memories

CEREBRUM: largest part of most vertebrate brains, with areas that control vocalizations, vision, hearing, smell, and taste, as well as voluntary skeletal muscle movements

CORTEX: thin layer of gray matter that covers surfaces of the cerebrum and cerebellum

GANGLIA: clustered cell bodies of neurons that may form a brain-like center in lower animals

GRAY MATTER: region of the brain or spinal cord that contains cell bodies of neurons, where information processing and storage occur

WHITE MATTER: region of neural tissue that contains axons of neurons that carry electrical nerve impulses from one processing center to another

Animals are multicellular organisms that obtain their nutrients by eating or ingesting other organisms, and many have locomotor abilities. Obtaining food and avoiding being eaten are behaviors enhanced by the ability of an animal to tell what is going on in its surroundings. Using information from sensory receptors and responding to changes in the environment are generally managed by a nervous system of some sort, usually with a center where processing occurs, a brain or brainlike structure. Invertebrate nervous systems are generally very primitive and may contain only a very rudimentary brainlike structure. Some animals, however, are so structurally simple that they have no neural processing center at all.

Invertebrates with and Without Brains

Sponges (phylum Porifera) are invertebrates with no brain or nervous system of any sort, in either the sedentary adults or the free-swimming larvae. Stimuli received at the body surface produce responses (movements) directly, over the entire body, in these and related lower metazoan animals. Other primitive invertebrates such as hydra, jellyfish, corals, and sea anemones (phylum Cnidaria) have one or more nerve nets. For these radially symmetrical animals, food or danger can come from any direction in the water, and the meshlike nervous system can respond directly without a central control region. Some jellyfish also have a nerve ring that helps coordinate their movements, but no brain.

Bilaterally symmetrical invertebrates include the flatworms (phylum Platyhelminthes), roundworms (Nematodes), mollusks (Mollusca), segmented worms (Annelida), and insects and their relatives (Arthropoda). Most of these show cephalization, the presence of an anterior head containing the main processing center of the nervous system, specialized sensory receptors, and the mouth. Echinoderms (Echinodermata) such as starfish are bilaterally symmetrical as larvae, but develop radial symmetry as adults, when they lack a head. Some mollusks are not symmetrical as adults, despite the bilateral symmetry of the larvae.

Among the flatworms, some have only nerve nets like those of cnidarians, while more complex planarians, tapeworms, and flukes generally have one or more pairs of ladderlike longitudinal nerve cords with ganglia at the head. These ganglia are clusters of cell bodies of neurons, the most primitive form of a brainlike structure. Nematodes or roundworms have a nerve ring and anterior ganglia organized around the anterior digestive tract, with nerve cords extending toward the head and tail from this center. Mollusks include clams and oysters (class Bivalva), snails and slugs (Gastropoda), and octopuses and squid (Cephalopoda). These animals have nervous systems that vary from simple and relatively uncephalized nerve rings and nerve cords, to a more centralized system with at least four pairs of ganglia.

Octopuses and squid have the most complex nervous systems of the mollusks and are the most intelligent invertebrates. The relatively large cephalopod brain contains many clustered or fused ganglia that manage sensory information from complex eyes and produce motor instructions for extremely rapid muscular responses. Giant nerve fibers in squid are the largest neurons known in any animal, up to one millimeter in diameter in a single cell, and are able to conduct rapid impulses that allow lightning-fast movements. Extensive studies of these neurons' structure and function have provided scientific insights that are also applicable to human neurons. Gastropods and cephalopods may show extremely complex behaviors, such as homing, territoriality, and learning. An octopus can have as many as thirty functional brain centers, some of which are memory banks used for experiential learning.

Annelids such as earthworms and leeches have paired cerebral ganglia near the mouth, connected by a solid ventral nerve cord to smaller paired ganglia in each body segment. Giant nerve fibers in the nerve cord allow rapid responses to escape from threats using reflex actions and patterned behavior. Earthworms can be taught to travel a maze by simple associative learning, in which repeated stimuli become linked to a specific behavior pattern, but this learning requires many repetitions and disappears within a few days if not reinforced.

Arthropods include spiders, scorpions, ticks, and mites (class Arachnida), lobsters, crabs, and shrimp (Crustacea), and insects (Insecta). The nervous system in arthropods is similar to that of annelids in its segmentation, but it is much more complex, and the anterior ganglia tend to be fused into a true brain. Many arthropods have giant neurons like those of some mollusks and annelids, capable of rapid nerve impulse transmission for efficient muscle control. Insects in particular, especially ants and bees, are capable of complex learning and very intricate social behavior. Habituation allows individuals to learn to ignore repeated stimuli that do not produce harmful effects, and cockroaches and ants can learn to run mazes.

Sea urchins, sand dollars, sea stars (starfish), and sea cucumbers are echinoderms, in which the bilaterally symmetrical larvae develop a secondary radial or biradial symmetry as they mature. The resulting radial nervous system is not greatly centralized, as there is a mouth but essentially no head. The nervous system consists of a nerve ring around the mouth that is connected to radial nerves and a nerve net. Thus, behavior generally involves only localized responses to stimuli, as along one arm of a starfish.

Evolutionary Development of the Vertebrate Brain

The location of most animals' brain or brainlike organ at the anterior or superior end of the body is important, since it places the brain at the leading end of the moving animal or at its highest point. Many sensory receptors are located in the head, and information from the eyes, ears, and nose can be rapidly received and processed if the processing center is in the same region.

In vertebrates, the nervous system is much more advanced than the primitive systems of invertebrates. The vertebrate brain is an anterior enlargement of the dorsal hollow nerve cord that develops above the notochord in all chordates. This swelling of the nerve cord allows development of a large collection of neurons that receive, process, and store information, and determine what the organism's response to that information will be. The central nervous system consists of the brain at the anterior end of the nerve cord and the spinal cord behind it, encased in a skull and vertebral column of bone or cartilage. The rest of the vertebrate nervous system is called the peripheral nervous system, with nerve fibers bundled into nerves. Clusters of the cell bodies of neurons in the central nervous system are called nuclei, while the same kind of clusters in the peripheral nervous system are called ganglia.

The components of the vertebrate embryonic brain are divided into three areas or primary vesicles, known as the forebrain (prosencephalon), midbrain (mesencephalon), and hindbrain (rhombencephalon). As development occurs, the three primary vesicles form five secondary vesicles that continue to develop into the mature brain structures. The forebrain becomes subdivided into the telencephalon, which matures into the cerebrum, and the diencephalon, which contains the thalamus and hypothalamus. The midbrain does not undergo further developmental separation. The hindbrain develops into the metencephalon, which will form the pons and cerebellum, and the myelencephalon, which becomes the medulla oblongata that is connected to the spinal cord. The lower or posterior part of the brain is called the brain stem, consisting of the medulla oblongata, pons, and midbrain, which manages the most primitive functions required for life. Higher brain functions reside in the cerebrum, particularly in the outer cortex of gray matter on its surface. The cerebellum coordinates skeletal muscle or motor activities, while the diencephalon processes and sends on sensory information to the cerebrum and cerebellum, as well as being the center of autonomic or visceral motor control.

The different classes of vertebrates are grouped into subphylum Vertebrata within phylum Chordata, with the main classes including cartilaginous fish (Chondrichthyes), bony fish (Osteichthyes), amphibians (Amphibia), reptiles (Reptilia), birds (Aves), and mammals (Mammalia). The brains of fish and amphibians are relatively primitive as compared to those of other vertebrates, with the main control over body functions handled by the medulla oblongata, the oldest part of the vertebrate brain. Olfactory lobes for processing sensations of smell and perhaps also taste, located in the cerebrum, and optic lobes for vision, in the diencephalon, are large in comparison to other parts of the brain, and responses are generally reflexive.

Animals that lay eggs with shells, called amniotes and including reptiles and birds, are adapted to the rigorous requirements of life on land, and have larger, more complex brains than fish and amphibians. The amniote brain has a larger telencephalon and is able to process and store more information about the land environment, which is much more likely to vary than is a watery environment. In addition to having a larger telencephalon, the brain contains more gray matter that is closer to the brain surface in amniotes than in fish or amphibians.

Mammals and some reptiles have much or all of the surface of the cerebrum covered in gray matter, which forms a structure called the cerebral cortex. The evolutionarily newer portion of this cortex is called the neocortex, while the older part is called the paleocortex. The paleocortex is the control center for drive-related behaviors, such as activities associated with feeding (licking, chewing, swallowing), sexual behavior, and primitive emotions (anger, fear). The limbic system occupies the paleocortex, which is sometimes called the reptilian brain, because it is the highest brain area present in reptiles and governs nearly all their behaviors. The neocortex is a "higher" control area that is well developed even in primitive mammals, but it is most completely expressed and covers the entire cerebral surface in humans. In cetaceans (whales and dolphins) and primates, the neocortex is the center of higher learning, logical thinking, and storage of many memories. The activities of the neocortex can override the more primitive responses of the paleocortex under most conditions, but when the higher brain areas are inactive, as in alcoholic intoxication in humans or when removed surgically in experimental animals, the lower areas reassert themselves and take control, often causing inappropriate behaviors.

Mammalian brains have convolutions on the surface of the cerebrum and cerebellum, with the neural cortex following and covering every "hill" and "valley" of the convolutions. This provides a much greater surface area occupied by gray matter, especially in humans, the species in which the convolutions and cerebral cortex are most extensive. Below the gray matter surface is white matter, myelinated neuron fibers that carry information from one area of gray matter to another. Deep to this white matter are basal nuclei, gray matter centers that help regulate subconscious and involuntary control of body functions.

The gray matter of the cerebrum in birds is nearly all in the deep basal nuclei, which are relatively much larger than they are in mammals, and in an overlying gray area specific to birds called the hyperstriatum. The avian brain lacks a neocortex entirely, with no equivalent of the cerebral cortex present. The area of the basal nuclei called the corpus striatum is apparently the center for complex behavior patterns, while the hyperstriatum manages learning and memory.

Humans have been found to show lateralization of the brain, where one side of the cerebrum (left) controls language production and interpretation, while the other side (right) controls spatial awareness and artistic creativity. This lateralization is not generally seen in other vertebrates, but recently it has been observed in some birds, where memories of song patterns and migratory homing directions are located in gray matter areas on specific sides of the brain.

Because the vertebrate central nervous system develops from a dorsal hollow nerve cord, the anterior end of its hollow, fluid-filled central canal enlarges into four ventricles or spaces. These are the first and second or lateral ventricles of the cerebral hemispheres, the third ventricle within the diencephalon, and the fourth ventricle associated with the pons, medulla oblongata, and cerebellum. The midbrain retains a simple canal called the cerebral or mesencephalic aqueduct that connects the third and fourth ventricle spaces.

The fluid that fills the canal and ventricle spaces is cerebrospinal fluid (CSF), produced by filtration of fluids from the blood at specialized capillary beds called choroid plexuses within the ventricles. Besides filling the hollow spaces of the central nervous system, CSF also washes over the surfaces of the brain and spinal cord in an area below the arachnoid layer, one of the central nervous system's coverings or meninges. It provides protection against traumatic injury, delivers nutrients, removes wastes, and helps regulate neurochemicals for the central nervous system.

The Primate Brain

Primates, the order of animals that includes monkeys, apes, and humans, contains species that show a higher level of brain development than most other mammals. Primate brains, especially in humans, are among the largest in the animal kingdom, compared to the body size of the animal. The primate brain retains in its structure the earlier forms and functions that have developed in lower vertebrates over evolutionary time, such as the brainstem and limbic system, but higher areas give new and more complex possibilities for learning and behavior.

Because humans are upright, bipedal walkers, the human brain is at the top of the spinal cord rather than somewhat in front of it as in other primates. The human brain weighs only about three pounds, or about 2 percent of the weight of a 150 pound individual, but that is still larger relative to body size than the brains of other primates, even chimpanzees. The cerebrum makes up about 87 percent of the volume of the brain, and the cerebellum occupies most of the remaining volume. The diencephalon and brainstem in primates are relatively smaller than in most other mammals, compared to the entire brain size. The cerebral cortex in humans contains only six layers of cell bodies in the gray matter on the surface of the cerebrum. Many axons extending down from these cell bodies into the underlying white matter cross-connect the neurons that receive stimuli, process information, determine responses, and store memories. Specific areas of this cerebral cortex determine the body's voluntary muscle actions, or receive and analyze sensory information from the skin, muscles, and joints. Other cortical areas process incoming information about smell, taste, vision, and hearing, and compare those sensations to previous memories or store them as new memories.

The most "human" aspect of the brain is the prefrontal cortex of the cerebrum, where logical analysis, predictions of the results of specific actions, and social interactions take place, although even in monkeys and apes the front of the brain manages social awareness and behavior. Since the primate brains of apes and monkeys are so similar to those of humans, many studies of brain function have involved experimentation on these animals, humans' closest relatives. Other mammals such as mice, rats, cats, and dogs have also served as subjects of brain studies that can be related not only to their own specific behavior, but also to how the human brain works in its various component parts. Since neurons are very similar to each other, whether they come from sea slugs, squid, or mammals, experimentation using these animals has produced insight into how all brains and nervous systems work.

—Jean S. Helgeson

See also: Anatomy; Communication; Emotions; Ethology; Habituation and sensitization; Imprinting; Instincts; Intelligence; Invertebrates; Language; Learning; Nervous systems of vertebrates; Reflexes; Sense organs; Vertebrates.

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BREEDING PROGRAMS

Types of animal science: Physiology, reproduction
Fields of study: Biochemistry, conservation biology, embryology, ethology, genetics, population biology, wildlife ecology, zoology

Breeding programs are used with domestic animals to improve their use for human needs, and are used with wild animals for conservation purposes.

Principal Terms

ACCLIMATIZATION: a process by which animals are adapted to new environmental conditions

ANIMAL HUSBANDRY: care and welfare of domestic animals

BIOTECHNOLOGY: methods used to manipulate biological processes (such as reproduction)

DOMESTICATION: a process by which animals are adapted biologically and behaviorally to a domestic (human) environment in order to tame and manipulate them for the benefit of humans

STUDBOOK: a record-keeping system that provides information on an animal's lineage

WILDNESS: characteristics that define the biological and behavioral life of a species in the wild

Keeping wild native animals began about 10,000 B.C.E. While the reasons for this remain obscured because of a lack of historical documentation, the physical evidence indicates an effort to keep animals in order to meet the population's needs. It was also more convenient to have animals nearby to avoid the dangers and difficulties of hunting. As time passed, these captive animals were bred in a manner that produced traits favorable to the people keeping these animals. This process of controlled breeding became known as domestication. Originally, this was an informal affair with little control by the caretakers. Eventually, individuals keeping animals recognized the benefits derived from captive breeding and began exercising more control over the process.

Certain native species were more compatible with the human environment and more adaptable to domestication. These species had attributes favorable to this kind of controlled situation, such as the ability to adapt to new environments, social gregariousness, a dominance hierarchy that recognized humans as an alpha species, adaptable reproductive behavior, mild temperaments, and a low tendency toward flight behavior (which allowed humans to approach them). However, these attributes were not recognized initially, so there was no conscious decision to keep only certain species. Several ancient societies maintained many species in captivity. Most species, those without the favorable attributes, remained wild, or at best were only tamed. Very few species were to become domesticated, and all of these were domesticated in the early years of human agricultural development.

Various attempts were made in Europe and the European colonies to domesticate additional species during the early 1800's, but none were successfully domesticated. The primary group of domesticated animals has remained the same throughout history: the dog, cat, goat, sheep, pig, cow, horse, camel, llama, reindeer, and elephant. Those species already domesticated have been bred over many generations to improve characteristics favored by humans, sometimes to the point that the domesticated animal no longer resembles its wild originator.

Breeding Domesticated Animals

To some extent, there were always animal breeding efforts taking place in agricultural animal herds, but for much of history they were not closely managed. This began to change in the seventeenth century, when science evolved into a reliance on observable and reproducible experimentation. That century saw improvements in livestock feeding, housing, and care, and conditions favoring the attainment of an animal's full genetic potential. Better educated and wealthy farmers were beginning to take notes and keep track of their animals, an important precursor to the breeding experiments that developed in the following century.

The eighteenth century was a time of increasing interest in agricultural improvement and experimentation. Originally, this involved breeding animals for improved adaptation to a local environment (that is, the local conditions where the farm was located). Eventually, however, this changed to breeding animals for improvements in the breed itself, without regard to its environment. Specific commercial advantages were sought, such as improved meat or milk production, or improved wool production. Eventually, as this effort at improving a breed's characteristics became widely practiced, it led to an international pedigree system, with studbooks that documented an animal's lineage.

Breed improvement and experimentation was enhanced through an exchange of information coordinated through the formation of farmers' clubs and societies. New techniques and successful experiments were publicized, and visits to breeding farms were reported upon. Journals were published that contained information previously limited to private correspondence. Monies were invested in improved breeding stock, which more widely distributed the improvements of the various breeds.

Originally these breeding efforts were conducted on the estates of wealthy farmers at their own expense. Toward the end of the eighteenth century, the governments of England and France became interested in promoting improved husbandry practices. France established the Comité d'Agriculture in 1775, and England established the Board of Agriculture in 1793. There was also an urgent need in the European colonies to adapt European domestic animals to colonial environments, or to convert colonial species to domestication. Acclimatization societies were formed for this purpose both in Europe and in the European colonies.

These developments increased significantly in the nineteenth century. In addition to practical improvements, theoretical improvements in animal husbandry were offered as the sciences of agricultural chemis-

Until the twentieth century, breeding programs concentrated on improving the quality of domesticated livestock. As the focus has turned to saving endangered species, one challenge is how to preserve the wildness of animals that will be returned to natural habitats. (Corbis)

Breeding for Wildness Rather than Domestication

Breeding domestic animals is done in order to improve characteristics that benefit humans, such as providing food and clothing. Much of animal husbandry throughout history has been devoted to the improved breeding of domestic stock for characteristics that are important to humans. Although the animal's welfare was provided for, there was no need to be concerned about characteristics that would be important to the animal.

However, when the goal is breeding wild animals, there are different breeding priorities. With wild animals, it is necessary to breed for characteristics that will favor the species, its survival, and its wildness. In fact, breeders wish to avoid what they strive for with domestic animals. This is particularly true if a species is extinct in the wild, endangered, or is to be returned to the wild to survive on its own. Even if this is not the case now, the situation may change in the future. Even species that are to remain in captivity within the foreseeable future should remain true to their wild conspecifics.

Maintaining an animal's wildness and related species characteristics through breeding is a relatively new concept. Even though studbooks are maintained for many wild species, there is no consensus on characteristics that define each species or what constitutes wildness. Unintentional domestication, or at the very least taming, may result from maintaining numerous successive generations in captivity, even though it is not intended to domesticate the animal. Thus, the problem is to overcome this domestication effect and maintain the wild characteristics of the species in those animals being cared for. This offers new challenges that have only recently been considered by those involved with wildlife conservation.

try, reproductive biology, and genetics developed. Advances in scientific knowledge aided the animal breeding efforts of farmers, and this information was better distributed once governments and universities developed agricultural departments, extension offices, and experiment stations to benefit the farmers.

Publication of *Die Organische Chemie in ihre Anwendung auf Agrikultur und Physiologie* (1840; *Organic Chemistry in Its Applications to Agriculture and Physiology*, 1840) by Justus von Liebig introduced agricultural chemistry to a wide audience and began what became known as scientific agriculture. Charles Darwin's book on evolution was published in 1859, and Gregor Mendel's work on genetics was published in 1866. Germany began a system of government-operated experiment stations in the 1870's. These combined laboratory experimentation with farm experimentation. In the United States, the U.S. Department of Agriculture was established in 1862, as were the land-grant colleges located in each of the states. Several states developed agricultural experiment stations in the late 1800's, and the federal government established a national system of experiment stations in 1887.

Implementation of federal and state programs developed in earnest during the early decades of the twentieth century. Scientific advances and a growing human population encouraged improvements in animal husbandry. Improvements in breeding techniques, improved knowledge about reproductive biology, improved veterinary care, and better housing for the animals also contributed to better animal husbandry. Eventually genetics and biotechnology began to play a major role in developing specific characteristics in each breed. After midcentury, farms decreased significantly as urban populations grew. Within this shifting demography, breeding programs gained new importance, as fewer farmers grew an ever-increasing number of domestic animals to meet the needs of a growing urban human population.

Breeding Wild Animals

Today's domestic species were once wild, but have been changed to suit human needs through the process known as domestication. Few species have been domesticated, even though attempts have been made to domesticate a wide range of species. The London Zoological Garden, the French Jardin Zoologique d'Acclimatation, and several acclimatization societies attempted to domesticate additional species in the late eighteenth century, but none were successful. The acclimatization facilities of these societies eventually closed or evolved into zoos that maintained, exhibited, and bred wild animals without changing them into tame or domestic animals.

Zoos and aquariums have always been concerned with wildlife conservation, although their effectiveness has been dependent on the era's zoological and animal husbandry knowledge, as well as the society's perceived importance of conservation. As the importance of conservation increased and the sciences related to wildlife conservation improved, zoo and aquarium conservation efforts improved. These conservation efforts included propagation programs that bred endangered species and species extinct in the wild. These propagation programs involve species studbooks, studying small populations of animals, introducing animals back into the wild, and other modern techniques.

Breeding wild animals over many generations, however, runs the risk of domesticating these animals. Of course, no such intentional domestication program has been successful. The greater risk is that the animals will become tame, will be unable to survive in the wild, and will lose their wildness. Because the breeding of wild animals is based on the animal's needs rather than human needs, propagation efforts with wild species are quite different from efforts made with domesticated animals. Nevertheless, the methods are similar.

Both wild animal breeding and domestic animal breeding require detailed studbooks in order to keep track of an animal's lineage, and the pairing of appropriate individuals is closely controlled. Many sciences provide knowledge important to the propagation programs, such as veterinary medicine, nutrition, reproductive biology, genetics, and biotechnology. Frozen tissues, artificial insemination, bioengineering, and recombinant deoxyribonucleic acid (DNA) technology play an increasingly important role in modern breeding programs.

Breeding wild animals is often more difficult than breeding domestic animals, since unusual breeding behavior is part of the reason some species are endangered. Improved knowledge about the species' social behavior and population biology needs are of assistance in the successful breeding of these difficult wild species, as is biotechnology. Frozen zoos have been established to maintain reproductive and other tissues for artificial insemination. Sometimes this artificial insemination involves the use of related surrogate species; for instance, using domestic cattle to give birth to endangered gaur. Back breeding is being attempted in order to revive extinct species; for example, breeding zebra so as to re-create the extinct quagga. As an increasing number of species become endangered and as their natural habitat continues to disappear, it is increasingly important to maintain these species through appropriate breeding programs.

—Vernon N. Kisling, Jr.

See also: Camels; Cats; Cattle, buffalo, and bison; Cloning of extinct or endangered species; Dogs, wolves, and coyotes; Domestication; Elephants; Extinction; Genetics; Goats; Horses and zebras; Mark, release, and recapture methods; Pigs and hogs; Population analysis; Population fluctuations; Population genetics; Population growth; Reindeer; Reproduction; Sheep; Wildlife management; Zoos.

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BUTTERFLIES AND MOTHS

Type of animal science: Classification
Fields of study: Anatomy, entomology, evolutionary science, invertebrate biology, physiology

Approximately 17,000 species of butterflies and 153,000 species of moths have been classified in the general order Lepidoptera (insects with scaly wings). They exhibit an incredible variety of color, pattern, shape, and size, as well as the ability to adapt to almost every climate.

Principal Terms

ANTENNAE: a pair of segmented sensory appendages located above the mouth parts

BATESIAN MIMICRY: an evolutionary trend in which an edible species mimics the form of a distasteful species to avoid predation

FRENULUM: a spinelike device that connects the front and hind wings in moths

INDUSTRIAL MELANISM: the rapid rise in frequency of the melanic form in many moth species downwind of manufacturing sites, associated with the advent of industrial pollution

METAMORPHOSIS: the process through which a larval form becomes a winged adult form

PROBOSCIS: a coiled, springlike sucking tube or "tongue" used to drink nectar

Butterflies and moths are collectively the second largest order of the insect class and are found on nearly every continent. Over 170,000 species have been classified and new species continue to be identified each year. While some are known throughout the world, most lepidopteran species have more limited distributions that reflect the presence of geographic barriers (such as mountains or deserts), food plant distribution, strength of flight, and degree of tolerance to environmental factors (such as temperature). Like other animal species, butterflies and moths exhibit their greatest diversity in the tropics.

Physical Characteristics of Butterflies and Moths

Butterflies and moths exhibit an enormous diversity of physical attributes. The smallest, the Western pygmy blue, is a butterfly with a wingspan of just 1.5 centimeters; the largest, the Atlas moth, has a wingspan that can reach 30 centimeters.

Like all insects, the bodies of butterflies and moths are divided into three regions: head, thorax, and abdomen. In most species, the head has prominent, large, compound eyes and a long pair of antennae used as "feelers" mounted above. Lepidopterans also have well-developed olfactory organs, and some moths are capable of hearing. Below the eyes is a coiled proboscis used to suck nectar. The thorax of the insect has three segments, each of which bears a pair of legs, the last two of which support pairs of wings, referred to as the fore and hind wings, respectively. The wings of butterflies and moths are supported by a series of tubular struts, called veins, that form complex patterns, which are often of great taxonomic significance in distinguishing species. The abdomen is a roughly tubular structure composed of ten segments ending with external genitalia which, because they vary greatly from species to species, are also of great taxonomic significance. The entire body, with the exception of the eyes, is covered with fine hairs, some of which are flattened to form scales. On the wings these scales are arranged like the shingles on a roof, with the exposed surface having minute longitudinal ridges visible under a microscope.

Lepidopterans vary greatly with respect to wing color and pattern. Wing coloration is usually caused by pigments deposited in the scales of the wings, but in some butterflies, such as the purple emperor, the iridescent and metallic colors are due to the construction of the scales themselves. Many butterflies are highly prized for their beautiful and brilliantly colored wings, including the blue morpho, whose brightly colored blue wings are thought to play an important role in mate attraction. In other species a conspicuous pattern may serve as warning coloration. One well-known example is the monarch butterfly, which has a bold pattern of black and orange that warns potential predators that it is distasteful. In this case, the warning is accurate because monarchs feed on milkweed plants that secrete a distasteful substance. It is interesting to note that the viceroy butterfly has evolved a nearly identical wing pattern, apparently to fool potential predators into thinking it is a monarch. The latter is an example of Batesian mimicry, or the evolution of form similar to a distasteful model by an edible species. Coloration, pattern, wing size, and shape in other species may, conversely, aid the lepidopteran by rendering it inconspicuous. For example, the pale form of the peppered moth is actually a complex pattern that effectively camouflages it against lichen-covered tree trunks.

While butterflies and moths are physically quite similar to one another, there are several distinct structural features used by taxonomists to distinguish them. Butterflies have antennae that are clubbed or at least swollen at one end, whereas the antennae of most moth species are featherlike. Butterflies all lack a true frenulum, which is a device that connects and coordinates the movement of the fore and hind wings of moths during flight. In general, butterflies have slender bodies, are brightly colored, and fly during the day, whereas moths are stouter, exhibit more drab colors, and fly at night. There are, however, some brightly colored, slender moth species, such as the coppery dysphania, and some representatives of one of the butterfly families known as "skippers" have stouter bodies, are dull-colored, and may be active at night.

The Life Cycle of Butterflies and Moths

Butterflies and moths share a complex life cycle consisting of four distinct phases: egg, caterpillar

Butterflies and moths play an important role in the pollination of many plants. (Corbis) (larvae), pupa, and adult. After mating, the female lepidopteran lays eggs, sometimes singly and sometimes in clusters, on the food plant of the caterpillar or larvae. After hatching, the larvae usually feed on the plant's leaves, although in some species, such as the skippers, the larvae feed on the stems and roots of the plant. During this time the larvae grow rapidly and shed their old skin or exoskeleton four or five times before they are fully grown. Upon reaching full size, the caterpillar undergoes a dramatic transformation, called metamorphosis, into a quiescent pupa or chrysalis stage, during which the larval organ systems are dissolved and rebuilt into the structures of the adult moth or butterfly. The caterpillar begins this process by spinning a small button of silk from which it hangs head downward. While grasping the shed larval skin between the edges of its abdominal segments, the pupa fastens itself to the button of silk. In some species, such as the swallowtails, the pupa is held upright by means of a silk girdle around its middle; in other species, such as the skippers, the larvae pupate in cocoons. After a period ranging from a few weeks to years, the lepidopteran emerges from the chrysalis and expands its wings by pumping blood into them from the body cavity. When the wings have dried, the lepidopteran is ready for flight.

Several lepidopteran species undergo migration. In some species, such as the monarch butterfly, the adult migrates on a seasonal basis. Experimental releases of monarchs suggest it is unlikely that any of the adult butterflies who start the journey complete the round trip—it is thought that the journey back is completed by their offspring.

Butterfly and Moth Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Arthropoda
Subphylum: Uniramia
Class: Insecta
Subclass: Pterygota
Order: Lepidoptera (butterflies, skippers, and moths)
Suborders: Zeugloptera (mandibulate archaic moths); Aglossata (kauri moths); Heterobathmiina (valdavian archaic moths); Glossata (swallowtails, sulfurs, orangetips, coppers, hairstreaks, blues, brush-footed butterflies, milkweed butterflies, wood nymphs, satyrs, skippers, sphinx moths, giant silkworm moths, geometer moths, tiger moths, noctuid moths, tussock moths, clear-winged moths, clothes moths)

Geographical location: Every continent except Antarctica

Habitat: Mostly fields and forests, but some are found within a few hundred miles of the North Pole far above the tree line on mountains, and in deserts (in the spring or after a rainstorm)

Gestational period: In tropical climates, a lepidopteran may have four generations in a single year; in Arctic regions where the growing season is much shorter, the cycle may take as long as two years, with larvae hibernating during the cold periods

Life span: Most live from four months to one year, but species in Arctic regions may live as long as two years

Special anatomy: Six legs, three on each side of the thorax; two pairs of wings; a proboscis for sucking nectar

Beneficial and Destructive Butterflies and Moths

Butterflies and moths play essential roles in the pollination of many plant species, are important sources of food for other animals, and are highly valued for their aesthetic qualities by collectors. Larvae of the silkworm moth have been used to produce silk in China since 2640 B.C.E. Several lepidoptera, however, are pests of important agricultural crops. The larvae of the cabbage butterfly do millions of dollars of damage to the cabbage crop each year; gypsy moth larvae are notorious for defoliating trees in North America and Eurasia.

—David W. Rudge

See also: Antennae; Camouflage; Flight; Insects; Metamorphosis; Migration; Mimicry; Nocturnal animals; Wings.

Industrial Melanism

The rapid life cycle and genetic variability of many butterfly and moth species makes them particularly useful for the study of evolution. One famous example is the classic investigations of the phenomenon of industrial melanism made by H. B. D. Kettlewell (1907-1979) in the early 1950's. Kettlewell worked with the peppered moth, a common species of moth throughout Britain and continental Europe. The moth was known to have two forms: a pale form that was very common and a dark form that was quite rare. Toward the end of the nineteenth century, this situation began to change. The first large-scale burning of coal, coke, and oil associated with the industrial revolution killed off the lichen cover of the unpolluted countryside downwind of manufacturing sites, visibly darkening the surfaces of trees. Coincident with these changes, naturalists and moth collectors alike began to notice that the previously rare dark form of this species (and others as well) was becoming more common. One way to explain this change can be stated with reference to natural selection. In unpolluted woods, the dark form is easily spotted by birds (the major predators on these moths) when it rests on pale, lichen-covered tree trunks, in contrast to the pale form, which is difficult to see. In polluted environments, the dark form is naturally camouflaged against visual predators when it rests on soot-darkened tree trunks, but the pale form is easily spotted. Kettlewell, using a series of investigations involving both experimental releases and field observations of differential bird predation, is generally credited as demonstrating that this explanation is indeed correct. It is interesting to note that since the advent of clean air legislation in Britain, the frequency of the dark form has declined once more.

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CAMELS

Type of animal science: Classification
Fields of study: Anatomy, conservation biology, developmental biology, ethology, physiology, reproduction science

Camels, the one-humped dromedary and the two-humped Bactrian, are well-adapted to the desert regions of Africa, the Middle East and Central Asia, where they are used for transport, milk, and meat. They can live without water longer than other large mammals.

Principal Terms

FERAL: domesticated animal no longer under the control of humans
HERBIVORE: animal solely dependent on plant material for its nutrition
INTERFERTILE: able to breed and produce fertile offspring
QUADRUPED: animal with four feet
RUMINATE: regurgitate and rechew ingested food

The ancestors of camels evolved in North America fifty million years ago. The oldest relatives were only twelve inches tall and lacked humps. About three million years ago, one branch migrated across a land bridge to Asia, becoming today's camels. Later, others moved to South America to become the lamoids, which include the vicuña, guanaco, llama, and alpaca. The North American camelids became extinct after the last ice age, perhaps due to climate change but more likely from overhunting by humans who were occupying the continent at that time. Dromedary camels were domesticated four thousand years ago in Arabia, while the Bactrians were independently domesticated five hundred years later in Central Asia. While primarily used for transport, they are also valued for milk, meat, hair, leather, and dung, which is dried and used for fuel. Although some wild Bactrian camels may still exist in remote regions such as China's western Xinjiang Province, most camels are domesticated or feral. Worldwide, camels are estimated at twenty million, 75 percent in North Africa (from Morocco to Somalia) and 25 percent in Asia (from Arabia to Mongolia), with twenty thousand in Europe and Australia.

Physical Characteristics of Camels

Camels, among the largest terrestrial animals at more than seven feet tall and ten feet long, are well adapted to arid regions of the world. Their long legs keep their bodies away from the hot surface of the ground. In addition, they have a thin profile when viewed from the front; this permits them to minimize absorbing solar radiation by facing the sun, which they do in the hottest periods of the year. Furthermore, they allow their body temperatures to rise up to 108 degrees Fahrenheit. They conserve water by having very efficient evaporative cooling and by producing very concentrated urine and dry, pelleted feces. They can also endure a substantial loss in body water, up to 40 percent of their body weight, with little harm or loss of appetite; they preserve the water in the blood at the expense of that in their tissues and alimentary tract. Furthermore, when rehydrating, they can consume up to fifty gallons of water without damaging their tissues or red blood cells; the latter can expand 2.4-fold without bursting. Contrary to popular myth, their humps do not provide water storage, consisting instead mostly of fat that can be used as a metabolic fuel. When camels are starved, their humps will regress or become limp.

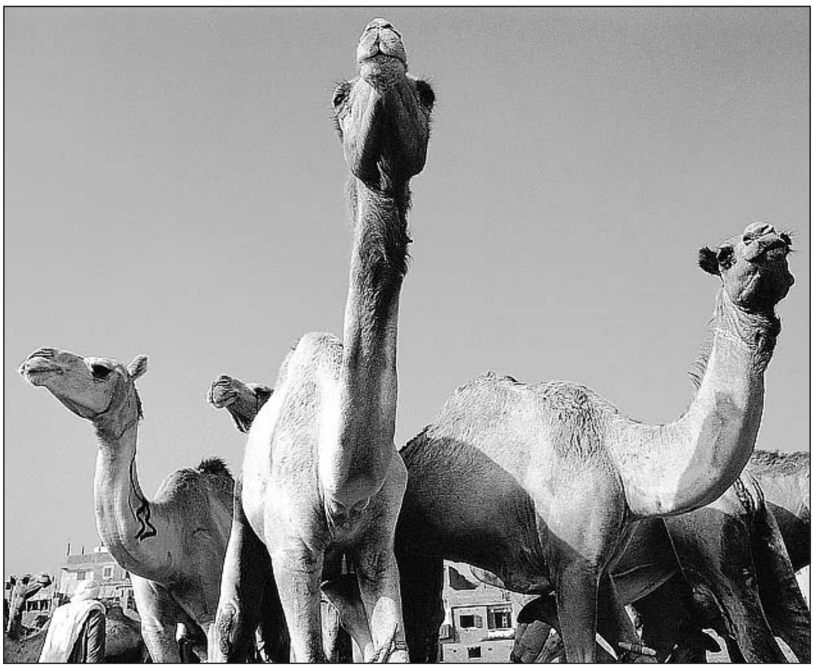
Camels are herbivores and eat a variety of plant material, grass, brush, and trees, subsisting well on browse with low nutritional value. As a result, their food preferences are complementary to those of other domesticated and wild animals. They can obtain much of their water needs from plants. With sufficient food and at moderate temperatures, they have been known to go months without drinking. They ruminate, permitting rapid ingestion of food and subsequent regurgitation and rechewing. Unlike cattle and sheep, they have three rather than four stomach compartments, although the first one, the rumen, is similarly used for microbial fermentation of plant material that would otherwise be indigestible.

Camels can carry loads of three hundred pounds and cover up to one hundred miles a day (although twenty-five to fifty is typical). They are loaded or mounted when they are in a kneeling position. They have a pacing gait, where both feet on each side move together, and their broad, padded feet keep them from sinking in sand. To deal with sandstorms, they have a third eyelid that comes up from below the eye, long eyelashes, and nostrils that they can close. Camels have very good eyesight; their eyes are protected from bright sunshine by a bony protrusion. They also have a keen sense of smell; reputedly, they can smell water a mile away.

Like their South American cousins, camels mate in a crouched position. Their pregnancies last thirteen months, resulting generally in single offspring. Females have relatively small mammary glands between their rear legs. They become sexually mature at three to four years, continue to grow until they are fifteen or older, and can live to be forty years old, although most are killed for meat before then.

Comparison of Dromedary and Bactrian Camels

The most obvious difference between the two types of camels is that dromedaries have one hump and Bactrians have two. During embryonic development, both have two humps, but one regresses before birth in dromedaries, although the vestige of that second hump is sometimes visible in front of the more prominent one. Bactrians are also shorter and hairier; these adaptations permit them to survive at the higher and colder elevations of the deserts of Central Asia. They survive at temperatures below freezing in winter and in the summer above 120 degrees Fahrenheit. They shed their hair in the spring and regrow it in the fall. Bactrians also have tougher foot-pads to deal with a more rocky terrain. Bactrians are slower animals; some dromedaries are bred as racing animals. These two types of camels are fully interfertile and, accordingly, belong to the same species. Dromedaries are much more numerous than Bactrian camels.



The camel's slender side-to-side body shape minimizes the amount of solar radiation it absorbs and helps keep the animal cool. (PhotoDisc)

Future of Camels

Camels are closely linked to the largely nomadic existence of their owners, whose lifestyle is succumbing to the demands of modern nation-states for more sedentary populations and respect for national borders, as well as the increasingly pervasive use of motor vehicles. These factors put the survival of camels at risk. However, they remain the best-adapted large animal in the most arid desert regions of the world and are not currently endangered as domestic or feral animals, although the remaining wild camels in Central Asia are under threat due to the fact that their natural habitat is China's nuclear test range. Camels could have increasing value for adventure vacations in the remote deserts of the world.

—James L. Robinson

See also: Deserts; Domestication; Endangered species; Fauna: Africa; Fauna: Asia; Ruminants; Thermoregulation; Water balance in vertebrates.

Camel Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Artiodactyla
Suborder: Tylopoda
Family: Camelidae
Genus and species: Camelus dromedarius (one-humped camel), *C. bactrianus* (two-humped camel)

Geographical location: Africa and Asia
Habitat: Deserts
Gestational period: Thirteen months
Life span: Up to forty years
Special anatomy: One hump or two humps on the back; several adaptations that permit them to conserve water

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CAMOUFLAGE

Type of animal science: Ecology
Fields of study: Ecology, ethology, evolutionary science

Both predatory and prey species use camouflage to minimize the chance that their presence will be detected. Although camouflage is often thought of as being exclusively a visual phenomenon, it must occur in all sensory modalities for it to work.

Principal Terms

APOSEMATISM: use of bright, noncamouflaged colors as a warning signal to indicate toxicity or dangerousness

COUNTERSHADING: a form of crypsis involving dark coloration on top and light coloration on the underside

CRYPTIC COLORATION: any color pattern that blends into the background

DISRUPTIVE COLORATION: use of stripes, spots, or blotches to break up the body outline and blend into a complex background

PROTECTIVE MIMICRY: use of both color and form to mimic an inanimate feature of the environment

Crypsis is the art of remaining hidden. Camouflage is usually thought of as color matching: a green aphid, for example, is likely to go unnoticed while feeding on a green leaf. Background matching, or cryptic coloration, is, indeed, the most common form of camouflage, but most crypsis involves far more than matching a single color. Very small animals such as aphids can get away with using a single camouflage color because they are much smaller than the plants on which they spend their entire lives: They only need to match one thing. Most animals, however—even most insects—are significantly larger than aphids and are likely to spend time in more than one place. Their camouflage must be more sophisticated if it is to be useful.

If a large organism is to remain undetected, it must be camouflaged with respect to an entire scene. One way to do this is with the use of disruptive coloration, that is, the use of stripes, spots, or patches of color for camouflage. Disruptive coloration can involve large color patches, as on a pinto pony, a tabby cat, or a diamond-backed rattlesnake, or may involve tiny variations of color on each scale, feather, or hair. Many brownish or grayish mammals actually have what is called agouti coloring, with three different colors appearing on each hair.

The irregular borders of multiple color patches on an animal's body help to obscure its outline against an irregular and multicolored background, just like the blotchy greens and browns on military uniforms. An animal that has a mix of browns in its fur, feathers, skin, or scales, for example, will blend into a forest or even an open desert or tundra much better than one that is a single solid color. Even the black-and-white stripes of zebras, which seem so striking, act as a form of disruptive coloration: From far away, and especially to an animal such as a lion, which does not have good color vision, the stripes of zebras help them blend into the tall, wavy grasses of the savannah.

Countershading is another form of crypsis involving differently colored patches. Countershaded animals appear dark when viewed from above and light when viewed from underneath. Animals with countershading include orca whales with their black backs and white bellies, penguins, blue jays, bullfrogs, and weasels. Countershading works and is found as camouflage in

Octopus: The Master Deceiver

Some animals such as chameleons (and anoles, which are mistakenly called chameleons) are famous for changing their color to match the background. Anoles can change from whitish to gray, brown, or green to match the sand, branches, or foliage where they rest. Some fish can go one better, creating complex disruptive color patterns to match different kinds of blotchy sand, rock, or coral backgrounds. The master of deception, however, is the octopus. No vertebrate can match the octopus in terms of the speed with which it changes color, the number of patterns it can create, or the variety of shapes and textures that it can take on.

Octopuses communicate with one another using complex and rapid changes in color, shape, and skin texture. They can also change color, shape, and texture to threaten, to bluff, or to hide from their enemies. Because they can transform themselves so quickly, octopuses are hard to follow and then hard to find again once lost from sight. They can squeeze into tiny crevices or, in a fraction of a second, turn into what looks like a piece of coral or seaweed or rotting wood—in fact, into virtually anything they might encounter in their environment.

Octopuses are also famous for another trick. When all else fails, they squirt a batch of jet-black ink into the surrounding water. By the time the ink has dissipated and the predator can see again, the octopus is long gone.

so many kinds of animals because no matter where one lives—a desert, a forest, a meadow, or an ocean—the sun shines from above. When looking up toward the sun and sky, dark things stand out and light colors blend in; when looking down toward the ground or the ocean floor, light colors stand out and dark colors blend in. Predators that are countershaded can thus approach their prey with equal stealth from either above or below; likewise, prey species that are countershaded will be equally hard to find whether a predator is searching from on high or from underneath. Countershading and other forms of disruptive coloration can occur in the same organism, so that dark spots, blotches or stripes appear on top while paler ones appear below.

Another way of remaining undetected in a complex scene is by using protective mimicry, that is, to mimic an inanimate object in both color and form. Some insects look like thorns on plant stems; others look like leaves or twigs or flowers. Some insects, frogs, and fishes look like rocks, lichens, or corals. Sea lions, sea dragons, and even eels can look like floating kelp or other forms of seaweed.

Some animals may not look much like the objects around them, but will disguise themselves by attaching pieces of plants or sand or other debris to their body. Some caterpillars use silk to tie bits of flowers and leaves to their body; others use saliva as a glue. Some crabs glue broken bits of shell and coral to their own exoskeleton. By using bits of local materials to camouflage itself, an animal can ensure that it matches the background. It can even change its disguise as it moves from one area into another.

Being transparent is another way to match whatever background happens to be present. Many marine invertebrates such as worms, jellyfish, and shrimp, are completely transparent. Complete transparency is less common among land animals, but some land invertebrates have transparent body parts, such as their wings, allowing them to break up the outline of their body and blend into whatever happens to be in the immediate background.

The Behavior and Ecology of Crypsis

Behavior is an important factor in the success or lack of success of any form of crypsis. For example, not even disruptive camouflage can hide something that is moving quickly with respect to its background. Because of this basic fact, predatory species that rely on speed or stamina to outrun, outswim, or outfly their prey generally have little use for camouflage. On the other hand, so-called sit-and-wait predators (such as boa constrictors or praying mantises), must be virtually perfectly camouflaged in order to remain undetected while their prey approach to within grabbing distance. In between are the stealth hunters that sneak up on their prey before making a final high speed attack; such animals must be camouflaged and slow moving when out of attack range, but do not have to be camouflaged or slow when at close range.

As with predators, prey species that rely on rapid escape maneuvers do not often bother with camouflage coloration, while prey species that cannot rely on efficient escape tactics must, instead, rely on not being seen in the first place. Prey species that can move quickly but not as quickly as their predators must detect their predators before their predators detect them, and then they must remain absolutely still until the danger has passed.

Some species use different strategies as they go through different stages in life. In many altricial species (species with dependent young that require extended parental care of the offspring), the eggs and/or young are camouflaged, even though the adults are not; the temporary spots on deer fawns and mountain lion cubs are examples. In other species, nesting or brooding females may be camouflaged while the adult males retain their gaudy plumage or attention-getting behaviors; the changing seasonal patterns of color and behavior of ducks and songbirds provide examples here. Some species may be toxic and gaudy during one stage of life, yet tasty and cryptic during another.

Finally, although camouflage is usually thought of as a visual phenomenon, crypsis is important in every sensory modality. If a prey animal is virtually invisible to its predators, but puts out a sound, a scent, or a vibration that makes it easy to locate, visual crypsis alone would be useless. For successful protection, prey species must be cryptic in whatever sensory modalities their predators use for hunting. Likewise, for successful hunting, predatory species must be cryptic in whatever sensory modalities their prey use to detect danger. For most species of both predator and prey, this

Zebras' stripes not only help them blend into their grassland habitat but also make it difficult for predators to pick out a single individual for attack. (Digital Stock)

Aposematism

Some prey animals use a strategy that is the opposite of crypsis: They attract attention to themselves, but advertise the fact that they might be dangerous to eat. This kind of advertising is called aposematism (or aposematic coloration or aposematic display).

A classic example of aposematism involves the monarch butterfly. The bright orange and black adults, as well as the orange, black, and white striped caterpillars, stand out against almost any background. Yet despite their obviousness, monarchs are generally left alone. As larvae, monarch caterpillars often feed on the toxic milkweed plant. Not only have they evolved an immunity to the milkweed's poison, but they take advantage of the toxin by incorporating it into their own body to act as a poison against potential predators. When birds first taste a monarch, they spit it out in disgust and learn to avoid other monarchs in the future.

Interestingly, viceroy butterflies are also distasteful and have evolved an appearance quite similar to that of the monarch. By adopting the same striking color pattern, each species is avoided after a bird first gets a taste of either one. This phenomenon, when two or more species use the same aposematic coloration, is called Müllerian mimicry. Occasionally, nontoxic prey species take advantage of the existence of an aposematic species by mimicking its warning coloration. Even though they are not toxic, these Batesian mimics are avoided by predators who have previously encountered the toxic species. For this deceit to work well, the models (the toxic species) have to outnumber the mimics (the nontoxic species) so that most predators encounter the distasteful species first.

means being camouflaged or blending into the background in several sensory modalities all at once.

—*Linda Mealey*

See also: Butterflies and moths; Chameleons; Displays; Ecological niches; Ethology; Fur and hair; Horses and zebras; Insects; Mimicry; Offspring care; Plant and animal interactions; Predation.

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CANNIBALISM

Types of animal science: Behavior, evolution
Fields of study: Anthropology, evolutionary science, population biology, reproduction science

Cannibalism is the act or practice of consuming the bodies or parts of the bodies of a species by members of the same species. Although its practice is not universal in the animal world, there are more than 1,300 kinds of cannibal animals in existence in the world today.

Principal Terms

ECOSYSTEM: a community of organisms in relation to each other and their physical environment

ENDOCANNIBALISM: a form of human cannibalism in which members of a related group eat their own dead

EXOCANNIBALISM: a form of human cannibalism in which unrelated humans are eaten

The most persuasive reason why cannibalism takes place within a species is the need to survive. Paramount to survival is the necessity to have a diet sufficient to support development and continued existence. Competition for survival begins at birth and continues throughout the life cycle of the animal. Since most animals produce more young than can survive, it sometimes occurs that the strongest of the young feeds on the weakest. Young mantids (praying mantises), black widow spiderlings, and varieties of young salamanders, for example, often feast on their brothers and sisters as soon as they are born. In some varieties of sharks, only one or two shark pups are born from the large number of eggs that the mother shark carried during gestation; the surviving shark pups consume their brothers and sisters before birth.

Another reason for cannibalism, also related to the need to survive, is the necessity to eliminate competitors within an ecosystem. Some young tiger salamanders, when living in extremely crowded conditions, develop special structures in their mouths that enable them to eat other salamanders that are their competitors. Adult male Kodiak bears often kill and eat young cubs, especially male cubs, as a means of both supplementing their diet and eliminating future competitors. Male lions and male feral cats are also known to kill and eat the cubs of another male, thus enabling them to mate with the mother of those cubs and ensure that their own offspring will survive. Male chimpanzees are also known to engage in the practice of killing and eating infants of females that they have not impregnated.

Sometimes cannibalism is related either to the lack of enough food or to a diet deficiency. Two popular household pets, guppies and gerbils, eat their young if there is not enough food available. Female gerbils also cannibalize their own or another female's litter as a means of gaining more protein in their diet. Furthermore, livestock may be forced into cannibalism by the practice of feeding them by-products of slaughtered animals to increase their protein intake; this practice is believed to have spread bovine spongiform encephalopathy, or "mad cow disease," among cattle.

One form of cannibalism still perplexes scientists. During the mating and reproduction process, some female members of the animal kingdom kill and later consume their suitors. Black widow spiders are perhaps best known for this practice, but not all black widows eat their mates after killing them. Scientists have discovered that if the female black widow spider is not hungry, she will not consume her dead mate. The female praying mantis, however, will always devour her mate after she has killed him.

Some animals appear especially capable of consuming members of their species if there is nothing else readily available. *Tyrannosaurus rex*, the famous prehistoric predator, was apparently in that category. Scientists have discovered that the North American *T. rex* may have devoured members of its own group in order to gain a fast and easy meal. South American horned frogs apparently feed on anything, including fellow horned frogs, that moves near them.

Human Cannibalism

While factors that explain cannibalism among animals can also be applied to humans, there are several other possibilities to examine in the case of humans. Prehistoric humans engaged in cannibalism as a means of survival, and modern human cannibalism because of a natural disaster or an accident has also been recorded. There are stories of shipwrecked sailors resorting to cannibalism of their dead and even murder and cannibalism in order to survive. Perhaps two of the most famous instances of modern cannibalism forced by starvation was the 1846-1847 experience of the Donner Party in California, and the 1972 incident involving the Andes mountain crash of a plane carrying a Uruguayan soccer team. In both instances, the survivors resorted to cannibalism (but not murder) in order to withstand the peril they faced.

However, the human animal is unique in that cannibalism is also practiced as a social and religious custom not involving subsistence and survival in the normal sense. One type of human cannibalism involves a genuine reverence by relatives for their dead. Called endocannibalism, this practice is based upon the belief that eating the flesh of departed relatives shows great respect and veneration of the dead. This type was practiced among the natives of islands of the southern Pacific Ocean until it was declared illegal following World War II.

Exocannibalism has ritualistic and religious overtones as well. Native warriors of the South Pacific, popularly referred to as headhunters, ate parts of their vanquished opponents as a means of controlling them and gaining their strength. Sixteenth century South American natives mixed the eating of captured slaves with religion, making the cannibalistic ritual into a festival. Indeed, it was actions similar to these, observed by the Spanish, that gave us the word "cannibal"— Columbus incorrectly transcribed the name of the human-eating Caribs of Cuba as *Canibalis*.

—Robert L. Patterson

See also: Carnivores; Competition; Digestion; Infanticide; Ingestion; Mammalian social systems; Offspring care; Reproduction; Reproductive strategies; Territoriality and aggression.

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CARNIVORES

Types of animal science: Anatomy, behavior, ecology, evolution
Fields of study: Anatomy, conservation biology, ecology, ethology, paleontology, wildlife ecology, zoology

Carnivores (literally, "flesh eaters") are one of the most successful orders of mammals. Most species are endangered by human persecution and habitat destruction.

Principal Terms

BODY MASS: the average weight of females of a species, expressed in kilograms
DIURNAL: active mainly during the daytime
GREGARIOUS: forming groups temporarily or permanently
NOCTURNAL: active mainly during the night
OMNIVORE: an animal that eats both plant material and animal material

Carnivores are a modern order of mammal that includes ten families: bears, cats, civets, dogs, hyenas, mongooses, pandas, red pandas, raccoons, and weasels. They first appear in the fossil record of the Eocene period, forty to fifty million years ago, and probably evolved from nocturnal, small, semiarboreal predators called miacids. Carnivores are recognizable by their teeth: enlarged canines, specialized for stabbing and holding prey, and carnassials, specialized for shearing flesh and skin. All carnivores eat other animals, which they capture in a variety of ways. Most are terrestrial, although the otters are aquatic. Carnivores are found on all continents except Antarctica. They are recent arrivals to Australia, apparently having reached this island continent along with humans ten to forty thousand years ago.

Bears, Cats, and Civets

Bears (family Ursidae) are widely distributed in Eurasia and North America, but only a few forms live in tropical areas of Asia and South America (the sloth and the sun and spectacled bears). At one time, a large predatory bear of the genus *Agriotherium* lived in Africa, but currently no wild ursids exist on this continent or in Australia. Today, the largest living ursid is the polar bear, with a body mass of 320 kilograms. Many Ursidae share with some of the Mustilidae a unique reproductive physiology, called delayed implantation, in which the fertilized egg may take many months to implant in the uterus and continue its development. This may be an adaptation to hibernation and wintertime shortages of food in temperate regions. Bears in cold climates spend much of the winter hibernating in a protected den. During this time, their heart rate and metabolism slow to conserve energy. Most bears are omnivorous, but the polar bear is a specialist hunter of seals.

Cats (family Felidae) are distributed throughout the world, from the heights of the Himalayas (the snow leopard) to the Amazon (the jaguar). The cats are among the most carnivorous of their order and the most adaptable. The earliest felids evolved in forested areas, and most retain adaptations for tree-climbing and use of cover as concealment. Millions of years ago, much larger forms of felids existed, including the extinct sabertooths whose long, bladelike upper canines were specialized for delivering killing bites to the necks of large prey, such as mammoths. Cats are a diverse family, ranging from the group-living lion (body mass 135.5 kilograms) to the solitary Geoffroy's cat (body mass 2.2 kilograms). Virtually all cats can hunt day and night, but nocturnal habits predominate. The cheetah is the only living cat that hunts exclusively by day. Often habitats will contain several species of cats, differing in size and specialized for different prey. For example, certain areas of the Amazon may contain jaguars, pumas, ocelots, and one or more forms of smaller cat, such as jaguarundi or margay.

Civets (family Viverridae) are restricted to tropical and subtropical areas in Africa and Asia. Civets retain many ancestral morphological features of the first carnivores. They are small (body mass range 1.2 to 13 kilograms), with adaptations for climbing trees and no specializations for pursuit or ambush of prey. Civets are nocturnal and, with one exception, arboreal. They eat both animals and fruits, although the fossa is almost exclusively predatory and the binturong eats almost only fruit. Viverrids are closely related to the mongooses.

Dogs, Hyenas, and Mongooses

Dogs (family Canidae) are almost as widely distributed as felids, being found from the Arctic and to the South American rainforest. However, canids evolved in open country habitats of North America and few have adapted to life in rain forests. The wolf was once the most widely distributed carnivore in the world. It evolved in east Asia and from there spread throughout Eurasia and the Arctic Circle, including migrating down into North America as far south as Mexico. Canids have reached their highest diversity in North American woodland-plains habitats (wolves, coyotes and foxes) and African savannahs (wild dogs and jackals). The dog family is diverse, but the domestic dog shows as much variation in body form (from tiny dachshunds to Great Danes) as all of the wild dog species put together. The smallest wild dog is the North African fennec (body mass 1.5 kilograms), and the largest is the wolf (body mass 31.1 kilograms). Although some canids, such as the gray fox, can climb trees to a limited extent, the dog family is highly adapted to fast running in open ground. Canids are characterized by complex social systems, often involving cooperative care of the young by older juveniles or nonreproducing adults. Dogs hunt animals by day and night, but many forms supplement their meat diet with fruit.

Hyenas (family Hyaenidae) are found mainly in Africa, with one species, the striped hyena, living in southern and western Asia. However, in the Miocene and Pliocene (two to twenty-two million years ago), the hyenas were numerous, diverse, and widespread through Africa, Eurasia, and

Predatory Behavior

Most carnivores pursue prey to obtain animal food. Four behavioral strategies for prey capture can be identified. The first and simplest is random encounter, in which the carnivore moves about its habitat and captures hidden or immobile prey. This predatory style characterizes most mongooses, civets, bears, and many mustelids. The second strategy involves following tunneling prey into their burrows. Many of the weasel group are specialized for this type of hunting, with their long, slender bodies and ability to lock their jaws on prey. The third strategy is ambush or stalking, in which predators rely on stealth to surprise prey. Any pursuit is typically a short chase that is abandoned if the prey outdistances the attacker. All cats are ambush predators. They have little stamina but can accelerate quickly. Vigilance gives early warning of attack and thus is very important for prey facing ambush predators. Finally, pursuit or coursing predators chase prey until the prey are exhausted or reach refuge. Stamina is more important than acceleration for these predators. Many canids and the spotted hyena are pursuit predators. Canids often survey fleeing prey, searching for individuals that run slowly due to age or infirmity. The coursing predators—wolves, dogs, and hyenas—commonly hunt in groups because through teamwork, the predators can run farther and faster than they could singly. The prey's best defenses are access to refuge or tireless running.

North America. Only four species of hyaenids exist today: the spotted hyena at 55.3 kilograms, the striped hyena at 35 kilograms, the brown hyena at 43.9 kilograms, and the aardwolf at 7.7 kilograms. The rise of the dog family has occurred in parallel with the decline of the hyenas. The unusual aardwolf eats termites and often digs a den in a termite mound. The other hyenas are specialized hunter-scavengers, adapted for bone-crushing with their reinforced teeth, jaws, and crania. Once considered scavengers only, field studies since the 1970's have documented the extensive hunting done by the large hyenas in Africa. All hyenas are solitary except the spotted hyena, which lives in clans. Members of clans usually disperse to hunt but also hunt in small packs, especially for large prey. Spotted hyenas are unique among carnivores because the females are larger than males and the males give the females priority of access to food and space.

Mongooses (family Herpestidae) are found only in Africa and warmer climates in Eurasia. They are closely related to viverrids but tend to be smaller (body mass range 0.5 to 1.5 kilograms), more terrestrial, and more often diurnal than the civets. Mongooses are renowned for their bravery in the face of snakes, but they generally hunt insects or small vertebrates, and may supplement their diet with fruits. Most mongooses are solitary, but Africa contains several forms of gregarious mongooses, such as meerkats, dwarf mongooses, and banded mongooses. These form long-lasting packs of up to thirty animals, using termite mounds or tunnels as dens during the night. It is believed that these mongooses have evolved highly social, gregarious habits because of the severe risk of predation by hawks, eagles, large carnivores, and snakes. The dwarf mongooses and meerkats show the most unusual social system, with one breeding male-female pair and multiple nonreproductive helpers feeding and protecting the young and the rest of the group. This system involves complex communication systems and a division of labor, including the use of sentinels to detect predators.


Carnivores' teeth are adapted for holding on to prey and shearing the meat from the bones. (Adobe)

Pandas, Raccoons, and Weasels

The giant panda is the only member of its family (Ailuropodidae), although it is considered closely related to bears. Its habitat is restricted to the Tibetan plateau. The panda bear is large (body mass 96.8 kilograms) and specialized to eat bamboo, as well as some animal foods.

The red or lesser panda has not yet been clearly related to other carnivores. Many scientists place it alone in its own

Carnivore Conservation and Human-Carnivore Conflict

Some carnivores come into conflict with humans, who destroy habitat, compete for the prey of carnivores, and hunt the carnivores themselves for meat or skins. Humans also kill carnivores to retaliate against real and perceived threats to human life and to livestock. For example, over a seventy-three year period in the twentieth century, Ugandan lions, leopards, and hyenas injured or killed 373 men, women, and children. Over the same period, thousands of lions and leopards were killed in retaliation for livestock attacks or for the trade in skins. Cheetahs and hyenas were driven extinct in Uganda by human eradication campaigns. Generally, large carnivores are subject to the most intense human persecution, but even mustelids may face trapping and lethal retaliation for raiding poultry.

Wolves present the best documented history of human-carnivore conflict. Wolves were once distributed widely throughout Eurasia and North America, until humans began raising domestic livestock. Then wolves would occasionally attack these tame, relatively defenseless prey. In turn, humans became ingenious in trapping, poisoning, and killing wolves. Wholesale decimation of wolves did not begin until the invention of firearms, but then it proceeded rapidly and without mercy. Wolves were virtually eliminated from most of the world. Now, fewer than 500,000 remain across the globe, and only a small fraction of these are legally protected.

More recently, public attitudes have changed, and respect for the wolf as a noble animal, coupled with awareness of the wolf's role in ecosystem function, have allowed the wolf to recover slightly in some countries.

family (Ailuridae), while others may group it with the raccoon family (procyonids). Its size (body mass 5.7 kilograms) and omnivorous diet is consistent with procyonids, but its distribution is not. The red panda is restricted to the Tibetan plateau, and part of its diet consists of bamboo, so it has sometimes been classified with the giant panda.

Raccoons (family Procyonidae) are found only in the Americas. This family is rather uniform in size (body mass 0.9 to 6.7 kilograms) and in diet. Virtually all of them eat a mixture of fruit, insects, and small vertebrates. Along with the familiar, widespread raccoons, there are less well-known forms in tropical regions, including the arboreal kinkajou, distinguished by a prehensile tail that permits it to hang from branch tips in order to reach fruit at the ends. Also among the tropical procyonids is the coati, which forms large groups with complex social organization. In a coati band, adult males live alone for much of the year, while adult females and young form groups of thirty or more individuals.

Weasels (family Mustelidae) are found everywhere except Australia. Scientists recognize four main subfamilies. The otters (body mass 5 to 40 kilograms) are adapted to aquatic life and eat fish and shellfish. The widely distributed badgers (body mass 0.6 to 10.9 kilograms) are adapted to digging and often specialize in eating earthworms. The true skunks of North America (body mass 0.4 to 2 kilograms) are terrestrial omnivores that have specialized anal scent glands used against predators. The weasel group (body mass 0.06 to 2.3 kilograms) includes a host of long, thin forms such as mink, ferrets, and martens. Mustelids are more numerous in temperate regions than in tropical ones, although otters are found around the world. Another tropical mustelid is the tayra, a weasel-like semiarboreal predator that may attack monkeys in the trees.

In summary, the order of carnivores is very diverse in body size, habits, social organization, geographic distribution, and basic ecology. Most members of this order are intelligent, predatory, adaptable, nocturnal, and solitary. However, among the exceptions to these general rules about carnivores are some of those species most familiar to humans: coyotes, lions, and wolves. Humans have long had a mixed view of carnivores. From the Egyptian reverence for cats and more recent romantic views of the noble wolf, positive impressions of carnivores have been countered by hatred for large predators, driven by economic concern over livestock-killing and attacks on humans.

—*Adrian Treves*

See also: Competition; Digestion; Digestive tract; Ecosystems; Food chains and food webs; Herbivores; Ingestion; Metabolic rates; Nutrient requirements; Predation; Teeth, fangs, and tusks; Vertebrates.

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CATS

Type of animal science: Classification
Fields of study: Anatomy, paleontology, physiology, wildlife ecology

The cat family contains some thirty-six extant species, usually grouped into four genera. They are native to every continent except Australia and Antarctica.

Principal Terms

CARNASSIALS: pairs of large, cross-shearing teeth on each side of the jaw

EPIHYAL: a hyoid bone whose presence or absence determines whether a cat generally purrs or roars

HYOID BONES: series of connected bones at the base of the tongue

PAPILLAE: sharp, curved projections on the tongue

VIBRISSAE: stiff hairs, projecting as feelers from the nose and the head

Catlike animals first appeared in fossil records approximately thirty million years ago. They shared typical anatomical features with later cats: long limbs ending in feet with retractable claws and skulls featuring slicing teeth and large, pointed canines. Some genera developed especially long, curved canine teeth, called "sabers." About 10 million years ago, small cats classifiable as members of the genus *Felis* appeared, and by 3.5 million years ago examples of the genus *Panthera* emerged. They did not immediately replace saber-toothed cats, whose fossils exist in deposits containing those of modern cats. The American saber-tooth, *Smilodon fatalis*, was still active toward the end of the last glaciation; some individuals were trapped in California's Rancho La Brea tar pits as late as ten thousand years ago. An estimated four-fifths of all cat species are now extinct, often having disappeared during the same period that their favorite prey species also vanished.

Classification

Living Felidae are usually classified into four genera containing thirty-six species. In 1916, R. I. Pocock, a taxonomist at the London Zoo, established the modern feline classification system using hyoid bones as the fundamental characteristic and the epihyal structure as distinguishing the two major cat genera. He defined the genus *Panthera* as cats whose epihyal bone is replaced by a thin ligament; these animals normally vocalize by roaring rather than purring. Included in this genus are the large cats of Africa and Asia—the lion (*P. leo*), the tiger (*P. tigris*), the leopard (*P. pardus*), the snow leopard (*P. uncia*), and the American jaguar (*P. onca*).

Pocock placed cats whose epihyal develops as a normal bone within the genus *Felis*. They are able to purr continuously and usually do not roar. For the most part these animals are small cats, including the African golden cat (*F. aurata*), the ocelot (*F. pardalis*), and many varieties of the European and African wildcat (*F. sylvestris*). This genus also includes the American cougar (*F. concolor*), which few persons regard as small. The lynx and its bobcat subspecies are sometimes placed in a separate *Lynx* genus, but most authorities classify them as *F. lynx* and *F. Lynx rufus*, respectively. The domestic cat, *F. catus*, is sometimes called *F. sylvestris catus* to emphasize its probable descent from the small African wildcat.

Two large cats do not fit the usual categories and are assigned separate genera. The Asian clouded leopard, a large cat with a rigid epihyal that inhibits roaring, is classified as *Neofelis nebulosa*. The cheetah, the only cat whose claws do not fully retract, appears to be evolutionarily distant from other felines and is named *Acinonyx jubatus*.

Recent deoxyribonucleic acid (DNA) studies suggest evolutionary relationships between cat species and subspecies that challenge standard classification systems. Several new schemes have been proposed, but none has yet achieved widespread acceptance.

Feline Anatomy

Every cat, from the smallest domestic cat to the largest tiger, is physically equipped to become a successful predator—coat color, legs, claws, mouth, teeth, sight, hearing, and touch are all highly adapted for hunting and devouring prey.

Coat colors help cats blend into their environment while stalking prey. Most cats display a pattern of spots, stripes, or rosettes on a yellowish background, providing camouflage within forest or broken terrain. The lion's uniform coat color blends into the grassy plains where it usually hunts. Lion cubs and the young of other species developing uniform coat color as adults are born with patterned coats, indicating that this was the primitive coloration of all cat species.

Cat legs are often long and muscular, permitting short, high-speed bursts when attacking prey. Cat claws are usually retractable, pulling inward when running, but extending outward when catching or holding victims. Although cheetah claws do not fully retract, the cat's powerful muscles permit speeds of over sixty miles an hour in full pursuit. Claws and muscles make cats agile climbers who can scale trees when escaping enemies or hiding in ambush.

Cat teeth are adapted for seizing and cutting meat. Four elongated, pointed canine fangs grasp prey, and small, chisel-like incisors tear meat. The scissoring action of large carnassial teeth quickly slices meat from carcasses. Food tends to be swallowed in relatively unchewed chunks, then broken down in the digestive tract. Sharp-pointed, recurved papillae on the tongue help remove remnants of flesh from bones and are also used for drinking fluid and cleaning fur.

Many cats are nocturnal hunters, possessing sensory organs well adapted to low light. Their large eyes contain an extrasensitive reflective retinal layer, making cat eyes appear to glow in the dark, while pupils vary swiftly from fully open to tiny slits. Hearing is acute, and ears swivel easily to pinpoint sources of sound. Vibrissae, or whiskers, on nose and head permit cats accurately to locate obstacles and open paths, even when moving through darkness. The vibrissae also inform cats of the best position for gripping prey with their mouths.

Feline Behavior

Most cats are solitary hunters leading solitary lives, joining other adults only during mating. Kittens, however, may remain with their mother for up to two years, learning how to hunt before set-

Cat Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Subclass: Eutheria
Order: Carnivora
Family: Felidae (cats)
Genera: Felis (small cats, twenty-eight species); *Panthera* (large cats, seven species); *Acinonyx* (cheetah); *Neofelis* (clouded leopard)

Geographical location: Native to all land areas of the world except Antarctica, Australia, and some oceanic islands

Habitat: Forests and grassy plains

Gestational period: Large cats, 3 to 3.5 months; smaller cats, approximately 2 months

Life span: Potential longevity is probably fifteen years for most species; some individuals have lived over thirty years

Special anatomy: Large eyes with excellent night vision; jaws adapted to seizing and gripping prey, teeth designed for tearing and slicing flesh ting off on their own. Most cats live within habitats providing little stimulus for cooperative action. Tigers stalking prey in the jungle or snow leopards living in open country with highly dispersed prey find individual hunting most efficient. Occasionally, male cheetahs join in hunting coalitions of two to four animals, but such groupings are rare.

Both solitary and social cats, such as lions, are highly territorial—clawing trees, spraying urine, or leaving uncovered feces marking area boundaries; loud roars advertise the presence of claimants. Solitary females tend to establish ranges respected by each other. Males inhabit larger territories, usually overlapping those of two or more females, but face challenges from neighboring or interloping males.

Cats use three hunting strategies: moving slowly through their home range stalking, seizing, and killing prey; setting up ambushes near burrows or climbing trees and patiently waiting to pounce upon unsuspecting victims; and inadvertently stumbling upon prey while engaged in other activities, such as searching for water. Cats prefer to kill their quarry before eating. Small animals are bitten at the nape of the neck with canine teeth, severing spinal cords; biting the throat ruptures air passages. A lion sometimes strangles an antelope, clamping its mouth over the muzzle and suffocating its victim.

Lions live in groups called prides, consisting of up to a dozen individuals who aid each other in hunting. Females and their young compose the pride's core; usually related to each other, they raise their cubs together. Two or three related adult males dominate and defend the pride, becoming the fathers of its cubs. When male cubs mature they are generally driven off, but females

The lynx belongs to the group of cats with an epihyal bone, which allows them to purr. Roaring cats, such as lions, have a ligament in place of the epihyal bone. (Digital Stock)

Domestic Cats

Most authorities consider *Felis sylvestris lybica*, a North African wildcat, the probable ancestor of modern domestic cats. In agricultural communities whose granaries attracted rats and mice, cat remains have been found associated with human artifacts as far back as 5000 B.C.E. Actual domestication is depicted in 1600 B.C.E. Egyptian tomb paintings showing cats sheltered under their owner's chair eating fish or gnawing bones; in one case, the cat is tied to the chair leg by a ribbon. Cat lovers enjoy believing that cats voluntarily joined human settlements, but Egyptians had been taming wild animals for more than a thousand years and probably deliberately adopted and tamed a tractable species of wildcat.

Cats became important symbols of Egyptian gods. Male cats represented the sun god Ra, daily battling the serpent of darkness as a tomcat. Females signified the mother goddess Bastet, symbolizing beauty, fertility, and motherhood. In contrast, during the Middle Ages Christians associated cats with paganism and witchcraft, burning many as agents of the devil.

After Rome conquered Egypt, the cat spread across Europe, eventually arriving in the New World and various oceanic islands. Human protection permitted genetic variation and mutation in coat color that would probably have been detrimental to survival in the wild. During the nineteenth century, people began to develop these variations into purebred strains. By the late twentieth century, cats had become the most popular companion animals in Europe and America. Yet the domestic cat retains the basic anatomy and behavior of its wild ancestors. As Alan Turner noted, "Structurally, it can be seen as simply a scaled-down model of a lion or a leopard."

may become permanent members of the pride. Group hunting by females, with occasional assistance from males on a difficult kill, is an economical procedure in open terrain containing abundant large prey.

Scientists studying feral cats—domestic cats returned to the wild—found two patterns of existence. Feral cats hunting widely dispersed prey tended to be solitary, occupying separate female and male territories. Cats gathered together only at concentrated and stable food sources, such as garbage dumps and barns. In either case, a group of related females and their kittens formed the core unit; adults often aided each other raising the young. Female offspring might remain group members, but strange females were driven off. Some resident males were tolerated but faced challenges from interlopers seeking access to females. Several groups might occupy areas particularly rich in food. In all cases, resemblance to the social structure of lion prides was striking.

Adapted to widely varying environments, the Felidae remains one of the most successful animal families. A single species—the tiger—can be found ranging from the tropics to Siberia. However, the tiger and other feline relatives are increasingly endangered. Hunters seek many cats as trophies; the fur trade also values their striped and spotted skins. Big cats are particularly vulnerable, as expanding human settlements constrict the large ranges needed for successful predation. Whether large cats will survive, or join the four-fifths of Felidae species already extinct, remains for future generations to decide.

—Milton Berman

See also: Cheetahs; Groups; Jaguars; Leopards; Lions; Mammals; Mountain lions; Nocturnal animals; Predation; Tigers.

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CATTLE, BUFFALO, AND BISON

Type of animal science: Classification
Fields of study: Anatomy, conservation biology, ethology, physiology, reproduction science, wildlife ecology

Cattle and buffalo are the major domesticated oxenlike animals in the world, while bison have never been domesticated, became nearly extinct, and have made a comeback in North America.

Principal Terms

DEWLAP: loose fold of skin hanging from the throat of some cattle
HERBIVORE: animal solely dependent on plant material for its nutrition
INTERFERTILE: animals able to breed together and produce fertile offspring
QUADRUPED: animal with four feet
RUMINANT: animal with four stomach compartments that regurgitates and rechews its food
UNGULATE: animal with hoofs

Cattle, buffalo, and bison belong to the Bovidae family of oxenlike animals. Cattle include both the humpless *Bos taurus* (comprising the so-called European breeds) and the humped *Bos indicus* (known as Zebu cattle); both are of the same species in that they are fully interfertile. Buffalo, or Asiatic or water buffalo, include the river buffalo and swamp buffalo. Bison come in three varieties (interfertile and hence of the same species), namely the European wood bison, the American plains bison, and the American wood bison; while the latter two are commonly referred to as buffalo, they are actually more closely related to cattle than to the Asiatic buffalo. Cattle, Asiatic buffalo, and bison constitute three of the five genera in this family, the other two being the African buffalo (*Syncerus caffer*) and the yak (*Poephagus grunniens*), although the latter is sometimes classified in the same genus as cattle (*Bos*).

All are herbivores, dependent solely on plant material for their nutrition. Furthermore, they are ruminants, having the ability to rapidly ingest their food and to subsequently regurgitate and rechew it. The first of their four stomach compartments, the rumen, is used for microbial fermentation of plant material, some of which would not otherwise be digestible. All the animals are four-footed and have split hooves. Both male and female have horns, except for those with a genetic variation leading to polled (hornless) animals. They have a keen sense of smell, and good sight and hearing. They are herd animals and generally produce a single offspring annually; when nutritionally or metabolically stressed, they may calve every other year. They usually give birth in the spring, except for intensively managed cattle, which can do so year-round.

Cattle evolved on the plains and forests of Europe and Asia. *Bos taurus* was first domesticated in the Fertile Crescent 6000 B.C.E. and *Bos indicus* independently in south Asia, probably India, about one thousand years later. They were likely first domesticated for religious purposes, and they are still considered sacred in India. They subsequently were developed for work (such as pulling carts and riding), milk, and meat. Their hides were used for shelter and clothing. In addition, their manure is used for fertilizer and, when dried, for fuel. Currently, they are the most numerous livestock species in the world, numbering 1.3 billion, and are found in most areas of the world, except Antarctica. Depending on the breed and nutrition, mature males weigh between 1,000 and 3,000 pounds (450 to 1,350 kilograms). Worldwide, cattle produce 85 percent of the milk consumed by humans. In developed countries, cattle have been highly selected for milk or meat production, leading to specialized breeds. Holstein-Friesian is the primary dairy cattle breed, while Hereford, Angus, and Brahman are three well-known beef cattle breeds; the latter is a *Bos indicus* breed. Various crossbred and regional varieties exist. The transportation of feed grains permits cattle to be raised in areas that would otherwise not support them.

The Asiatic buffalo evolved in the forests and swamps of south and east Asia. It was also probably domesticated in two locations, the river buffalo on the Indian subcontinent 3000 B.C.E. and the swamp buffalo in east or southeast Asia about one thousand years later. Depending on the breed and nutrition, the mature male buffalo can weigh up to two thousand pounds (nine hundred kilograms). It lacks a hump and a dewlap. Like cattle, it is used for work, meat, milk, clothing, fertilizer, and fuel. While most of the world's 150 million buffalo are still found in Asia, some are around the Mediterranean (Italy and Egypt), in eastern Europe (Romania, Bulgaria, and Russia), Brazil, and Australia. In the developing world, its use as a work animal is paramount, particularly in plowing rice paddies. However, breeds of river buffalo have been selected for milk production and account for fully half of the milk production in India. Mozzarella cheese was originally made from buffalo milk in Italy, and the very best continues to be so made.

The bison evolved in the colder regions of Europe and Central Asia; it came to North America over a land bridge from Asia during the last ice age. It was never domesticated, in large measure because of its unpredictable behavior, including a tendency to stampede. The European wood bison was hunted nearly to extinction and only survives in a few small herds. After the last ice age and the demise of mammoths, the bison was the largest animal in the Western Hemisphere; the mature male weighs around two thousand pounds (nine hundred kilograms). In 1500 C.E., over forty million bison roamed the plains and woods of North America. The Plains Indi-

Cattle Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Artiodactyla
Suborder: Ruminantia
Family: Bovidae (oxenlike animals)
Genus and species: Bos primigenius, also known as *Bos taurus* or *Bos indicus* (cattle); *Bubalus bubalis* (Asiatic or water buffalo), *B. depressiicornis* (lowland anoa), *B. quarlesi* (mountain anoa), *B. mindorensis* (tamarau); *Bison bonasus* (European wood bison), *B. bison* (American bison)
Geographical location: Cattle—originally the plains of Europe and Asia, currently worldwide, except for Antarctica; buffalo—mostly south and east Asia; bison: plains and prairies of North America
Habitat: Cattle—grasslands; buffalo—tropical and subtropical forests, swamps, or grasslands; bison—temperate grasslands
Gestational period: Cattle—nine months; buffalo—ten to eleven months; bison—nine to ten months
Life span: Up to twenty-five years, depending on management
Special anatomy: Cattle—may have a hump over the shoulders and a dewlap (*B. indicus*) or neither (*B. taurus*); buffalo—a thick hide, which makes it resistant to some disease-carrying insects; few sweat glands, necessitating wallowing in water or mud in hot environments; breeds exhibit a wide variety of horns; bison—large head and a hump over the shoulders; two layers of hair, a dense undercoat and a coarser outercoat, hardy and able to withstand cold winters; a Jacobson's organ on the roof of the mouth to enhance its sense of smell

Image Not Available

ans depended on the bison for food, shelter, clothing, and fuel. With the completion of the transcontinental railroad, the American bison was decimated for meat, hide, sport, and sometimes no apparent reason. By the end of the nineteenth century, fewer than one thousand survived. However, conservation efforts by the American Bison Society were successful and today over 200,000 animals are found in hundreds of herds, including twenty-five with more than 500 animals each. The Bronx Zoo was particularly important in preserving seventy-seven animals from five founding herds, from which most American bison today are descended.

Comparison of Cattle and Buffalo

Compared to cattle, the Asiatic buffalo is big-boned, massive, and set on strong legs with large hooves. It can pull heavier loads, but is slower. It is better suited to muddy conditions because of its larger hooves and lower susceptibility to foot rot; accordingly, it is much more useful in working flooded rice paddies. On the other hand, its hooves are softer; if used extensively on hard surfaces, it must have its hooves protected by metal plates, wooden shoes, or straw pads. Perhaps surprisingly in view of its origin in the hot and humid areas of Asia, the buffalo is more susceptible to heat stress because of its limited sweat glands. It is best worked in the early morning or evening and must have access to water or mud to wallow in and dissipate heat. It is not tolerant of cold because it lacks hair and the added insulation it provides. It is relatively slow growing and, hence, is not as efficient as a producer of meat. Under similar environments and management in the Third World, buffalo and cattle produce similar amounts of milk. In the developed world, the milk production of buffalo is much lower, probably because of the greater genetic selection that has been practiced on dairy cattle. Its hide is very thick and tough; this appears to provide some protection from tick-borne diseases. The disposition of swamp buffalo, especially, is very placid, with its care often entrusted to children. However, it does have a strong hunger reflex and requires heavier fencing than cattle generally do.

Comparison of Bison with Cattle and Buffalo

Compared with cattle and the Asiatic buffalo, the bison has never been domesticated. However, it can be farmed, and around 90 percent of the animals are currently in private herds. Compared with cattle and buffalo, it is the most homogeneous in terms of color, with mature animals often a dark brown, although a few white bison do occur. While it will charge to defend itself, its preferred defense is to run; it can maintain a speed of thirty-five miles per hour (fifty-six kilometers per hour) for half an hour. Because of its hardiness, it can survive severe winters, with temperatures down to –50 degrees Fahrenheit (–45 degrees Celsius). It is easily more cold tolerant than the buffalo and even most cattle. It is susceptible to many diseases that affect cattle, specifically brucellosis, which causes abortions in cattle and undulant fever in humans. Controlling the disease in wild animals is more difficult than in cattle. Accordingly, it is important to keep bison and cattle separate unless both are known to be brucellosis-free. Bison require sturdier fencing than do cattle and probably buffalo.

—James L. Robinson

See also: Claws, nails, and hooves; Digestion; Domestication; Fauna: Asia; Fauna: North America; Herds; Horns and antlers; Lactation; Mammals; Ruminants; Ungulates.

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CELL TYPES

Types of animal science: Anatomy, physiology
Fields of study: Anatomy, developmental biology, genetics, histology, invertebrate biology, zoology

Living cells are the basic units that make up the animal body. Cells are variable in size, shape, structural components, and function. Understanding the functions of cells provides insights into various diseases.

Principal Terms

ADENOSINE TRIPHOSPHATE (ATP): a molecule produced in the cell that provides energy for cell processes

AMINO ACID: the subunit that makes up larger molecules called proteins

CYTOPLASM: the living portion of the cell that is contained within the cell membrane

DEOXYRIBONUCLEIC ACID (DNA): the molecular structure within the chromosomes that carries genetic information

DIFFERENTIATION: the process during development in which specialized cells acquire their characteristic structures and functions

GAMETE: the sex cells of an animal; each gamete contains only one chromosome from each available pair of chromosomes found in normal body cells

GENE: the part of the chromosome that includes the DNA and is the carrier of heredity

NUCLEUS (pl. NUCLEI): a central cell structure that controls the activity of the cell because of the genetic material it contains

ORGANELLE: a subcellular structure found within the cytoplasm that has a specialized function

PROTEIN: a substance made up of amino acids; proteins are the chief building blocks of cellular structures

The cells that make up the body of an animal are the most basic units of life. Living cells use nutritional sources for energy to maintain structure as well as to maintain life processes such as growth and reproduction. Life requires structure, and cells have the minimal architectural design that enables them to retain life and to pass life on to future generations of cells. Typically, cells are joined in the animal body to form larger structures called tissues. By definition, a tissue, such as connective or muscle tissue, is an aggregate of similar cells and intercellular materials that are combined to perform a common function. An organ, such as the skin or the biceps, is frequently composed of several types of tissues.

Cell Structure

There are essential structural characteristics of animal cells that enable them to maintain life. Most fundamentally, there must be a border that limits the physical portion of the cell from its environment or surroundings. In animal cells, that border is called the cell membrane. Within the membrane lies the cytoplasm (literally, the plasm of the cell); outside the membrane is the environment from which the cell must extract its nutritional needs and into which the cell must pass the waste products that result from the numerous chemical reactions that are continually occurring inside the cell.

Structurally, the cell membrane consists of a double layer of lipid molecules. These molecules are bipolar: The head end of each molecule has an attraction, or affinity, for water molecules (it is hydrophilic), while the tail end of the molecule tends to repel water molecules (it is hydrophobic). In the formation of the membrane, these molecules are found parallel to one another and arranged in a double row. Their heads face the inside of the cell in the inner row, and their heads face their environment in the outer row. The hydrophobic tails form the interior of the membrane and provide an effective barrier that prevents the free passage of water and water-soluble substances. Interspersed among the lipid molecules, like boats in the waves of a lake, are numerous protein molecules. Some of these proteins, called transmembrane proteins, extend entirely through the lipid bilayer and have ends exposed to both the interior and exterior of the cell.

Others, called integral proteins, are found only on one side of the membrane and extend only part way into the lipid bilayer. Finally, some proteins, called peripheral proteins, are attached to the outside or inside surfaces of the membrane. Transmembrane proteins may function as channels or pores allowing specific ions or molecules to pass through them. Integral proteins may also function as transmembrane carriers in that they can bind to specific products outside the cell—such as a certain amino acid—and then flip-flop across the membrane to the inner side and release the product into the cell's interior. Peripheral proteins on the outer surface of the membrane may serve as identification markers for other cells. The membrane itself functions to maintain the integrity of the cell's cytoplasm by holding essential things inside and preventing the cell from drying out.

The cytoplasm is a general term for the viscous fluid within the cell's membrane. In the cytoplasm are numerous small, specialized structures called cell organelles. An essential structure for living cells is the nucleus, which contains genetic information in the form of DNA. DNA determines a particular cell's structure and function. Other organelles in the cytoplasm are designed for specific processes such as manufacturing energy, building structural proteins, or storing cell products prior to exporting them. Some organelles are enclosed within their own membranes, which are structurally very similar to the membrane forming the cell's outer boundary.

The Nucleus and Its Contents

The nucleus is an essential control center of the cell. It is enclosed within a unique membrane—the nuclear envelope—that has relatively large pores, through which large information-carrying molecules called ribonucleic acid (RNA) pass from the nucleus to the cytoplasm. Resident within the nucleus is a dark material called the chromatin. During cell division, the chromatin material condenses into clearly observable structures called chromosomes. When the cell divides into two, each daughter cell contains equal numbers of chromosomes from the original maternal cell. The chromatin material within the cell's nucleus is made up of two major types of material—DNA and associated proteins.

The DNA is organized into discrete packets of information called genes, which form the backbone of the chromosomes. The genes determine the characteristics of the specific cell or organism. The DNA-associated proteins regulate the gene's expression. At times, the genes may express themselves by replicating their information into chemical messengers called RNA. The RNA may diffuse out through the nuclear pores into the cytoplasm. Within the cytoplasm, RNA may bind to an organelle called the ribosome, which produces new protein molecules. Normally, the nucleus also contains one or more very dark round structures called nucleoli. The nucleoli assist in the production of the cell's ribosomes. A single nucleolus is made up of protein and RNA.

A particular cell may also contain hundreds of mitochondria, also typical organelles. The mitochondria are complex, double-membraned structures, and they are found throughout the cytoplasm of the cell. Mitochondria are the energy producers of the cell. These oval-shaped structures contain numerous enzymes that stimulate energy-producing reactions. The net sum of these reactions results in the formation of high-energy ATP molecules. These molecules diffuse throughout the cell to various other organelles and release their energy, thereby fueling most cell processes.

Lysosomes are cell organelles that are round in shape and are enclosed within a membrane; they contain many different enzymes. The enzymes function to break down, or digest, many substances into simpler substances that the cell can use. The endoplasmic reticulum (ER) consists of membrane-enclosed spaces in the cytoplasm. These complex membrane arrays are extensions of the outer cell membrane. Some of this membrane system is covered with ribosomes that function to produce protein. These parts of the ER are called rER, for rough ER or ribosomal ER. Other ER portions, that lack ribosomes, have a smooth appearance and are called smooth ER (sER). Another cellular organelle, the Golgi apparatus, appears as a bunch of flattened bags. This organelle is usually not far distant from the ER. After the rER produces a protein product, the Golgi apparatus further processes the product and packages it for cellular export.

Cell Size and Function

Animal cells have great variations in size. Among the smallest are some bacteria, which may be about 0.1 micron in diameter. (One micron equals 0.001 millimeter.) The largest known cell is the single-cell ostrich egg, which is about seventy-five millimeters in diameter—more than 750,000 times larger than the smallest bacterium. Somatic cells, the cells that make up the body structures of animals, are typically more intermediate in size. For example, the human red blood cell is about seven microns in diameter, while an intestinal epithelial cell is about thirty microns in diameter. Most animal cells are approximately the same size and typically have diameters between ten and twenty-five microns.

An essential characteristic for cell survival is the ratio of the cell's surface area to the volume of the cell, or its surface-to-volume ratio. Typically, cells with small diameters have large surface-to-volume ratios, while large cells have small surface-to-volume ratios. Many of the substances that are needed for the cell's survival, such as oxygen or nutrients, enter the cell through the surface membrane by simple diffusion. The cells that have high rates of metabolism tend to be very small and have larger surface-to-volume ratios. Alternatively, larger cells either have lower metabolic rates or have specialized shapes such as numerous membrane enfoldings to optimize diffusion of essential materials into their interiors.

In multicellular animals, cells are differentiated. Differentiated cells are those that have a specialized modification in their structure to enable them to perform a specific task. Thus, a striated muscle cell contains numerous myofibrils that shorten as the cell contracts, while a glandular cell may contain numerous secretory granules filled with products for export.

Animal cells can be classified on the basis of the number of chromosomes that they contain. Somatic cells, or body cells of an organism, are called diploid, because they contain the total number of chromosome pairs that is characteristic for that organism. For example, somatic cells in mosquitoes contain four pairs of chromosomes (or eight individual chromosomes). Each chromosome in the pair contains genetic information for the same genes that the other paired chromosome contains. Alternatively, sex cells or gamete cells—sperm and egg cells—contain a haploid number of chromosomes, which consists of a single chromosome from each of the possible pairs. Thus, a human sperm cell contains a total of twenty-three individual chromosomes, whereas a human skin cell contains a total of forty-six individual chromosomes.

Another way to classify animal cells is to consider the primary way that they use proteins. Some animal cells are primarily protein-secreting and manufacture much of their proteins for body use outside the cell that produced the protein. An example of this is the pancreatic acinar cell, which produces numerous digestive enzymes (proteins) and secretes them into the pancreatic duct for transport into the digestive tract, where the enzymes break down complex foods into simpler forms. Other animal cells are primarily protein-retaining cells in which much of the manufactured protein is retained for use by the cell itself. An example of this is the keratinocyte, the prominent cell type found in the skin. This cell produces a large amount of the protein keratin, which remains stored in the cell's cytoplasm. Because of the presence of the keratin, the skin is able to maintain its waterproofing, protective function. Without keratin, the skin would lose body water.

Cell Shapes and Types

Animal cells have a wide variety of shapes. Individual cells that are mobile within an aqueous environment tend to be spherical in shape. The neutrophil, a type of white blood cell, is an example of this. Cells that are mobile within tissues and that migrate from one area to another often have long cytoplasmic extensions. An example of this is the macrophage, which has long, changeable, armlike processes (projections) that enable it to migrate through tissue spaces and ingest bacteria that may be found there. Other migratory cells have a tail called a flagellum. Sperm cells, for example, use their flagella to propel themselves through the female reproductive tract to reach the egg.

Some cells have branching, stationary cytoplasmic processes through which information molecules move. Often, these processes form a complex network with similar cells such as the network of neuron cells in the brain. Body tissues are made of cells that have tight cell-to-cell connections between their membranes. These cells may provide a covering or form the wall of a particular structure. Protective cells, such as skin cells, are often many layers thick.

A typical animal's body is composed of about two hundred recognizable different cell types. Most of these are variations of four main categories: epithelial cells, connective cells, movement cells, and message cells.

Epithelial cells form a continuous layer over surfaces that are external or internal to the body. Skin is an external protective tissue that is made of many such layers of cells. The inner lining of the digestive tract, for the most part, consists of a single layer of epithelial cells that absorb and secrete materials. Connective cells provide the structural support of the animal body. Examples of these cells are fibrocytes, found in the dermal layer of the skin, and osteocytes, found in the matrix of bone.

Cells responsible for body movement are typified by the muscle cells. Muscle cells that are attached to bone and cause limb movement are called striated muscle cells. Muscle cells that are found in the walls of body organs such as the stomach are called smooth muscle cells; contraction of these cells causes the contents of the stomach to be mixed and stirred. Cardiac muscle cells are found in the heart, and they contract to force the movement of blood throughout the circulatory system.

Message or conveyance cells are very diverse. Branching nerve cells have long processes that carry information molecules (for example, from the spinal cord to the finger). Red blood cells carry oxygen from the lungs to the body cells. Gamete (sperm or egg) cells transfer genetic information from one organism to the next generation of organisms.

Studying Cells

Ever since the 1600's, when Antoni van Leeuwenhoek first used a simple magnifying lens system to study the structure of single-celled life forms, microscopes have been an important tool in cytology (the study of cells). Several types of microscopes are commonly used to study cells, whether alive or preserved.

Light (bright-field) microscopes with two sets of magnifying lenses are most commonly used to study animal cells today. These microscopes have magnification powers ranging from about forty to two thousand times. In their natural state, most cells are essentially colorless. In order to make microscopic viewing more effective, cells are often stained so that their structures are more readily visible. A phase-contrast microscope is a modified light microscope that can produce visible images from quite transparent objects. This type of microscope is frequently used to study unstained or living cells. Its magnification range is similar to the light microscope.

A transmission electron microscope (TEM) uses electrons instead of light rays to visualize objects. A TEM passes its electron beam through very thinly sectioned cells. The density of the stained cellular structures absorbs electrons in a differential fashion so that an image corresponding to the cell's architecture can be visualized. The TEM can magnify cellular structures from 1,000 to 250,000 times. Consequently, this type of microscopy is often used to study the small subcellular organelles.

Another popular technique used to study animal cells involves growing them in cultures outside an animal's body. This technique, called in vitro cell culture, involves obtaining a group of living cells from an animal, usually in the form of pieces of tissue. An enzyme solution is commonly used to digest the cell-to-cell connections and to produce a suspension of free individual cells. These cells are then placed in petri dishes along with a liquid medium that contains essential nutrients. Some types of animal cells, especially fibrocytes found in the connective tissues, are easily cultured with this technique. These cell cultures, if properly maintained, will grow and reproduce for generations. Experimenters can use such cell cultures to investigate how living cells function and respond to varied environmental influences.

Since cells are the basic units of life, an understanding of their function is essential in comprehending the way living organisms function. Many diseases are caused by a malfunctioning group of cells. For example, a group of cells normally undergoes an orderly sequence of growth and reproduction. At times, however, some cells become disordered and began to multiply rapidly without stopping. This may be caused by an abnormality that appears in the genetic code or by the presence of a virus that takes over the genetic controls of the cell. This situation is typical of some types of cancer.

As scientists learn more about how cells live and why cells die, they will gain valuable insights into the aging process and may thereby increase the span of life. As differentiation is better understood, scientists may be able to change mature cells or even replace them if they become damaged, destroyed, or simply worn out with age.

—Roman J. Miller

See also: Adaptations and their mechanisms; Asexual reproduction; Biology; Cleavage, gastrulation, and neurolation; Cloning of extinct or endangered species; Determination and differentiation; Embryology; Fertilization; Gametogenesis; Gas exchange; Genetics; Homeosis; Morphogenesis; Multicellularity; Mutations; Osmoregulation; Protozoa; Reproduction.

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CENTIPEDES AND MILLIPEDES

Types of animal science: Anatomy, classification, reproduction
Fields of study: Anatomy, invertebrate biology, zoology

Over twelve thousand species of the arthropods centipedes and millipedes are known. Centipedes are carnivorous, and millipedes are usually vegetarians.

Principal Terms

DIPLOSOMITE: millipede trunk segment, formed by the fusion of two body segments

MANDIBLES: jaws of insects and other arthropods

NOCTURNAL: active at night

PALP: oral sensory organs of arthropods

Centipedes and millipedes are somewhat similar organisms. Together, they make up approximately twelve thousand species of long, flattened, segmented animals, grouped among the Myriapods. A major difference between centipedes and millipedes is diet. Centipedes are carnivores, living on other animals, and millipedes are herbivores, living on dead plant matter. Millipedes have cylindrical bodies, while centipedes are wormlike.

When a centipede or millipede runs, it picks up each leg, one after the other. However, it only moves the legs on one body side at a time. The result is that legs move in rhythmic waves along the body. Millipedes are much slower than centipedes.

Physical Characteristics of Centipedes

Centipedes belong to the class Chilopoda of the phylum Arthropoda, which includes insects, myriapods, crustaceans, and spiders. Centipedes resemble worms. Their heads contain paired, jointed, sensory antennae; brains, connected to ganglia; compound eyes, simple eyes, or no eyes at all. Centipedes also have two pairs of jaws. The first pair are toothed mandibles and the second pair, the underjaws, have palps.

A centipede body is divided into between twelve and one hundred segments, each having two legs, so the name "centipede," which means "hundred-footed," is appropriate. The first pair of legs, in the segment behind the head, holds poison claws that are used to fight or kill prey. These claws are full of a venom made in the head. Each of the paired legs in all segments but the last one are shorter, of similar length, and clawed. Those in the last segment are longer than the others. A thin, tail-like cercus projects from a centipede's rear. Centipedes breathe through air tubes (tracheas) on the sides of their bodies.

The Lives of Centipedes

Centipedes are carnivores that eat worms and insects, which they poison. Nocturnal, they hide under stones, logs, or ground litter during the day. Some species bear live young, but most lay eggs. Small centipedes of temperate climates (such as the United States) are harmless to humans. Larger, tropical centipedes are much more dangerous, as exemplified by the families Scolopendridae, and Geophilidae.

The reproductive cycle of centipedes often begins in spring or fall, when a male places his semen on the ground. In the spring, a female puts the semen inside her body, immediately using it to fertilize her eggs. If the female takes in the semen in the fall, she may carry the semen for months before fertilization occurs. After fertilization, females lays their eggs, which hatch in two to four weeks. Newborns have smaller numbers of segments and legs than adults. They grow by molting. After each molt, new body segments and legs are produced. Mother centipedes tend their young until they can hunt. Centipedes mate at two to three years old and may live for six to ten years.

Centipedes Large and Small

Scutigeridae have compound eyes, long antennae, and fifteen pairs of long legs. Found in Europe and the United States is a two-inch species with a brown, striped body, the common house centipede. Lithobiidae, stone centipedes, are also short-bodied. They and scutigerids are the fastest centipedes. Stone centipedes have simple eyes, the same number of legs as scutigerids, and antennae about 35 percent the length of their bodies. Neither family delivers stings harmful to humans.

Scolopendridae have over twenty pairs of legs, short antennae, and simple eyes or none at all. These slow-moving, tropical centipedes are the largest species, reaching lengths of one foot. The fourth family, Geophilidae, known as soil centipedes, are also slow moving. They have up to 350 legs, short feelers and no eyes. They burrow in the ground. Scolopendrids and geophilids deliver bites harmful to humans.

Millipedes

Millpedes are arthropods of the class Diplopoda and occur worldwide, except for polar regions. They are 0.1 to 12 inches long. The largest American species, the four-inch, red and black *Narceus americanus*, lives in southern forests.

Millipede heads are round and hold a pair of short antennae, two simple eyes (or no eyes), and mandibles. "Millipede" means "thousand-

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footed" but none have over five hundred legs. The legs arise from the characteristic feature of diplopods, 9 to over 110 diplosomites. These double trunk segments form by the fusion of two body segments. Each diplosomite holds two pairs of legs, except for the legless head segments and the next three segments, each with one pair of legs. Every four-legged diplosomite contains two pairs of ganglia and two pairs of heart arteries. Millipedes grow in length and diplosomite number by molting. They live one to seven years and reproduce by laying eggs.

Millipedes are covered with thick, calcified chitin back plates. Their protective strategy, when threatened, is to curl into a ball with their head inside and excrete a smelly, toxic liquid from "stink glands." This liquid kills or repels predators. Millipedes inhabit dark, damp places and eat decaying—or in some cases live—plants. Their actions damage some crops but, more often, enrich the soil.

—*Sanford S. Singer*

See also: Arthropods; Exoskeletons; Insects; Locomotion.

Centipede Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Arthropoda
Subphylum: Uniramia
Class: Chilopoda (Centipedes)
Families: Geophilidae (soil centipedes), Lithobiidae (stone centipedes), Scolopendridae (tropical centipedes), Scutigeridae (house centipedes)

Geographical location: Worldwide, in temperate, warm, or tropical regions

Habitat: Under stones, logs, leaves, other ground litter; in human habitations

Gestational period: Eggs hatch in two to four weeks

Life span: Six to ten years

Special anatomy: Sensory antennae; compound eyes; toothed jaws and underjaws; segments, each with two pairs of legs; poison claws; cercus; air tubes

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CHAMELEONS

Types of animal science: Anatomy, classification, reproduction
Fields of study: Anatomy, zoology

Chameleons, the family Chamaeleontidae, have long, sticky tongues to capture prey. Other unique characteristics include eyes that operate independently of each other, leaflike body shapes, ability to change skin color, zygodactyly, and prehensile tails.

Principal Terms

ARBOREAL: dwelling in trees
CHROMATOPHORE: a color-causing cell
COLD-BLOODED: animals whose body temperatures equal the temperature of their surroundings
PREHENSILE: able to grip things
ZYGODACTYLY: having toes pointing forward and backward in the same foot

Chameleons are a group of over one hundred lizard species living in Madagascar, Africa, Asia, and Europe. They are famous for the ability to change color, first noted in the third century B.C.E. by Aristotle. In most cases, chameleons are brown, green, or yellow. Their skins can change to almost any combination of those colors, as well as to pinks, reds, blues, and purples.

Chameleon species are mostly arboreal. They inhabit southern Spain, Crete, the Saudi Arabian peninsula, Sri Lanka, India, Madagascar, Pakistan, and most of Africa. North American color-changing lizards, particularly anoles, are wrongly called chameleons.

Physical Characteristics of Chameleons

Chameleon maximum body lengths range from one inch to three feet, depending on species. Like other reptiles, chameleons are cold-blooded, with body temperatures the same as those of their surroundings. A chameleon body is flat from side to side; it both looks smashed out of shape and has dorsal and ventral crests, which provides camouflage by making it resemble a leaf.

Chameleon eyes, placed on the sides of their heads, can rotate in a full circle, and rove separately or together. This is thought to be partly because chameleons have short necks that do not turn. It is useful for carnivorous chameleons seeking food (insects, spiders, scorpions, and mammals) and not wishing to be eaten themselves. Using independent eye motion, they may seek to eat an insect seen out of the left eye and use the right eye to check for predators that might eat them.

Arboreal chameleons have feet that grasp branches like hands. This is because their feet are zygodactyl, with toes of each foot facing in opposite directions, and can wrap around twigs and branches. This helps them to navigate safely in trees. For the optimum arboreal equilibrium, chameleons have prehensile tails to grip branches. The tails curl into snail-like spirals when not needed. Ground-dwelling chameleons lack the prehensile tails and zygodactyly.

Some chameleons have on their heads horns which, spearlike, stick out from spaces between upper lips and eyes. They are used in mating and protecting territory. The heads of most chameleons are flat on top and wide on each side, making it seem that they are wearing helmets. Chameleons move slowly and carefully on tree branches. However, their rapidly moving, body-length tongues quickly shoot out of the mouth to catch prey on sticky, mucus-rich ends, and bring it back before escape is possible.

Chameleon color changes are due to skin chromatophorea, which hold pigments and pigment-making components. To change color, chameleons send hormone signals through the blood, changing the identities and thus the colors of chromatophore pigments. Chameleon color changes indicate fear, changes in light intensity and body temperature or other environmental changes, and attempts to blend into surroundings and to attract or deter potential mates.

Life Cycle of Chameleons

Most chameleons are arboreal. Exceptions include pygmy (stump-tailed) chameleons, which are small, ground-living, and lack prehensile tails. Male chameleons are territorial. In many cases, male invaders of a territory are fought actively and the battle ends in the death of one male. In some cases, the combat is ritual, though the male who is faced down leaves.

Males and females are solitary, coming together only to mate. Most color changes indicate breeding intentions, pregnancy, or, on the part of females, disinterest. Regardless of species, chameleons mate year round. Females can lay fertilized eggs several years after mating because they store sperm and can delay their fertilization.

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Females lay batches of ten to sixty eggs, in some cases in burrows, in others in trees. In vivaparous species, the young, developed from eggs carried by mothers, are expelled onto tree branches. After laying eggs or depositing their young, females have no further contact with offspring.

Young chameleons break out of their eggs via egg teeth, designed for this purpose. The egg teeth later fall out, as they have no other use. Chameleons live for five to ten years, if they reach old age.

Three Representative Chameleon Species

Common chameleons (*Chamaeleo chameleon chameleon*) inhabit southern Spain, northern Africa, and the Mediterranean coast of the Middle East. Arboreal, they grow to ten-inch body lengths, with ten-inch tails and ten-inch tongues. They eat only insects, and mate in late summer. Females lay batches of twenty to thirty eggs.

Flap-necked chameleons (*Chamaeleo dilepts dilepts*) are named for skin folds near their necks and ears. They are arboreal and inhabit South Africa. They eat insects, spiders, and scorpions, and grow up to about fourteen inches long. These chameleons change color extensively, starting from a mix of brown and yellow.

Panther chameleons (*Chamaeleo pardalis*) of Madagascar are arboreal, grow to twelve inches long, and eat insects. They are aggressive and territorial, named for their ferocity, and fighting between males is to the death. Females lay thirty to fifty eggs.

Chameleons are not harmful to humans. They are actually ecologically beneficial, eating many insect pests. Chameleons are also thought desirable pets by many people. However, they are difficult to maintain in captivity.

—Sanford S. Singer

See also: Amphibians; Camouflage; Cold-blooded animals; Lizards; Reptiles; Salamanders and newts; Thermoregulation.

Chameleon Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Reptilia
Subclass: Archosauria
Order: Squamata
Suborder: Sauria (lizards)
Family: Chamaeleontidae (chameleons)
Genera: Chamaleo (twenty-four species), *Brookesia* (four subgenera, eight species)

Geographical location: Madagascar, Africa, Asia, and Europe

Habitat: Land-dwellers; mostly arboreal, though some live on the ground

Gestational period: Females lay ten to sixty fertilized eggs, which hatch on their own

Life span: Five to ten years

Special anatomy: Eyes that rotate 360 degrees, zygodactyl feet, prehensile tails, spearlike horns for mating and combat, long sticky tongues

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CHAPARRAL

Types of animal science: Ecology, geography
Fields of study: Ecology, environmental science

Chaparral is the name of a major ecosystem (or biome) found in areas with moist, cool to cold winters and long, dry hot summers (Mediterranean climate).

Principal Terms

ELFIN FOREST: a stunted forest growing at high elevations in warm, moist climates

FIRE ECOLOGY: an ecosystem that depends on periodic fires to clear underbrush; the seeds of many plants in such an ecosystem require fire in order to germinate

Chaparral ecosystems with different names occur in the Mediterranean, South Africa, Chile, Australia, and Mexico. The word "chaparral" is a colloquial adaptation of the original Mexican name, *chaparro*. While the chaparral communities in other parts of the world have the same basic characteristics and very similar adaptations, this article will focus on the chaparral of California and the American Southwest.

Chaparral is an interesting and unique ecosystem. It is an elfin (stunted) forest dependent on a fire ecology, and its adaptations to a harsh and variable climate are remarkable. The chaparral's geology, latitude, altitude, and climate are all related and have played a role in its formation.

In California, the chaparral is located mainly along the central and southern coastal areas, primarily between elevations of 500 and 2,500 feet. It is also found in some areas of the Sierra Nevada foothills, one hundred miles or more inland, and in the lower elevations of some other interior mountains. The geology of most of the areas where this ecosystem occurs is believed to have started with massive upheavals from half a million to ten thousand years ago. The most common substrate was granite. Relentless disintegration resulted in rocky and sandy debris which would allow increasing amounts of plant life to grow. As the organic matter became more abundant, its debris (leaves, twigs, and decaying dead plants) became more and more mixed into the materials of the granite decomposition. This resulted in a rich, sandy loam.

Chaparral Flora

Because of the cool, moist winters and dry, hot summers, plants evolved to survive these marked changes. In most of the chaparral, there are quite extreme diurnal temperature changes, with fluctuations of fifty to sixty degrees or more. Compounding these harsh conditions are frequent strong, dry winds, often reaching forty miles per hour.

The plants that have become the residents of the chaparral are mainly shrubby, small-leaved evergreens with leathery, thick stems. Shrubs predominate, but there are also small trees, and wildflowers are in abundance in many areas. All plants are adapted to conserve water. There is little humus in the soil, which is relatively nutrient-poor. The sandy nature of the soil and the variable periods of dry and sudden rain can cause a quick run-off.

The predominant plants are between three and nine feet in height, with some trees being taller. They hug close to the ground to provide shade. The ratio of the surface area of the leaves and stems to their body mass is reduced, and they tend to have thick, heat-resistant surfaces. Some of the plants are capable of turning their leaves so the edges face the sun, which cuts down the warming effect on their surfaces. All these mechanisms greatly reduce evaporative water loss. Most of the bushes and trees also have unusually long tap roots. A three-foot plant might have a tap root that goes ten or more feet below the surface, enabling it to get more water and nutrients.

The most common plant in the chaparral is the greasewood-chamise bush (*Adenostoma fasciculatum*). Others that predominate are the christmasberry-toyon bush (*Photinia arbutifolia*), the scrub oak (*Quercus dumosa*), the yucca (*Yucca Whipplei*), and the hoary manzanita (*Arctostaphylos canescens*). The chamise is characterized by numerous small, club-shaped leaves with a waxy substance that protects them from drying. When there is a fire, the chamise burns with an intense heat and creates a very black smoke (hence the name "greasewood").

The Role of Fire

The role of fire in the maintenance and regeneration of the chaparral is of paramount importance. The hot, dry summer weather, often fanned by winds, makes the chaparral very prone to fires. Because of the high fuel content in the dense plants, with their waxy and oily components, these fires are very intense and can spread rapidly. Fire is necessary to clear excess growth and allow new seeds to germinate. Indeed, several of the key species need fire to release their seeds or they will not germinate. The amount and distribution of the canopy fuel can have a marked effect on regrowth and even spatial variation. Naturally recurring fires are usually good for germination. Unusually intense fires, often from years of fire suppression, may do harm by damaging the plants severely.

In much of the chaparral, human interference has allowed the fires to become more damaging when they occur. This creates a difficult paradox, since many people now reside in the chaparral and chaparral fires can spread very rapidly, especially with strong winds. Conversely, in some areas where fire has been controlled, the chaparral has been retreating. A good example of this is on the southern slopes of Mount Tamalpais, a mountain just north of San Francisco.

Chaparral Fauna

A wide variety of reptiles, birds, and mammals make the chaparral their home. They have developed adaptations to survive and thrive in this harsh environment. Several species of skinks, lizards, and a variety of snakes, including gopher snakes, the California king snake, and both the red diamond and western rattlesnakes are residents. There are dozens of birds, from several species of hummingbirds to the large birds: the turkey vulture, barn owl, roadrunner, and golden eagle. There are many species of rodents, including kangaroo rats, chipmunks and gophers. The variety of medium to large mammals of common interest is impressive and includes the coyote, gray fox, badger, lynx, bobcat, mountain lion, and mule deer.

—*C. Mervyn Rasmussen*

See also: Deserts; Ecological niches; Ecology; Ecosystems; Fauna: North America; Grasslands and prairies; Habitats and biomes; Mountains; Tundra.

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CHEETAHS

Type of animal science: Classification
Fields of study: Anatomy, behavior, physiology, reproduction

The fastest land mammals, cheetahs originated millions of years ago, before any of the other big cats, but are now an endangered species.

Principal Terms

GESTATION: pregnancy or the term of carrying young in the womb

HYOID: central part of the arch which joins the tongue to the skull

MUTATIONS: sudden variations of inherited characteristics

POLYESTROUS: multiple sexual heats or periods of sexual excitement

Except for rare mutations, cheetahs (whose name is the Hindi for "spotted ones") have tawny or grayish white coats covered with round or oval black spots roughly an inch in diameter, located everywhere except for the throat and abdomen. The hair on the coarse coats is slightly longer at the nape, and the tail has four to six black rings (distinctive to each cheetah) and a white tuft at the end. Cheetahs purr, yelp, and bark rather than roar, owing to the lack of an ossified hyoid.

Cheetahs have long bodies and legs and a small domed head with high set eyes, short ears, and a black line (resembling a teardrop) that runs from each eye down to the mouth. These lines aid vision by reducing solar glare. The whiskers are smaller than those of most cats, but cheetahs hunt by sight alone. Mature cheetahs weigh between 110 and 130 pounds and reach an average height of thirty-two inches at the shoulder, while their bodies extend to roughly fifty inches in length. Male cheetahs are slightly larger than females, but both sexes have small teeth and large lungs and nasal passages which produce a high volume of oxygen. One set of leg muscles is designed for walking, while another is for high-speed sprinting. Cheetah paws are round and hard, and have semiretractable claws that provide traction during sprints and help the cheetah make quick turns. By a combination of running and leaping, the cheetah can accelerate from 0 to 45 miles per hour in two seconds, and can reach recorded speeds of up to 71 miles per hour—but for no more than 300 yards.

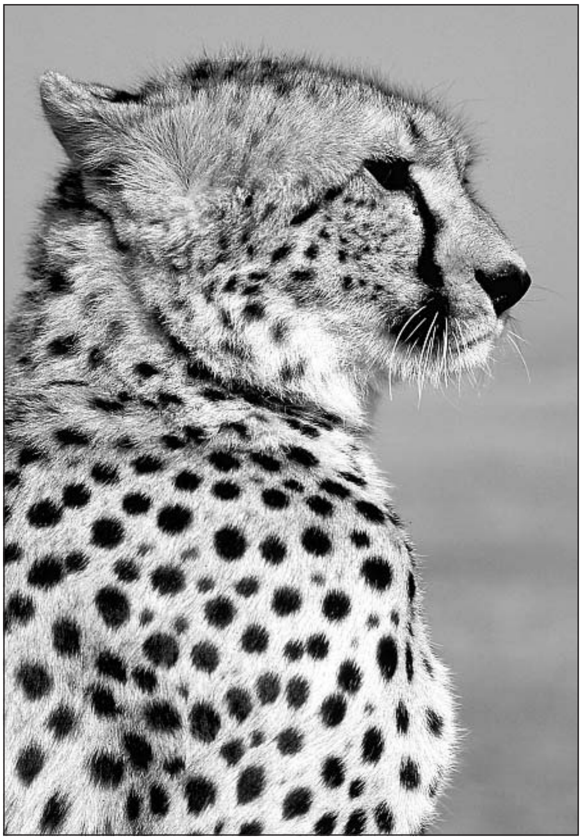
Habitat and Behavior

While about 75 percent of mammals in North America and Europe were eradicated during the Ice Age, the cheetah survived. However, the isolation of its small population created genetic problems because close relatives must mate. Cheetahs used to abound in India, but were wiped out there by the 1950's. They are not usually found in forest habitats but are mostly found in the drier parts of sub-Saharan Africa (especially Namibia and Ethiopia).

Though they are frequently observed on open, grassy plains, they also appear in bush, scrub, and woodlands. They can adapt to arid environments, having the ability to travel an average of fifty miles between drinks of water. The blood or urine of prey satisfies their thirst, as does the flesh of *tsama* melons.

Unlike lions, cheetahs hunt in early morning and late afternoon. They scan the countryside from a tree limb, the top of a termite mound, or even the roof of a safari car. Being carnivores, they feed primarily on gazelles, impalas, game birds, rabbits, and the young of warthogs, kudu, hartebeest, oryx, roan, and sable. Once they have located prey that has somehow strayed from its group, they approach stealthily to within fifty yards before sprinting. However, the sprints, though extremely swift, are brief, lasting anywhere from a few seconds to a minute. Most hunts are unsuccessful, but in successful ones, the cheetahs knock down their prey by the force of their charge or trip it, and strangle it by seizing the throat. Smaller prey are killed by a bite through the skull. A female with cubs hunts daily, whereas lone adults hunt every two to five days. Cheetahs eat quickly because they fear challenges from lions and hyenas, and they often haul their prey to high branches of trees.

Male cheetahs form coalitions to help them in hunting prey and defending territory. Unrelated males are sometimes accepted into coalitions, but lone males can secure territory only if there are no coalitions nearby. Unlike males, female cheetahs leave their natal groups, though they do occupy the same home range as their mothers. Also unlike males, they are solitary, except when they have new litters. Males and females mix to mate, but only females rear cubs. Life spans in the wild average seven years.



The black line that runs from the cheetah's eye down to its mouth serves to cut solar glare and aids the cheetah in scanning for prey. (Corbis)

Cheetah Facts

Classification:
Kingdom: Animalia
Subkingdom: Acinonychinae
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Carnivora
Family: Felidae (cats)
Genus and species: Acinonyx jubatus
Geographical location: Sub-Saharan Africa and northern Iran
Habitat: Areas with tall grass and shrubs, or areas with elevated points
Gestational period: Three months
Life span: Up to twelve years in the wild, seventeen in captivity
Special anatomy: Body is approximately four feet long; long, thin legs; a tail about half as long as the total body; a deep, narrow chest; small round skull; rounded ears set far back; large nasal passages and lungs; large heart, adrenals, and arteries; spine gives spring for back legs

Reproduction

Cheetahs reach sexual maturity in two years. Being polyestrous, females have an average reproductive cycle of twelve days, with fertility lasting from one to three days. Gestation lasts about three months, and litters usually number three to five cubs, though some have as few as one and as many as eight. Newborn cubs are about a foot long and weigh less than half a pound. They have a mantle of hair along their back which helps camouflage them in the grass, but this mantle eventually disappears.

Mothers move their cubs every few days to avoid predators. However, infant mortality rates can be as high as 90 percent, with lions being the biggest killers. Cubs are weaned at 3 to 6 months, but usually remain with their mothers between 1 and 1.5 years, while she teaches them how to hunt and kill prey.

—Keith Garebian

See also: Carnivores; Cats; Endangered species; Fauna: Africa; Lions; Locomotion; Predation.

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CHICKENS, TURKEYS, PHEASANT, AND QUAIL

Type of animal science: Classification
Fields of study: Anatomy, zoology

The chicken, turkey, pheasant, and quail are related members of the family Phasianidae. Chickens are probably the most numerous bird in the world.

Principal Terms

CHICKS: baby birds from chickens, turkeys, pheasant, or quail
CLUTCH: a group of eggs in a nest
COCK: male chicken, pheasant, or quail
COCKEREL: young male chicken, pheasant, or quail
COVEY: flock of quail
EGG: a round, hard-shelled object produced by the female bird that may produce offspring, but is often used as a food product for human consumption
FLOCK: group of birds
HEN: adult female chicken, turkey, pheasant, or quail
ROOSTER: male chicken or pheasant
TOM: male turkey
WATTLE: a large, rather long, finger-type growth that hangs off the upper beak of a tom turkey

The chicken is the most widely raised of agricultural animals. It is estimated that over eight billion chickens are produced annually in the world for both meat and egg production. The chicken was domesticated over four thousand years ago in southeast Asia. The general history of domesticated fowl is not very clear. It appears that the world's chicken population was developed from at least four different wild jungle fowl. Crossbreeding allowed for the introduction of new breeds that continued to develop and change. Today's domesticated birds all come from the Asiatic birds. The wild red jungle fowl is considered to have had the most influence in chicken development. It was the most widespread of the chicken's probable ancestors, was the most calm and compact, and could be the foundation bird of the domesticated chicken.

Chickens

There are three distinct categories of domesticated chickens: meat, egg, and dual purpose. The meat-producing bird is referred to as the broiler breed, and it was developed to be a very fast-growing, quickly maturing, large-bodied bird. The purebred broiler breed chicken is usually crossbred with another breed of chicken to produce an even faster-growing bird. The broiler breed does not lay well and is seldom used as a farm flock bird for egg production.

The egg production chicken is a very lightweight bird, for it was genetically developed to produce eggs and stayed away from any kind of meat characteristics. Most of the egg production breeds come from the Mediterranean region of the world. In general, they are very quick birds, easy to scare, and excellent converters of feed into white-shelled eggs. The Leghorn breed is probably the most well known of the Mediterranean breed of chicken. The dual purpose breed of chicken was primarily developed in the United States for the American farmer or the small flock owner. In the latter part of the nineteenth century, a bird was needed that had relatively good egg production value but also was large enough so a family could use extra birds for food. Most of the American dual purpose breeds have a calm demeanor, lay a good-sized brown-shelled egg, and are easy to keep. The two most common breeds are the Plymouth Rocks and the Rhode Island Reds.

Chickens come in all different sizes and shapes. There are also enormous color and color pattern differences. Many chickens are solid colors, others are striped, splashed, dotted, tipped, or checked. In just about all cases, the rooster is more colorful than the hen. Since the hen sets on the eggs for hatching purposes, she needs to blend into the surrounding area so that a predator will have a harder time in finding her and the nest. The modern farmer, however, usually does not allow hens to set in the wild, and most chicks are now hatched in an incubator.

The chicken's comb varies in type: It may be single, or shaped like a rose, a vee, a pea, or a strawberry. The comb structure is the same for a rooster or a hen. The weight of chickens can vary also, with the rooster weighing anywhere from six to twelve pounds and the hen weighing about two pounds less, depending on the breed and age of the chicken itself. The Asiatic chicken breeds weigh the most, and the Mediterraneans the least.

The incubation period of a chicken is twenty-one days. The baby chicks are rather well-developed when hatched and can survive a day or so with little or no feed. They have a yolk-sac attached that gives them enough food until they are able to figure out how to eat and drink. Newborn chicks need a higher protein base than do older chickens. The growing chicks need between a 20 to 24 percent growth formula in order to survive and flourish.

A chicken has much in common with other birds. The bone structure is similar to that of most birds in that it is lightweight, with hollow cavities, yet strong. The muscle structure is well defined and powerful, allowing the chicken to fly, although not far. The digestive system is typical of all birds. Chickens take in food through their beaks; then it is moved to a pouch where it is stored before being passed on through the gizzard, a hard, rough muscle whose function is to crush the food with small stones that have been picked up to assist in the breaking up of the food particles. Chickens always need a new supply of stones, or grit, to help them in their dietary function. The feathers cover the bird's outer frame and serve as an insulator to keep body temperature even. Feathers constitute 4 to 10 percent of the bird's total weight, depending on the breed and age of the bird. The feathers are replaced on a regular basis, called a molt. The female molt is more dramatic than the male's.

Wild turkeys have exceptionally keen eyesight and are considerably smarter than their domesticated counterparts. (PhotoDisc)

A hen will start laying eggs when she is about six months old and will do so for about twenty weeks, when she goes through her first molt. The average laying hen will lay about 220 to 250 eggs in her first year of production. In the year following, the hen lays about half as many, and the following year, about as half as many again. Many chicken producers will get rid of the chicken after she has her first molt because egg production tends to drop off dramatically afterward.

Chicken, Turkey, Pheasant, and Quail Facts

Classification:
Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Class: Aves
Subclass: Neornithes
Order: Galliformes (chicken, turkey, and pheasant)
Suborder: Galli
Families: Megapodiidae (mound birds, two tribes); Cracidae (curassows, two tribes); Phasianidae (grouse, three tribes), with subfamilies Perdicinae (three tribes), Tragopaninae; Phasianidae, with subfamilies Meleagridinae (turkeys), Argusianinae (argus pheasant), Pavoninae (peafowl), Afropavoninae (congo peacocks), Numidinae (guinea fowl), Phasianinae (pheasant)

Geographical location: Chickens and pheasant originated in Southeast Asia from the wild jungle fowl; turkeys are strictly a North American bird that is now well received as a domestic fowl; quail are located on all continents except Antarctica

Habitat: The original habitat of chickens and pheasant was the warm region of Southeast Asia and now has spread worldwide; turkeys are an American ground bird; quail are found in forests, dryland areas, and plains

Gestational period: Eighteen to thirty-two days, depending on the species

Life span: Chickens will live about four years; pheasant live about the same length of time, but less in the wild; turkeys and quail live between three and six years

Special anatomy: Males are very colorful; females tend to be dull and drab-colored

Turkeys

The turkey is a rather large, ground-feeding bird that is native only to North America. There are two varieties. The eastern wild turkey, also called the common turkey, had a natural range that covered the southern portion of Canada to northern Mexico. The second turkey is called the ocellated turkey of southern Mexico and northern Central America. The eastern turkey had a much greater natural range, but because much of its natural cover has been destroyed over the years by human population growth, the range is now much smaller. In many cases, the eastern turkey has been wiped out of existence in numerous locales.

The domestic turkey is economically important to many regions in America. The turkey is traditionally served on Thanksgiving all across the United States. The wild turkey has a rather dark plumage, and eats nuts, bugs, and other things it finds on the forest floor. It roosts in trees during the night. The wild turkey is very wily and is alert to all danger. The wild turkey male, or tom, is rather large for a bird that can fly with ease. He weighs about twenty pounds when full grown. The female is not as large but is just as alert. She will try to hatch out ten to fifteen eggs in her clutch every year. Turkeys tend to band together after the reproduction season is over, and they stay together until the following year.

The domestic turkey does not come from the eastern variety but from the ocellated strain. The Native Americans of Mexico and Central America domesticated the bird sometime before Columbus discovered the region. Currently, there are several kinds of domesticated turkey used in agriculture, with the Giant White being the one chosen for human consumption. The domestic turkey has been bred to have huge breasts and other dominant portions. It grows rapidly but cannot reproduce by itself very easily, having become too large. Most turkey insemination is now done through artificial means.

Quail

The quail is a relatively small, very fast-flying bird that is found in the western hemisphere as well as Europe, Asia, and northern Africa. It is a ground bird that prefers to hunt for seeds, bugs, insects, and other food on the ground near cover. Quails need a high-protein source of feed because of their fast heartbeat, so they usually hunt meaty invertebrates. The quail is generally monogamous in nature. When babies arrive, both parents tend to the offspring.

There are several closely related varieties of quail in the world. All have adopted a slightly different way of living, but are recognizable by their general patterns of flight, group activity, and food-hunting tactics.

Quail belong to the Phasianidae family, which includes pheasant, turkeys, and several other fowl. The males and females are similar in color and size. Quail are nonmigratory and will establish a territory in which they want to live and stay. Quail are sportsmen's favorite bird because they are fast flyers and elusive. They serve as a challenge.

Pheasant

The pheasant also belongs to the family Phasianidae. The history of the pheasant suggests that it originated from one of several wild jungle fowl of southeast Asia at least five thousand years ago, if not more. The greatest variety is located in Asia, but there are several native species in Europe as well as in Africa. The pheasant in North America were imported as sport gamebirds. North America has no native pheasant.

The pheasant does not roam very much and prefers to keep itself in a specific territory. The bird will forage on the ground, but at night will try to sleep in trees or in some other specific cover. The pheasant male is very polygamous and will mate with as many females as he can find. He does not help in the rearing of the babies and actually serves no function other than breeding and calling out when danger is near. The male has a much different color pattern than the female. He is colorful and bright-feathered; she is dull in color. The pheasant builds her nest on the ground and needs to blend in to the surrounding area in order to elude predators that might kill her or rob her nest.

The pheasant is a strong flyer, but does have to run before taking off on most occasions. It has a long neck, very strong legs and feet, and a powerful beak that is hooked at the end. There are several species of pheasant in the world, with the most numerous being the domesticated chicken.

—Earl R. Andresen

See also: Beaks and bills; Birds; Domestication; Feathers; Flight; Molting and shedding; Nesting; Respiration in birds; Wildlife management; Wings.

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CHIMPANZEES

Types of animal science: Anatomy, behavior, classification
Fields of study: Anthropology, ethology, zoology

Two species of chimpanzees exist and are classified under the order Primates, an order of extreme physical variability and complexity. Chimpanzees are humans' closest relatives and exhibit significant learned behaviors.

Principal Terms

DOMINANCE HIERARCHY: ranking or status system found in some primate societies
FUSION-FISSION COMMUNITY: a society whose members are of both sexes and all ages, which can form and dissolve subgroupings
HOME RANGE: a primate's territory
KNUCKLE-WALKING: terrestrial locomotion, in which the animal walks on the knuckles of the forelimbs and soles of the hind feet
SOCIAL GROOMING: an activity maintaining social interaction, whereby debris is removed from a primate's hair

Chimpanzees are highly intelligent and emotional animals. They demonstrate many humanlike traits, such as a rudimentary culture, in their adaptive responses to environmental challenges.

Physical Characteristics of Chimpanzees

Woodland chimpanzees weigh between 73 and 132 pounds. The bonobo weighs from seventy-three to ninety-nine pounds. Females are about 10 percent smaller than males. Chimpanzees have powerful arms and shoulders and locomote through knuckle-walking, a form of quadrupedalism, although they are occasionally bipedal, and can also brachiate (swing through trees and branches). Chimpanzee forelimbs (arms) are longer than their hindlimbs. Vision is in color and highly acute. Chimpanzees have short thumbs, and their grasping ability is somewhat impaired relative to humans.

Both *Pan troglodytes* and *Pan piniscus* are promiscuous. Females of each species exhibit sexual swelling when they are receptive to mating; however, there is no consistent breeding season.

Ecology and Diet

Chimpanzees at one time inhabited a three-thousand mile belt across equatorial Africa. Today their distribution is limited, and in some regions they are extinct or disappearing.

Chimpanzee home ranges vary in size depending upon food resources and other ecological dynamics. The home range of the woodland chimpanzee can be from 2 to 215 square miles, whereas the bonobo's home range is from 7 to 19 square miles. Water availability, nesting trees, and seasonal food resources define ranges, and chimpanzees can cover several miles in a day. Adult male chimpanzees patrol their ranges to ensure the exclusiveness of a community's domain. Aggression as a result of invasion and intercommunity destruction has been documented by Jane Goodall.

Chimpanzees are omnivorous: Their diet consists of a great variety of vegetal foods, as well as insects, grubs, bird eggs, and small mammals. While leaves and fruit define much of the chimpanzee's diet, colobus monkeys, young bush bucks, and young baboons obtain supplemental protein through cooperative hunts.

Group Life and Learning

Chimpanzees of both species reside in fission-fusion communities. Membership within community subgroups can change throughout the day.

Jane Goodall

Born: April 3, 1934; London, England
Fields of study: Ethology, zoology
Contribution: Goodall, a primatologist, was the pioneer in long-term field studies of the woodland chimpanzee (*Pan troglodytes*). Her research documented previously unknown behaviors including tool manufacture, cooperative hunts, and numerous other humanlike traits.

Image Not Available

Jane Goodall was awarded a Ph.D. in ethology from Cambridge University in 1965, one of a few to not earn a bachelor's degree prior to graduate study. In 1967, she became the scientific director of the Gombe Stream Research Centre in Tanzania. In addition, she has held university teaching appointments at Stanford University, the University of Dar es Salaam, Tanzania, Tufts University, the University of Southern California, and beginning in 1996, at Cornell University as A. D. White Professor-at-Large. She holds memberships in numerous scientific organizations and has been awarded honorary degrees from many prestigious institutions, including the University of Pennsylvania in 1990, and the University of Edinburgh, Scotland, in 1997. The recipient of dozens of awards from worldwide organizations, Goodall received the Centennial Award from the National Geographic Society in Washington, D.C., in 1988 and was recognized for her scientific contributions by being made a Commander of the British Empire by Queen Elizabeth II in 1995.

Goodall demonstrated an early interest in the primates and wildlife of Africa. As a young woman she worked with famed paleontologist Louis Leakey at Olduvai Gorge in Tanzania. With Leakey's encouragement and advice she began her research in 1960 with a population of free-living chimpanzees in the Gombe National Park.

Through rigorous observations, Goodall documented numerous behaviors of *Pan troglodytes* which exploded previously held myths. Perhaps Goodall's most significant accomplishment was to demonstrate that the woodland chimpanzee possessed the capacity for rudimentary culture. Goodall's research documented that woodland chimpanzees could modify and use natural objects such as branches, twigs, and stems of grass. These tools could be employed to extend the food quest, for example in "termite fishing," intimidate other animals such as baboons, and make their daily lives easier by doing such things as using leaves as sponges to soak up drinking water.

In an early and important book, *In the Shadow of Man* (1971), Goodall described chimpanzee family and social life, basic tool-making, aggression, and predation. That chimpanzees organized themselves into distinct groups for hunting entranced a worldwide audience. Many behaviors were filmed by Goodall's first husband, Baron Hugo van Lawick, a wildlife photographer. Later contributions to the literature, particularly *The Chimpanzees of Gombe: Patterns of Behavior* (1986) and *Through a Window: Thirty Years Observing the Gombe Chimpanzees* (1990), underscored the value of long-term field studies.

Goodall's fieldwork might be characterized as a combination of patience and determined effort. By the 1980's, this effort culminated not only in an enormous amount of knowledge on woodland chimpanzee behavior but also in the establishment of the Gombe Stream Research Centre as one of the world's foremost primate research facilities.

Since the mid 1980's, Goodall has spent large amounts of time away from the Gombe Centre in worldwide lecturing and in lobbying for chimpanzee and wildlife-related issues. In addition, she has been actively involved in chimpanzee conservation and has worked to halt the illegal trade in chimpanzees.

—Rene M. Descartes

Males and females strive to attain dominance, or elevated status, which provides access to preferred food resources and desirable mates. Physical size, strength, and age influence the attainment of position within a dominance hierarchy. Hierarchies function to minimize chaos within the community. Woodland chimpanzee communities range from 20 to over 100; bonobo groups range from 50 to 120 individuals.

Social interaction is enhanced on the individual level through social grooming. Mutual grooming, or cleaning the hair carefully, is an act denoting friendship and intimacy.

Learning accounts for much of chimpanzee behavior, acquired through play and observation. Tool use, a learned behavior, has been observed frequently among woodland chimpanzees, much less so among the bonobo. Tools (sticks, rocks, branches, leaves) have been used, and in some instances modified, in order to access and extract underground termites from their nests for consumption; to intimidate other animals; to facilitate drinking; to clean the body; and to crack open nuts.

Chimpanzee behaviors associated with meat eating include begging and the subsequent sharing of the kill by the hunters. Cannibalism and infanticide among chimpanzees have also been observed.

Chimpanzees are emotional animals that require reassurance that they are part of the community. Touching and embracing among individuals are common behaviors.

—Rene M. Descartes

Chimpanzee Facts

Classification:
Kingdom: Animalia
Subkingdom: Metazoa
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Subclass: Eutheria
Order: Primates
Suborder: Anthropoidea
Family: Pongidae
Genus and species: Pan troglodytes (common or woodland chimpanzee), *P. piniscus* (pygmy chimpanzee or bonobo)

Geographical location: Africa; *P. troglodytes* is found from west to east Africa, from Senegal to Tanzania, including the Ivory Coast, Gabon, Sierra Leone, Congo Republic, and the Democratic Republic of the Congo; *P. piniscus* is found in the central and western regions of the Democratic Republic of the Congo

Habitat: *P. piniscus* prefers rain forests and swampy forested areas; *P. troglodytes* has been observed in diverse habitats—tropical rain forest, wooded savanna, primary and secondary forest

Gestational period: 7.5 to 8 months

Life span: Forty to fifty years

Special anatomy: Large complex brain (390 cubic centimeters average) in relation to body size

See also: Apes to hominids; Baboons; Cannibalism; Communication; Communities; Evolution: Animal life; Evolution: Historical perspective; Fauna: Africa; Gorillas; Groups; Hominids; *Homo sapiens* and human diversification; Human evolution analysis; Infanticide; Learning; Lemurs; Mammalian social systems; Monkeys; Orangutans; Primates.

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CHORDATES, LOWER

Type of animal science: Systematics (taxonomy)
Fields of study: Anatomy, evolutionary science, physiology, zoology

Lower chordates are those members of the phylum Chordata other than the vertebrates. They are small marine organisms, chiefly of interest for the light that they shed on the history of vertebrate development.

Principal Terms

CHORDATA: a phylum of organisms characterized by the presence of a notochord, a dorsal nerve cord, and gill slits

DEUTEROSTOMES: echinoderms, hemichordates, and chordates, a group linked by features of cell development including retention of the blastopore as anus

LOWER CHORDATES: a group within the Chordata that shows chordate characteristics in the larvae but is separated from vertebrates by the lack of a skeleton

NEOTENY: a process by which larval features are retained into the reproductive adult stage

NOTOCHORD: a flexible stiffening rod found in primitive chordates

PROTOSTOMES: annelids, mollusks, flatworms, and arthropods, a group linked by features of cell development including retention of the blastopore as the mouth

The phylum Chordata is chiefly of interest because it includes the human taxonomic group, the vertebrates. Yet the phylum also includes a number of lesser-known groups, termed the lower chordates. Chordates as a whole are characterized by the presence of a longitudinal cartilaginous stiffening rod (the notochord), a single tubular dorsal nerve cord, and perforations in the pharynx comparable to gill slits. The subphylum that includes humans, the Vertebrata, is further characterized by the presence of a bony skeleton that forms an internal support and protects vital structures such as the spine and brain. In land-dwelling vertebrates, gill slits are present only in the embryonic stages. The other two subphyla currently included within the Chordata and making up the lower chordates are the Urochordata, or tunicates, and the Cephalochordata, all of which are small marine organisms. In the past, an additional group, the Hemichordata (acorn worms and pterobranchs), were also considered chordates. They possess a dorsal nerve cord and gill slits but do not have a notochord; they are now placed in a separate phylum, although they are considered to be closely related to chordates. In addition, a group of fossil organisms with echinoderm affinities have been interpreted as chordates and given the name Calcichordata. Most specialists on this group (generally known as mitrates) consider them to be echinoderms, however, as their chordate affinities are based entirely on soft-part reconstructions.

Sea Squirts

The largest group of lower chordates, containing about 1,300 species, is the Urochordata. These organisms, commonly called tunicates, little resemble chordates in their adult form: Only the tadpolelike larval stage possesses distinct chordate characters. Three classes are recognized—the Ascidiacea, Thaliacea, and Larvacea—and of these the most common and typical tunicates are the ascideans, or sea squirts.

Adult sea squirts are sessile (attached to the ocean bottom) marine organisms commonly found in coastal waters worldwide. They are sack-shaped, range from a few millimeters to a few centimeters in length, and have two siphons, inhalant and exhalant, extending from the upper surface. The outer part of the body is called the tunic. This is a protective structure made of proteins and polysaccharides, which is often quite thick and may vary from a soft, delicate consistency to one that is tough and similar to cartilage. Within the tunic, much of the space is taken up by the pharynx (an expanded part of the digestive tube), which has small perforations in its wall, creating a net. Small, hairlike structures called cilia create currents that pull water in through the inhalant siphon. The water then passes through the openings in the wall of the pharynx into the atrium (the surrounding cavity), and from there it passes out through the exhalant siphon. Food particles are trapped on the pharynx wall by a mucus sheet, which moves constantly to the midline of the pharynx and then posteriorly to the gut, where digestion takes place. This is a very effective system, and it can filter out particles only one to two micrometers in diameter.

Sea squirt larvae, unlike the adults, are tadpole-shaped and mobile. They are generally very small and are mobile for only a few hours before settling and becoming sessile adults. The tail of the larva has a notochord, which acts in much the same way as the vertebral column of vertebrates. As it is flexible but of a fixed length, it will not shorten when muscles on either side contract; it thus makes them antagonistic, bending the tail from side to side. Above the notochord is a dorsal nerve cord that swells anteriorly into a light detector and an organ sensitive to tilting. The larvae tend to swim down and away from light—behavior that takes them to sites such as overhanging rock faces that are suitable adult habitats.

Thaliacea, Larvacea, and Cephalochordata

The Thaliacea and Larvacea are both planktonic (that is, they float near the surface of the ocean). The Thaliacea, or salps, are colonial forms that may reach two meters in length. Their inhalant and exhalant siphons are at opposite ends of the body, and water is pumped through by rhythmic muscular contractions. This class has no tadpole-like larvae, but instead develops directly into the adult form. The Larvacea do develop from larvae, but they retain the tail as a permanent organ. Water is filtered through a mucus sheet in the pharynx as in other tunicates, but in this group the entire animal is surrounded by a delicate gelatinous "house" that is probably homologous to the sea squirt's tunic. The house has mesh at the inhalant and exhalant openings that helps to concentrate food particles; this concentrate is then passed through the mucus sheet, and food particles are trapped. The house is continually shed and replaced, probably to counteract clogging of the filters, and may not last more than a few hours.

The subphylum Cephalochordata includes only about twenty species of two genera of organisms that are often referred to as amphioxus. These are small, fusiform, and rather fishlike organisms up to seven centimeters long that live in sandy and shelly bottoms in shallow coastal waters. They burrow head down in coarse sediments and can filter-feed even when buried by filtering the water that penetrates between grains.

In cephalochordates, the notochord extends almost to the snout. This is further forward than in fishes, and it may aid in burrowing by stiffening the snout. The swimming muscles are arranged in myomeres (muscle segments) down the body and are similar to those found in fish, though simpler in shape. A hollow dorsal nerve cord runs above the notochord and is enclosed in a tube of collagen fibers that enclose the cord in a way similar to the vertebrae in fish. There is no anterior swelling of the nerve cord that might be comparable to the brain in vertebrates. The nerve cord, however, sends a ventral motor nerve and a dorsal sensory nerve to each myomere, an arrangement identical to that found in vertebrates. As it is in the urochordates, the pharynx is pierced by numerous slits, and food particles are trapped by a mucus sheet that moves across them and back to the gut. The blood system is more complex, however, and is similar in general arrangement to that of fish, although there is no heart; blood is propelled by pulsations of some of the vessels.

Hints About Vertebrate Origins

The cephalochordates and urochordates are particularly interesting for what they suggest about vertebrate origins. Although in the past it has been suggested that vertebrates evolved from various invertebrate groups such as annelids (segmented worms) or cephalopods (squid and octopuses), it is now recognized that fundamental patterns of development distinguish chordates and echinoderms from mollusks and advanced segmented invertebrates. These differences involve the way in which cells divide and the relative potential of the cells.

In mollusks and annelids, spiral cleavage results in cells that are nested between one another in successive rows. They are also determinate—that is, the fate of each cell is predetermined, so that the removal of one results in the developmental failure of part of the organism. In chordates and echinoderms, however, the cells are directly above one another in layers (radial cleavage), and if a cell is removed, adjacent cells will compensate for its loss (indeterminate cleavage). In both groups, cells initially form a ball, termed the blastula, and cells at one end grow in to form a second layer of tissue, the endoderm, which forms the lining of the gut. The external layer, or ectoderm, forms the outer surface of the body. In the mollusk-annelid group, the opening in the blastula (the blastopore) is retained as the mouth, while in the echinoderms and chordates it becomes the anus.

Despite the fact that this information points to a close relationship between echinoderms and chordates, there are too many differences for them to make convincing vertebrate ancestors. The larvae are similar to those of lower chordates, but the adults are quite different. The same can be said for hemichordates, although they are probably more closely related to chordates than echinoderms are. Adult urochordates are also too specialized to be suitable candidates for the vertebrate ancestor, and the same can be said of cephalochordates, although amphioxus does show many vertebrate-like features. It is currently accepted that the echinoderms, hemichordates, and lower chordates must have diverged from vertebrate ancestors no later than the lower Cambrian period (about 550 million years ago). This is substantiated by the presence of a fossil cephalochordate in the Burgess shale, which is middle Cambrian in age.

It has been suggested that the lower chordates show how the vertebrate ancestor may have arisen by a process of neoteny or pedogenesis, in which larval characteristics may be retained in the adult. Sexual development is accelerated, and the development of other organ systems is arrested, so that the nonreproductive larvae of the ancestor become the reproductive adults of the descendant. In this case, a notochord and tail muscles are found in sea squirt larvae but not in the adults; however, they are retained in the Larvacea. Further retention of larval features could have given rise to cephalochordates and, by a further step, to vertebrates.

Studying Chordates

Lower chordates, small marine organisms, are often difficult to study because of their size and delicacy. The gelatinous covering of the Larvacea, for example, is so easily damaged as to be almost impossible to observe. Many modern techniques, however, have been developed to aid in the study of organisms such as these. Cinematography is used in studies of movement, and high-speed photography is particularly useful; the film can then be shown at a much slower speed to enable detailed analyses of complex movements. Electromyography can also be used to trace muscular action, as it follows the electrical changes that take place in muscles when they are active. The lower chordates are all filter feeders, and it is possible to carry out experiments that show how effective they are at removing small particles from the water. Sea squirts can be placed in a dish containing a suspension of colloidal graphite, and their filtering ability can be seen as a function of the rate at which the water clears. In addition, the size of particles can be varied to show how efficient the filtering apparatus is; this has shown that sea squirts can remove particles as small as one to two micrometers in diameter, although the diatoms on which they normally feed are closer to two hundred micrometers in diameter.

Fossil lower chordates are extremely rare; however, a probable cephalochordate, *Pikaia*, is known from the Burgess shale of British Columbia, which is dated as middle Cambrian (530 million years ago). The Burgess shale contains a variety of soft-bodied organisms preserved as films of carbon on the bedding surfaces. Study is difficult because the material is compressed and because it is the same color (black) as the rock that contains it. Specimens can be prepared by picking rock away with needles. Details can then be studied by observing the specimens under low-angle light, which picks out differences in reflectivity of the rock surfaces and carbon films, or by immersing specimens in water or alcohol, which also enhances differences between the fossil and the surrounding rock.

These techniques make it possible to determine which characters are important in determining relationships within the lower chordates. Studies on relationships rely heavily on a methodology called phylogenetic systematics, or cladistics. In this taxonomic method (taxonomy is the study of interrelationships), only advanced characters shared between species (termed synapomorphies) are used to develop a picture of relationship. These relationships are expressed as branching diagrams termed cladograms (*klados* is Greek for "branch"), hence the name cladistics. Studies using this technique have advanced understanding of the relationship between lower chordates and the vertebrates. The picture is by no means clear, however, and much still waits to be done.

Understanding the Route of Evolution

The lower chordates are of particular interest for the light that they shed on the way in which the group to which humans belong, the vertebrates, may have developed and when this may have occurred. Vertebrates differ from lower chordates in possessing both an internal skeleton and a brain; however, there is only limited fossil record of the earliest members of the group. The earliest known vertebrates are fish that are found in rocks of the Ordovician period (450 million years ago) in Australia, South America, and North America. These animals had an external bony armor, but knowledge of both their external appearance and their internal anatomy is restricted by poor fossil preservation. It is clear, however, that these animals were already relatively advanced and, hence, that a fairly long period of vertebrate development is not represented in the fossil record. As the lower chordates are the nearest relatives of the vertebrates, they can provide some information on how this development may have taken place.

It has been suggested that the process of neoteny, or pedogenesis, might explain the development of vertebrates. In this process, development of adult characters is retarded, and the organism reaches sexual maturity while still in the larval stage. This process may already have operated in the lower chordates, as the urochordates show chordate characters in the tadpolelike larval stage only, whereas the more advanced cephalochordates retain the chordate characters in the fishlike adult stage. It is fairly easy to see, therefore, how a continuation of this process could lead, by fairly small morphological changes, to organisms similar to the larvae of modern lampreys, jawless fish that represent the most primitive modern vertebrates.

It is clear, however, that vertebrates did not evolve directly from cephalochordate ancestors. Although the modern cephalochordate amphioxus shows many features that one would expect to find in a vertebrate ancestor, it also has a number of basic differences that are inconsistent with a position on the direct evolutionary lineage of the vertebrates. In particular, the presence of a notochord extending to the anterior end of the rostrum and the lack of a clearly differentiated head make cephalochordates unlikely ancestors of organisms with large brains. It seems more likely, therefore, that both vertebrates and cephalochordates represent divergent lineages from a common ancestor, probably of urochordate type. The presence of the fossil cephalochordate *Pikaia* in rocks of Middle Cambrian age (530 million years ago) indicates that the division had already taken place then and that the first vertebrates must have been present some time in the early Cambrian period.

—David K. Elliott

See also: Anatomy; Circulatory systems of invertebrates; Development: Evolutionary perspective; Echinoderms; Evolution: Animal life; Evolution: Historical perspective; Extinction; Heterochrony; Marine animals; Marine biology; Muscles in invertebrates; Physiology; Vertebrates.

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CIRCULATORY SYSTEMS OF INVERTEBRATES

Type of animal science: Anatomy
Fields of study: Evolutionary science, histology, invertebrate biology, systematics (taxonomy)

Any circulatory system provides transport for materials required by cells that cannot be supplied quickly or efficiently enough by diffusion. Invertebrates possess a great variety of circulatory systems. Some are closed systems; some are open systems.

Principal Terms

BLOOD: the fluid connective tissue within blood vessels that carries raw materials to cells and carries products and wastes from them

CLOSED CIRCULATION: a circulatory pattern in which blood is always contained within blood vessels

DIFFUSION: the process whereby a substance moves from an area of greater concentration to one of lesser concentration, as through a cell membrane

HEMOLYMPH: the transport fluid of organisms with open circulation systems in which there is no clear distinction between blood and intercellular tissue fluid

LACUNAE: small spaces among tissue cells through which hemolymph flows in open circulatory systems

OPEN CIRCULATION: a circulatory pattern in which the blood is not always contained within blood vessels

SINUSES: larger spaces, thought to represent through channels, for hemolymph in open circulatory systems, sometimes bound by membranes

TRACHEAL SYSTEM: the respiratory system of insects and other terrestrial invertebrates; it consists of numerous air-filled tubes with branches extending into tiny channels in direct contact with body cells

Circulatory systems are necessary when the process of diffusion no longer provides an organism with sufficient gas, nutrients, and waste exchange with its environment. Some invertebrate groups, such as sponges, coelenterates, and flatworms, have such thin body walls that diffusion can meet all their needs. For most invertebrates, however, the distance from the organism's surface to the cells in the interior is too great for diffusion to support their metabolic requirements. A circulatory system is composed of three parts: the pump, the fluid that is pumped, and the vessels in which the fluid is transported. As in the design of invertebrate body plans, there is great diversity in the design of invertebrate circulatory systems.

The Components of the Circulatory System

The pump may be a simple tube lined by muscle fibers. Alternate contraction and relaxation of these muscles produces a peristaltic wave that pushes the blood along. The pump may be a heart: a localizable, discrete organ whose muscle layers are the primary generators of the power that propels blood through the blood vessels. The heart can be a simple muscular enlargement, or it can be complex and multichambered, depending on the evolutionary history and the needs of the organism. Some organisms may have more than one heart.

If the pumped fluid remains within the blood vessels, it is usually called blood. If it leaves the blood vessels to enter cavities surrounded by tissue cells with which it exchanges materials, it is called hemolymph. In the cavities (called lacunae if small and sinuses if large and lined with a membrane) blood mingles with intercellular fluid. Whatever it is called, the fluid is composed of water, solutes (such as salts, sugars, and other nutrients), and, in some cases, cells and formed elements. The blood may also contain a respiratory pigment that helps deliver oxygen to the cells.

Fluid Transport Systems

Blood vessels may extend only a short distance from the heart or may provide a continuous path for the transport of blood. If the blood vessels are incomplete and blood is pumped from arteries into body spaces—sinuses and lacunae—it is an open circulatory system. If the blood vessels are continuous and the blood never leaves these circulatory channels, it is a closed circulatory system. These are generalized terms for convenience; there are actually many intermediate cases. Some open systems have membrane-lined sinuses and lacunae, and exchange takes place by diffusion just as it does in the tiniest vessels of closed systems. Blood vessels are categorized according to their function. Arteries carry blood away from the heart; veins carry blood back to the heart. Closed circulatory systems have tiny tubules, called capillaries, connecting small arteries to small veins. The exchange of materials between the tissue cells and the blood takes place only in the capillaries.

A few generalities based on physical principles indicate the rules guiding fluid transport. Organisms relying on diffusion alone to circulate nutrients and eliminate wastes are limited to certain shapes and sizes: They are often only two cell layers thick. Organisms using bulk transport of fluid, on the other hand, may be as complex and as differently shaped as plants and animals are.

A fluid transport system is any system in which internal fluid movement reduces diffusion distances—either between points within an organ or between a point within an organism and the external environment. While diffusion is always used for short-distance transport, bulk flow augments diffusion for any long-distance transport. Bulk flow requires a pump and a fluid that must come into intimate contact with tissues and the environment for efficient transfer. Either the tissue layers must be thin (as in open circulatory systems) or the vessels must have a small radius (as in a closed circulatory system). The circulatory fluid should spend the majority of its time in the transfer regions (sinuses and lacunae or capillaries) and not in transit.

Such transport systems use both large and small vessels. Large vessels move fluid from one exchange site to another, and small vessels allow diffusion at the exchange sites. The total cross-sectional area of the small vessels must exceed that of the large vessels so that the flow rate in small vessels will be less than the velocity in large vessels. High-speed pumps in large vessels are preferable to low-speed pumps in the small vessels. This means that accessory hearts are only used when the "cost" of operation is not a major factor or when the pump serves some additional functional role—as when active cephalopod mollusks, such as squid and octopods, use accessory hearts to ensure adequate blood flow through their gills.

Closed and Open Circulatory Systems

Circulatory systems are traditionally divided into two categories. Closed systems are those in which the blood is always contained within distinct vessels and is physically separated from the organism's intercellular fluids. They are usually characteristic of organisms with high metabolic demands. High volumes and high pressures can be maintained in the closed vessels to aid transport and diffusion. Annelids, cephalopod mollusks, and vertebrates usually have closed circulatory systems.

Open systems are those which possess large, usually ill-defined, cavities (sinuses if bound by an endothelial layer, lacunae if not) and in which the blood is not physically separated from the intercellular fluids. Arthropods and noncephalopod mollusks have open systems.

Open circulatory systems are not always sluggish, low-pressure arrangements. Some spiders generate sufficient pressure in their open systems to use hydraulic pressure as a substitute for extensor muscles in their legs. In addition, capillaries often exist in open systems, particularly in areas such as the excretory organs and the cerebral ganglion. The major sinus in the foot of gastropod and bivalve mollusks is not a large, open cavity but a network of channels in a spongy tissue that function as capillaries. The lack of return vessels in these systems is usually a result of the fact that fluid simply has nowhere to go other than in the direction of low pressure: back to the heart. These volume constraints are sufficient to develop pressure, although this system is incompatible with high pressure and flow rates.

In the two major groups with open circulatory systems, arthropods and noncephalopod mollusks, the circulatory sinuses play an additional role: In bivalve and gastropod mollusks, the hemocoel (main body cavity) functions as a hydrostatic skeleton in locomotion and burrowing. In aquatic arthropods, it serves the same function during molting, when arthropods lose the support of the exoskeleton. In insects, the tracheal system has assumed the respiratory function, and the blood merely delivers nutrients and removes wastes. In large flying insects, the circulatory systems may also have the primary responsibility of removing heat to maintain thoracic temperatures.

Pressure Patterns in Heart Action

To function effectively, the circulatory system must have a regular pattern of pressure increases that will push the blood along through the vessels. The heartbeats that accomplish this may be initiated and maintained by nerves, or they may be self-generated. If nerves initiate the contraction of the heartbeat, the heart is called neurogenic, meaning that nerve impulses generate the depolarization that results in the contraction of the heart's muscle cells. In these hearts, the heart muscle will not contract without a nerve impulse. Some species with neurogenic hearts are crustacea, horseshoe crabs, some spiders, and scorpions.

Heart muscles that continue to beat even when nervous connections are severed are called myogenic, meaning that the heart muscle contracts without external stimuli. Under these circumstances, the contraction of the muscles may occur at a different rate from that imposed by the nervous system when active. Myogenic hearts are found in mollusks and many insects.

All heart action must be modulated to respond to external and internal conditions, so even myogenic hearts usually receive some innervation. Modulation occurs through the mediation of nerves, hormones, or intrinsic controls in the heart. In the lobster, for example, nerves are crucial to maintaining the best rhythm and amplitude, but neurohormones released from a pericardial organ influence the heart action. Stretching the heart muscle, an intrinsic control, will also increase the vigor and rate of contraction.

In many cases, the structure of the heart and its suspensory ligaments contributes to the functioning of the circulatory system. Values at the openings (ostia) to the heart prevent backflow when the heart contracts. This pulls at the ligaments. Their elasticity pulls back the walls of the heart, creating low pressure that enables the heart to fill on relaxation. In effect, the heart sucks blood from veins to refill itself for the next contraction.

In many species, the contraction of body parts contributes to the circulation of blood. Arthropods have a rigid exoskeleton; contraction in one part pushes the blood into another segment. In American lobsters, a quick flexion of the abdomen (an important locomotor movement) raises pressure in the abdomen and increases the rate of blood flow to the thorax and into the heart region.

All flow depends upon pressure differences, regardless of whether the circulatory system is open or closed, and there are two kinds of pressure. Background pressure is the pressure that prevails everywhere in the animal. Since pressure differences are responsible for flow, these pressure differences are imposed on the background pressure. If the body changes posture and increases background pressure, the blood pressure must similarly increase in order to maintain flows at the same level they were before the postural change. The blood-pressure gradient and the resistance to flow in the system affect blood flow.

The low resistance in open circulatory systems probably permits relatively high rates of blood flow with relatively low pressure. The high blood-flow rate compensates for the low oxygen-carrying capacity of the blood.

Open and closed systems differ; neither is necessarily superior. The inherent weakness of the open circulatory system is that the peripheral blood flow cannot be as well controlled as that of closed circulatory systems. Yet the large sinuses are often subdivided, thereby providing discrete channels of flow, and the peripheral blood flow may be more regular than previously thought. Closed circulatory systems have a flow that is easily controlled. Flow through particular regions can be managed by using muscles to close off certain channels. Cardiac output can be distributed to meet tissue demands. In open systems, this is not possible after the blood leaves the major vessels, although muscle contractions and accessory hearts may influence peripheral flow. Whatever their patterns, the circulatory systems of invertebrates are adequately matched to their needs; they have enabled these creatures to survive and proliferate for millions of years.

Studying Invertebrate Circulation

Methods used to study invertebrate circulatory systems are varied. One basic problem is that 95 percent of all animal species are invertebrates, and many of these creatures are not known and have never been studied. The larger, more common organisms that are easiest to study have been subjected to experimentation. Many invertebrates are difficult to maintain in the laboratory, but techniques to maintain them in good health are being developed and improved. Without these culture techniques, experimenters must use recently caught subjects whose condition is doubtful.

Most knowledge of invertebrate circulatory systems is anatomical. Even a common animal must be described so that a physiologist can apply appropriate techniques to study the functioning of the heart, vessels, and blood. Descriptions are usually derived from dissection and from microscopic study. These painstaking methods have been used on known species for centuries. Larger invertebrates, such as lobsters, crabs, clams, squid, and octopods, have been studied by techniques similar to those used in vertebrate circulation physiology. A heart can be exposed and either attached to a lever that can record its contractions or attached to an electronic force transducer, which can measure the strength of contraction.

The heart is large enough to be punctured for blood samples, and hemolymph can be withdrawn from the larger sinuses. These blood samples can be analyzed for the presence and activity of cells, respiratory pigments, nutrients, and wastes, using ordinary biochemical techniques. The development of microanalytic techniques in biochemistry allows the sampling of body fluids from small insects, worms, and rare organisms that might be damaged by taking larger samples.

In addition, force transducers can be placed along blood vessels and in hemocoels to determine the pressure exerted during flow. Electronic devices can monitor the flow rate by detecting cells or the passage of a dye or magnetic substance. Radioactive tracers can be injected and their path followed. All these less invasive techniques allow the animals to survive longer and to deliver data that can be more reliably interpreted because they are from a healthy subject. The use of fewer organisms in research and the survival of rare creatures are important both to the environment and to the development of a full understanding of these complex systems.

Advantages of Closed Versus Open Systems

Invertebrate circulatory systems occur in two plans, closed or open, and both styles of circulation have benefits for their users. Although open circulatory systems are usually thought to be sluggish and inefficient, they are not necessarily so. Active animals such as crustaceans and insects have open circulatory systems and metabolic rates (oxygen and nutrient demands) that equal those of the most active invertebrates, squid and octopods, which have closed circulatory systems.

Nemertean worms (Rhynchocoela) are a small group of inconspicuous and inconsequential worms that have an interesting circulatory system. These worms may reach thirty meters in length (although they are only a few millimeters wide), but they have a simple blood system. There may be two or three blood vessels, with connections between them, running the length of the body. The vessels have a layer of muscle in the walls. Contraction of these muscles and the main body muscles move blood—in any direction—along the vessels.

Annelids (wormlike animals) also have a closed circulatory system. The major blood vessel has pulsatile regions, often called hearts, which drive the blood forward. The pattern of blood vessels, including capillaries, is repeated in each segment of the animal, although most segments do not have "hearts." Accessory hearts occur in different segments, and the overall pattern of circulation varies greatly among species (and even within a single individual's many segments).

Arthropods and most mollusks have open circulatory systems; these invertebrates have a well-developed central heart. The heart pumps blood through an extensive arterial network, which may end in capillaries. The blood eventually leaves the blood vessels and enters lacunae. Diffusion of materials takes place in the capillaries or in the lacunae. Sinuses collect the blood for return to the heart. In these organisms, the blood follows an ill-defined path. Contractions of the body musculature affect the speed and volume of blood flow in any region.

The crustacean arthropods are a group having inactive members, which lack a heart and blood vessels entirely, and active members, which have a high level of circulatory system organization. The inactive members pump their body fluid through sinuses and lacunae using the pressure developed by muscle contraction. Decapod crustaceans, the familiar crabs, have a heart whose contraction drives blood into well-defined arteries; the return of blood to the heart from the veins occurs because of the elastic recoil of the ligaments suspending the heart in the pericardial cavity. Part of the beauty of this pattern is that only veins from the gills enter the pericardial cavity. Therefore, only oxygenated blood enters the heart and is pumped into the body. Thus, although there may be body spaces in which flow is indeterminate, the important blood flows are well controlled and can meet the needs of complex and active organisms.

—Judith O. Rebach

See also: Anatomy; Arthropods; Chordates, lower; Circulatory systems of vertebrates; Digestion; Endocrine systems of invertebrates; Endocrine systems of vertebrates; Gas exchange; Heart; Invertebrates; Kidneys and other excretory structures; Lungs, gills, and tracheas; Muscles in invertebrates; Muscles in vertebrates; Nervous systems of vertebrates; Physiology; Reproductive system of female mammals; Reproductive system of male mammals; Respiration and low oxygen; Respiration in birds; Respiratory system; Water balance in vertebrates.

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CIRCULATORY SYSTEMS OF VERTEBRATES

Type of animal science: Physiology
Fields of study: Anatomy, histology, zoology

Vertebrates' circulatory systems consist of a closed system of blood vessels with a centrally placed heart, which receives oxygen-poor blood from the body and pumps it to the organs of respiration, where it is oxygenated and returned to the body's tissues. It is here that the oxygen and nutrients are unloaded and carbon dioxide and excretory products are picked up.

Principal Terms

AORTA: the major arterial trunk, into which the left ventricle of the heart pumps its blood for transport to the body

ARTERY: a blood channel with thick muscular walls which transports blood from the heart to various parts of the body

ATRIA: the two chambers of the heart, which receive venous blood from the body (via the right atrium) or oxygenated blood from the lungs (left atrium)

CAPILLARIES: the very fine vessels in various tissues, which connect arterioles with venules; it is here that the exchange between blood and the extracellular fluid takes place

CARDIAC OUTPUT: the amount of blood ejected by the left ventricle into the aorta per minute

DIASTOLE: relaxation (filling with blood) of the heart chambers

PACEMAKER: a specialized group of cardiac muscle cells in the right atrium which initiates the heartbeat; also called the sinoatrial node

SYSTOLE: contraction (emptying of blood) of the heart chambers

VALVES: specialized, thickened groups of muscle cells in the heart chambers, major arterial trunks, arterioles, and veins which prevent backflow of blood

Cells, the units of the animal body, need a constant supply of blood. Blood effects the transport of important materials needed for metabolic, synthetic, and degradative activities, supplying energy and materials necessary for growth, repair of worn-out components of cells, reproductive activity, and other functions of the body. Among the many products that blood transports through a system of closed channels are oxygen, nutrients, metabolic wastes, heat, and hormones. The circulatory system links all tissues with one another and with the external environment to and from which many of these materials are transported.

Basically, the circulatory system of vertebrates consists of two parallel systems of blood vessels: One, the arterial system, actively transports blood and its constituents from a central pumping station, the heart; the other, the venous system, more or less passively brings the blood back to the heart. The two systems branch again and again until they ramify all tissues. In the extracellular space of tissues, the finest branches of each system, called arterioles and venules, are connected by means of a network of fine capillaries that allow the movement of blood in one direction, from arterial into the venous system, in which the valves prevent any backflow of blood. A head of pressure, generated in the heart, pumps the blood in this direction, facilitating the transport of substances as well as their movement and filtration out of the capillary membranes and into the extracellular fluid.

Circulatory Systems of Fish, Amphibians, and Reptiles

The simplest level of organization of the circulatory system of vertebrates is seen in fishes. The heart in fishes consists of two chambers, an atrium (auricle) and a ventricle. The oxygen-poor, carbon-dioxide-rich blood returning from the body via a system of veins is first received by an enlarged vein, the sinus venosus, prior to entering the atrium. The atrium empties its blood into the thick-walled, muscular ventricle, which then pumps it into an enlarged artery, the conus arteriosus. The blood then passes through a major arterial trunk, the ventral aorta, going directly to the gills. The arteries in gills branch profusely and are connected via capillaries with other arteries. In the capillary bed, the blood becomes oxygenated and provides nutrients to the tissue. The oxygenated blood then flows to the head and the rest of the body, and from there returns to the heart through the venous system.

In preparation for their journey to land, ancient aquatic vertebrates had to evolve lungs for aerial breathing and had to evolve a complementary circulatory system. As demands for oxygen for a terrestrial existence increased, greater blood pressure and a new way of oxygenating blood were in order. The atrium became divided into two, the right one receiving the deoxygenated blood returning from the body and the left one receiving the oxygenated blood from the lungs (which replaced gills). The deoxygenated blood, entering the right part of the single ventricle, is pumped into the pulmonary artery, all the way to the lungs. The left part of the ventricle, receiving oxygenated blood from the left atrium, pumps it into the body. This three-chambered heart is present in amphibians and most reptiles. The oxygenated and deoxygenated bloods mix partially in the ventricle. In some amphibians, flaps and partial valves tend to prevent such mixing. Reptiles have a partition between the right and left parts of the ventricle, which is complete in alligators, crocodiles, and turtles.

Circulatory Systems of Birds and Mammals

Later reptiles, birds, and mammals developed four-chambered hearts. This complete division of the heart into two separate right and left pumps enables birds and mammals to achieve high speeds. One pumping circuit, the pulmonary, receives blood from the body and pumps it to the lungs; the other pumping circuit, the systemic, receives oxygen-rich blood from the lungs and pumps it into the systemic circulation. Valves within the heart prevent the blood from flowing through it in the opposite direction.

The contractile tissue of the heart consists of muscle cells that receive sympathetic and parasympathetic nerve impulses. The vertebrate heart is myogenic; that is, all of its muscle cells and fibers possess an inherent capacity to contract (electrically depolarize) rhythmically; however, all these fibers are under the control of a group of specialized heart muscle cells which have a lower threshold for depolarization than other heart muscle cells: the pacemaker. In fish, amphibians, and reptiles, the pacemaker is located in the wall of the sinus venosus (the first heart chamber before the atrium). In higher vertebrates, which lack a sinus venosus, the pacemaker is found in the wall of the atrium and is called the sinoatrial node. The wave of electrical depolarization initiated here is conducted through the atrioventricular node via a special group of fibers called the Bundle of His, which branch out into the ventricular muscle. The depolarization enters and traverses the atrioventricular node only relatively slowly but spreads down the atrioventricular bundle and its branches much more rapidly than it could travel through ordinary ventricular muscle. This regulates the sequence of contraction of the heart chambers: The atria contract first and the ventricles later, each group of muscles contracting approximately in unison.

Since the pulmonary (right) circuit is much shorter than the systemic circuit, it contains less blood volume and offers less frictional resistance to blood flow; also, the right ventricle has muscular walls that are less thick than those of the left ventricle, which has to pump large volumes of blood to the entire body via the systemic circuit. After the two ventricles are completely filled (a condition referred to as diastole), they contract simultaneously (called systole). During systole, the maximum arterial pressure is generated; during diastole (just before systole), arterial pressure decreases to a minimum. The pulmonary side of the heart contains the funnel-shaped valve between the atrium and the ventricle known as the atrioventricular valve, the right one having three flaps, or cusps (and hence named the tricuspid valve), and the left one (the bicuspid or mitral valve) having two. The free edges of these cusps hang down into the ventricular cavities and are anchored by tendonlike cords of connective tissue called chordae tendinae, each of which is attached to the ventricular wall by a lump called a papillary muscle. The pulmonary artery and the aorta originate at the base of the right and left ventricles, respectively, each having a semilunar valve at its origin. Each of these valves opens in the direction of the blood flow and prevents the backflow of blood. The ventricular contraction and the resulting turbulence in the blood produce the long, low-pitched "lub" sound that can be detected with a stethoscope. The sudden closure of the semilunar valves is similarly perceived to emit a relatively short, high-pitched "dup" sound.

Blood Volume and Blood Vessels

The volume of blood that is pumped by the heart each minute is called the minute-volume, whereby the heart beats (contractions) per minute (cardiac stroke rate) eject a typical quantity of blood per beat. This rate is altered by the body's activity and by the volume of blood returning to the heart from the veins each minute. If the venous blood volume is adequate, then increase in stroke rate can increase minute-volume. The increased stroke rate, however, involves a decrease in the ventricular filling time, and as a result, the ventricles do not fill completely. Thus, the stroke volume is decreased; at rapid heart rates, even the minute-volume may be decreased, so that it offsets the stroke rate. During systole, the ventricles do not empty completely. A small residual volume of blood remains in them. An increased venous return may cause more complete filling and emptying of the ventricles, thus increasing the cardiac output without changing the stroke rate.

The vessels at various points in the circulatory path differ anatomically and functionally. The great arteries have thick walls heavily lined with smooth muscle and contractile tissue to enable them to transport blood under pressure from the heart to peripheral tissues. The arteries become smaller and thinner-walled as they branch out toward the periphery. The systemic arteries deliver blood to the microcirculatory beds of the tissues and organs. These "capillary beds" consist of microscopic arterioles, capillaries, and venules. The contraction (vasoconstriction) and relaxation (vasodilation) of the smooth muscles in the terminal branches of the arteries play an important role in regulating blood flow in the capillary bed. Control of the arteriole muscles is mediated by sympathetic neurotransmitters, hormones, and local effects. From the arterioles, the blood enters the capillaries, minute vessels whose walls consist of a single layer of cells, facilitating transfer of oxygen and nutrients to the tissues and the loading of metabolic waste and carbon dioxide, all via the extracellular fluid. Their density depends on the need of the particular tissue for nutrients and oxygen. The capillaries drain into small, thin-walled but muscular vessels called venules, whence the blood begins its return to the heart through the veins. The veins have elastic walls but are without muscles. The venous vasculature serves as a reservoir, storing about 60 percent of the blood.

Studying Vertebrate Circulation

Circulatory systems of vertebrates have been studied since ancient times through dissection and observation of animal and human cadavers: The heart can be cut open to examine its chambers and their structures, and the body wall can be cut open from the ventral side to expose the circulatory organs. Preserved, dissected animals, including fish, amphibians, reptiles, and mammals, are available from suppliers for students of anatomy who wish to conduct their own dissections. The venous systems of these animals are dyed blue and the arterial systems are dyed red. Plastic models of the circulatory system can be purchased for classroom use.

Scientists are also interested in microcirculation, or circulation at the capillary level. One can fasten a live frog on a frog board and observe the capillaries in the frog's foot web under a microscope. The movement of the red blood cells into the capillary is observed; it is slow and intermittent. The blood flow is regulated by the central nervous system (the vasomotor center in the medulla), as well as by local conditions (such as levels of carbon dioxide, acidity, histamine, temperature, and inflammation). One can then immerse the foot in hot or cold water and observe the resulting change in blood flow. Histamine can be applied to cause vasodilation, which can be controlled by epinephrine. Drops of dilute hydrochloric acid can be applied to the foot to cause vasodilation and inflammation. Thus, it is clear from the foregoing discussion that the heart and circulatory system are of vital importance to the health of an animal.

—M. A. Q. Khan

See also: Anatomy; Arthropods; Chordates, lower; Circulatory systems of invertebrates; Digestion; Endocrine systems of invertebrates; Endocrine systems of vertebrates; Gas exchange; Heart; Invertebrates; Kidneys and other excretory structures; Lungs, gills, and tracheas; Muscles in invertebrates; Muscles in vertebrates; Nervous systems of vertebrates; Physiology; Reproductive system of female mammals; Reproductive system of male mammals; Respiration and low oxygen; Respiration in birds; Respiratory system; Water balance in vertebrates.

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CLAMS AND OYSTERS

Types of animal science: Anatomy, classification, ecology
Fields of study: Anatomy, ecology, marine biology, zoology

The category of clam is confusing, because there are some organisms found in freshwater or marine environments that are termed clams and some that are termed mussels. In sea water, fourteen marine organisms called clams are commercially valuable. Chief among these are the Atlantic surf clam and the ocean quahog. Scientists recognize twelve living genera of oysters but, as more studies are made by classification experts, the actual number may be slightly more or slightly fewer. In the United States, four species are commercially important, with the eastern oyster, Crassostrea virginica, *leading the list.*

Principal Terms

ESTUARY: a bay where seawater is diluted by freshwater from a river or land runoff

NACRE: shiny, pearly lining of some seashells; mother of pearl

PLANKTON: floating or weakly swimming plants and animals, usually very small in size

SALINITY: a measure of the quantity of dissolved salts in seawater

SESSILE: a type of existence in which organisms are permanently attached and incapable of moving

TIDE: periodic rise and fall of sea level influenced by gravitational attraction of the Sun, Moon, and Earth

Clams and oysters have long been of value to humans as food, while their shells have been valued as ornamentation. Paleolithic shell middens, some twenty-five feet high and seventy feet in base diameter, consist almost entirely of the discarded shells of clams and oysters. Oysters were especially prized because they lay on the surface of the estuary bottom and were easily gathered. Clams, buried a few inches deep, required some effort to gather. To prepare the shellfish for food, they were often simply placed on a fire and roasted in the shell. The fleshy contents were removed, eaten as they were, or cooked in a stew with some vegetables.

Physical Characteristics of Clams and Oysters

There are more than fifteen thousand different species of clams worldwide. They range in size from the *Condylocardia*, about 0.004 inches long, to the giant clam (*Tridacna gigas*) of the southwest Pacific Ocean, which grows up to nearly five feet long and weighs about 550 pounds.

Classified as bivalves, the animals have two shells that protect the soft body parts. In clams, two syphons, one incurrent and one excurrent, draw in and discharge seawater. The water supplies the shellfish with oxygen as well as plankton and other organic matter for food. A muscular projection (the foot) enables the clam to burrow into the sandy bottom. The valves are held together by two adductor muscles that slowly contract and relax to pump water into the shell. When the shellfish senses danger, the adductor muscles contract, closing the valves tightly and effectively sealing the soft body parts from a potential predator.

Oysters vary in shape depending on the type of bottom on which they lie. The shells usually are elongated with a rough surface. They do not have siphons. Instead, seawater, containing food organisms, is drawn into the body by a pumping action of the valves. Oysters do not have a foot and are sessile.

Clam Facts

Classification:
Kingdom: Animalia
Phylum: Mollusca
Class: Bivalva, with ten orders, fifty-seven families
Geographical location: Worldwide
Habitat: The bottom of all marine waters, from coastal subtidal to great depths of the sea
Gestational period: Larval stage varies according to species but generally lasts around one month
Life span: For the edible clam (quahog), harvest occurs in three to five years; some researchers estimate a life span of up to three hundred years for this species, if it is not eaten
Special anatomy: Shape of the shell varies only slightly and is generally roundish; lips of the *Tridacna* shell are wavy; some species have a powerful tongue or foot that enables the clam to dig quickly into the sandy bottom to escape predators

The Life Cycle of Clams and Oysters

In clams and oysters, the sexes are separate and spawning is triggered by favorable water temperature. The eggs and sperm, several hundred thousand to several million each, are broadcast into the water through the excurrent siphon. Of the millions of eggs, only a very few reach adulthood; many fail to be fertilized, some are eaten by small fishes and other predators, some succumb to molds and bacteria, and some adults are eaten by eels, sea stars, and whelks. Each year, more than 112 million pounds of clams and nearly 26 million pounds of oysters are taken for human food.

Shellfish that grow in polluted waters may ingest disease organisms which accumulate in their tissues. These can cause disease in humans. Some toxic plankton may cause illnesses, such as paralytic shellfish poisoning in humans who eat the clams or oysters uncooked (“on the half-shell”). Commercially canned shellfish are cooked under pressure and are safe to eat. The incidence of human illness from eating toxic clams is very low. One species of clam, the teredo, or shipworm, burrows into wood and leaves it honeycombed.

Pearls

Most clams and oysters produce pearls but not all are of gem quality. The pearl is made of the same material as the lining of the shell. It is deposited around some irritant such as a grain of sand. The giant clam produces pearls as large as golf balls.

—Albert C. Jensen

See also: Invertebrates; Jellyfish; Marine animals; Marine biology; Mollusks; Shells; Tidepools and beaches.

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CLAWS, NAILS, AND HOOVES

Type of animal science: Anatomy
Fields of study: Anatomy, marine biology, ornithology, zoology

Claws, nails, and hooves are widespread among animals, including vertebrate herbivores and predators, as well as invertebrates such as crabs and lobsters. The functions of these growths include defense, obtaining food, and safe locomotion.

Principal Terms

CHITIN: a transparent, horny substance of invertebrate exoskeletons

CRUSTACEANS: lobsters, shrimps, crabs, and barnacles

EPIDERMIS: the outer, protective layer of the skins of vertebrates

KERATIN: a tough fibrous substance found in hair, claws, nails, and hooves

MATRIX: the skin beneath a nail, involved in its growth

UNGULATE: a hoofed mammal

VASCULAR PAPILLA: a protuberance having a blood supply

Claws, nails, and hooves are very often special growths of the outer skin (epidermis) of warm-blooded, vertebrate animals. Nails are considered to be claws whenever they are thicker, longer, harder, and sharper than those of humans. Nails and claws contain large amounts of keratin, the hard substance present in the skin and nails of human fingers and toes. The skin below a nail or claw, from which it grows, is called the matrix. If a nail, claw, or hoof part is torn off, it grows again, as long as the matrix has not been overly damaged. Nails and claws occur on the digits of fore limbs and hind limbs of vertebrates.

Nails and claws are made of dead skin cells, very rich in the fibrous substance keratin. Each nail or claw consists of a root, concealed within a fold of skin at its base; a body, the exposed part attached to the skin surface; and an anterior edge overlapping the end of the digit to which it is attached. In clawed animals such as badgers, moles, rodents, wolves, and cats this edge can become quite long. The matrix, the skin below the root and body of a nail or claw, is thick and covered with highly vascular papillae. The matrix color is sometimes seen through transparent horny tissue, in humans and in some other species with relatively thin nail bodies or claws. A nail or claw grows forward by a combination of continual growth of new cells both at the root and under its body.

The body of the nail or claw in the predatory and burrowing animals is much thicker than in humans. Unlike human nails, the claws of burrowing animals do not have to be trimmed; they are worn down by use. The claws of cats, from house cats to lions and tigers are retractable. This allows these animals to walk easily without wearing their claws down and to unsheathe them for the serious business of capturing and killing prey. Predatory animals, especially cats, that have retractable claws must hone them down from time to time. Cats use scratching posts—whether fallen tree limbs found in the wild or specially made carpet-covered posts provided by hopeful pet owners—for this purpose, as well as to sharpen the claws.

Ungulate Hooves

A hoof is a thick, hard growth at the front of a foot of a horse or other mammal in the order Ungulata (the hoofed mammals). The ungulates include elephants, pigs, horses, and many horned animals, such as deer and cattle. A hoof, really a "hoof-nail," is also made of keratin and it arises from the outer skin layer, or epidermis. A hoof differs physically from a nail or claw in that it is blunt and encases a toe or foot. Hooves are thought to have developed from animal toes, and ungulates are divided into those with even and odd numbers of toes. For example, a horse hoof developed from one toe. It almost completely circles the bottom of the foot. Zebras and donkeys are also animals whose hooves are single toes, not divided (or cleft). Even-toed ungulates have two or four toes. Usually, the two middle toes are developed into a cleft (divided) hoof. This vertebrate group includes deer, antelope, sheep, goats, cattle, pigs, and hippopotamuses. Hooves adhere to the earth well and give animals that have them a firm footing for pulling, running, walking on slippery or icy ground, and climbing mountains.

Lizard and Bird Claws

Lizards, reptiles in the order Squamata, which also includes snakes and crocodiles, are the largest extant group of reptiles, with about three thousand species. All have dry scaly skin, clawed feet, and external ear openings. In many cases, lizard claws are used for traction on slick surfaces, or in climbing trees. They are also used by large carnivorous and omnivorous species to pick apart or tear apart food.

Most land birds have clawed feet, which help them to perch in trees. The claws are thought to have derived partly from the evolution of birds from ancient lizards. The most extensive claws seen in the birds are the talons of birds of prey (the raptors). Raptors include the night-hunting owls and the day-hunting hawks, eagles, falcons, and vultures. All are meat eaters, although the meat devoured by the small species is insects. All of the raptors have powerful bills, and all but vultures

Hooves are adaptations of the nails on two or three of an animal's toes; they help protect the foot on rough or rocky terrain. (PhotoDisc)

Ungulates: The Class of Hoofed Animals

Ungulates, the hoofed mammals, belong to the subphylum Vertebrata. Their name comes from *ungula*, Latin for "hoof." Ungulates with an odd number of toes belong to the order Perissodactyla, including horses (one-toed) and rhinoceroses (three-toed). Even-toed ungulates belong to the order Artiodactyla, including pigs (four-toed) and camels, giraffes, antelope, deer, cattle, sheep, and goats (all two-toed).

The other ungulate orders contain elephants and hyraxes. Ungulates vary in size extremes, from the seven-ton male African elephant to rabbit-sized antelope. Ungulates are herbivores and the only mammals that possess horns or antlers. In every case, the toes of an ungulate hoof are the correct size and right number to make the animal sure-footed, whether on mountain trails, in the desert, or in icy and snowy conditions. Ungulates are widely dispersed around the world, occurring on all continents except Australia. They can live for up to twenty-five years.

have grasping toes tipped with large, curved, sharp talons. It is believed that the weak talons of vultures are part of the reason why they eat carrion, not live prey. That is, they cannot strike live prey like the other raptors or carry it off in strong claws.

Invertebrate Claws

Among invertebrates, insects, scorpions, and crustaceans are examples of organisms that possess claws. Examples are praying mantises and beetles, among the insects; scorpions, among the arthropods; and lobsters and crabs, among the crustaceans. In all cases, the claws are restricted to the first two legs of these invertebrates. Also, unlike those of vertebrates, the claws are not keratin-containing epidermis outgrowths. They are portions of the chitinous invertebrate exoskeletons, and therefore part of their shells.

Crustacean claws are huge, compared to animal claws. Most often, both claws are of somewhat similar size and used to capture prey. However, some crustaceans, such as hermit and fiddler crabs, have claws where one is much larger than the other. In those cases, the larger of the claws is usually used in protection and/or mating.

Lobsters have two huge, body-length claws used to grasp prey, and to dig burrows in which they live. In "true lobster" species, the claws are especially huge. One claw is heavier than the other and has blunt teeth to crush prey. The other is somewhat smaller and has sharp teeth to tear up prey. Not all lobsters have the heavy claw on the same side. They are "right clawed" or "left clawed." During the day, a lobster stays in its burrow awaiting prey. At night it comes out to seek food, catching it and tearing it up into eating-sized chunks with its claws. Lobsters grow by shedding their shells (molting). When they do this, their claws are soft. They cannot use them well for hunting until the new shells harden. At those times, they mostly eat carrion.

Crabs, related to lobsters, are also clawed decapods. Like other cephalopods, the crab body is sheathed in tough chitin. A crab has five pairs of walking legs, and two front legs which hold claws for feeding and defense. Male hermit and fiddler crabs have one claw that is huge compared to the other. The oversized claw in hermit crabs is used defensively, to close off the mollusk cell it uses as its abode to protect its soft, vulnerable body. Fiddler crabs also have one oversized huge claw; they use it in mating and combat.

Claws, nails and hooves are very important to animals. They are weapons used for protection and to secure food, appendages that impress potential mates, and locomotor appendages that assure safe, optimized movement around habitats. It is interesting that in organisms as far apart, evolutionarily, as lobsters and ungulates, claws and hooves are made of similar, tough insoluble materials, chitin and keratin, respectively.

—Sanford S. Singer

See also: Beaks and bills; Birds; Bone and cartilage; Crustaceans; Fur and hair; Horns and antlers; Mammals; Physiology; Predation; Skin; Teeth, fangs, and tusks; Ungulates.

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CLEAVAGE, GASTRULATION, AND NEURULATION

Type of animal science: Reproduction
Fields of study: Anatomy, cell biology, invertebrate biology, physiology, reproduction, zoology

A single-celled zygote goes through the processes of cleavage, gastrulation, and neurulation to become a many-celled embryo. By learning about normal development, scientists are finding ways to prevent abnormal development.

Principal Terms

ARCHENTERON: the primitive gut cavity formed by the invagination of the blastula; the cavity of the gastrula

BLASTULA: an early stage of an embryo which is shaped like a hollow ball in some animals and a small, flattened disc in others; contains a cavity called the blastocoel

CLEAVAGE: the process by which the fertilized egg undergoes a series of rapid cell divisions which result in the formation of a blastula

GASTRULATION: the transformation of a blastula into a three-layered embryo, the gastrula; initiated by invagination

GERM LAYERS: the embryonic layers of cells which develop in the gastrula: ectoderm, mesoderm, and endoderm

INVAGINATION: the turning of an external layer into the interior of the same structure; formation of archenteron

MORULA: a solid ball or mass of cells resulting from early cleavage divisions of the zygote

NEURULATION: the process by which the embryo develops a central nervous system

NOTOCHORD: a fibrous rod in an embryo which gives support; a structure that will later be surrounded by vertebrae

ZYGOTE: the fertilized egg; the first cell of a new organism

A fertilized egg divides into many smaller cells, which then undergo rearrangement and differentiation to form the embryo of a new individual. The division of the one-celled zygote into smaller and smaller cells is called cleavage. The cellular rearrangement is known as gastrulation, and the proliferation and movement of cells into position to form the beginnings of the central nervous system is termed neurulation. The significance of these events lies in the fact that a single cell with genetic information from two parents is transformed into a multicellular structure with three germ layers that will give rise to all the organs and systems of the body.

Cleavage

After fertilization, the resultant zygote undergoes many rapid cell divisions. The cleavage process results in smaller and smaller cells, called blastomeres. The cell divisions are by mitosis, which produces identical chromosomes in each new cell. When between sixteen and thirty-two cells have been formed, the structure is called a morula, from the Latin for “mulberry,” which it resembles.

The morula stage is short-lived because, as soon as it is formed, processes are initiated that bring it to the next stage, known as the blastula. A cavity begins to form in the center of the morula as water flows in and pushes out the cells. The new cavity is called the blastocoel and the embryonic stage the blastula. Cleavage continues until the blastula consists of hundreds of cells but is still no larger than the original zygote. The blastula is the terminal cleavage structure. The egg, much larger than an average cell, has been fertilized and subdivided into hundreds of normal-sized cells. The blastomeres all appear to be similar to one another, but studies have shown that the individual cells are already destined for the tissues they will become.

The principles of cleavage are the same in all vertebrate groups, but the mechanics differ according to the amount of yolk in the egg. Eggs with large amounts of yolk undergo only partial cleavage, because the yolk retards the cytoplasmic division. In birds, reptiles, and many fishes, the yolk is so dense that the cytoplasm and nucleus are crowded into a small cap or disk on one side of the cell. The cleavage divisions all occur in this small area, resulting in a flattened blastula atop the large inert yolk.

Eggs with but a moderate amount of yolk, such as amphibian eggs, are able to cleave completely. Because division proceeds more slowly through the part of the cell where yolk has accumulated, the cleavage is uneven. The cells are formed more slowly on the yolky side and are larger and fewer in number. The blastocoel is smaller and displaced to the side, with less yolk. The side with smaller blastomeres will develop into the embryo and is called the animal hemisphere. The side containing larger amounts of yolk is called the vegetal hemisphere and will provide nutrients for the embryo.

Eggs with very little yolk undergo total and equal cleavage divisions. The blastula has a large, centrally located blastocoel, and blastomeres are uniform in size. Starfish and the primitive chordate amphioxus undergo this kind of cleavage. They are often used to demonstrate the successive cleavage stages which are more easily seen in the absence of yolk. Though mammalian eggs do not have large amounts of yolk, their development is similar to that of birds. The outer layer of cells of the morula develop into a membrane, called the trophoblast, that surrounds the embryo. The embryo forms from cells in the inner region known as the inner cell mass. A large, fluid-filled blastocoel forms within the trophoblast, giving rise to the term "blastocyst" for the mammalian blastula. The inner cell mass develops atop the blastocoel as the bird embryo on the yolk.

Gastrulation

Gastrulation is the next process in embryonic development and consists of a series of cell migrations that result in cellular rearrangement. The final gastrula will have three embryonic germ layers destined to give rise to all body structures and systems.

The first step in gastrulation is an indenting or invagination in the blastula at a spot known as the dorsal lip. Cells begin to move over the lip and drop into the interior, forming the lining of a new cavity, the archenteron, or primitive gut. Continued inward movement of cells forms a middle layer between outer cells and inner ones which have dropped in through the opening, or blastopore. The three embryonic germ layers have now been formed, and they are called ectoderm, mesoderm, and endoderm.

In animals with little egg yolk, such as the starfish, gastrulation begins when a few cells lose their adhesiveness and drop into the blastocoel. That causes a dent or depression in that area. Cells move in and deepen the depression, forming the archenteron. As the archenteron expands, the inner blastocoel shrinks and is finally obliterated. This process may be visualized as punching in the side of a hollow rubber ball with one's finger. The hole the finger makes is the blastopore; the new cavity formed by the hand represents the archenteron; and the original space inside the ball represents the blastocoel. The indentation forms two cell layers, and a third one is formed as cells continue to move in and take position between the inner and outer layers.

The outer ectoderm is destined to become epidermis and nerve tissue. The inner endoderm will form digestive glands and the lining of the digestive and respiratory systems. The middle germ layer, the mesoderm, will give rise to bone, muscle, connective tissue, and the cardiovascular and urinary systems. Additional mesoderm forms a rodlike structure known as the notochord, which lies in the roof of the archenteron. The notochord is a distinctive characteristic of chordates and gives embryonic support. The mesoderm lateral to the notochord will segregate into paired masses known as somites, each with prospective skin, bone, and nerve segments.

Gastrulation in blastulas with moderate quantities of yolk, such as amphibians have, proceeds similarly, but the archenteron is displaced toward the animal hemisphere and is filled with yolk cells. The early stages are similar to those in starfish.

Gastrulation in birds and mammals is initiated in a manner different from that in starfish and amphibians, because of the discoidal configuration of the blastula. Both groups have incomplete cleavage with embryonic development on a disk-like area on one side of the egg. The upper cells of the disk separate from the lower ones, forming two layers, the epiblast and the hypoblast. After the two layers are formed, a thickening occurs in one quadrant of the blastula and soon becomes noticeable as a distinct streak, the primitive streak. The streak becomes grooved, and cells from either side begin to migrate to the groove and sink down through it. The cells then move into position between the epiblast and hypoblast. The three embryonic germ layers have been formed.

The primitive groove in the gastrula is considered homologous to the blastopore in the starfish and amphibians. After the germ layers have been established, cells continue to move in to the new cavity, the archenteron, and form a mesodermal notochord in the roof of the archenteron.

Neurulation

Neurulation is the final stage of early embryonic development. Studies have shown that the notochord induces the neurulation process to begin. Cells just above the notochord are induced to proliferate and thicken, forming a neural plate. After the neural plate is formed, a buckling occurs in it, forming a depression known as the neural groove. Modern microscope techniques have revealed microfilaments and microtubules lying beneath the surface of the plate. Contraction of the microfilaments and elongation of microtubules appear to cause cell buckling and folding of the plate. The neural groove deepens at its cephalic end, and folds on either side continue to grow higher until they actually touch each other, forming an enclosed tube, the neural tube. At the same time that the neural tube is forming, the head is growing forward and tissue is folding beneath it so it projects forward free from the surface. Brain differentiation begins with the enlargement of the anterior end of the neural tube. The undilated caudal portion will give rise to the spinal cord. The brain forms several constrictions, so that three bulges appear. These will become the three embryonic brain divisions: the forebrain, the midbrain, and the hindbrain.

Upon completion of the three brain divisions, the embryo undergoes forward flexion of the forebrain and a lateral torsion so that the embryo comes to life with its left side on the yolk. A final caudal flexion causes the embryo to take its typical C-shaped configuration.

Extraembryonic membranes form from tissue outside the embryo to provide oxygen, nutrients, and waste storage. In birds, an outer chorion and amnion fuse to form a membrane with a large blood supply which provides for the exchange of oxygen and carbon dioxide between the embryo and the atmosphere. The allantois is a membranous sac to contain waste secretions.

In mammals, the outer chorion becomes extensively vascularized on one side and interconnects with the uterus to form the placenta. Nutrient and waste exchange between mother and baby take place in the placenta. The amnion forms a fluid-filled sac that lies closely around the embryo and cushions it. The allantois is not needed for waste storage and is not well developed.

Embryology

Humans have always been intrigued by the processes of gestation and birth. Aristotle questioned whether the embryo unfolds from a preformed condition and then enlarges to adult proportions or progressively differentiates from simple to complex form. Not until the eighteenth century were actual observations made of a developing embryo. The chick egg was the first to be studied, because of its large size. Early studies were descriptive, as each stage of the embryo was observed and carefully described. It was found that development does proceed from simple form to forms increasingly complex.

In the late nineteenth century, great interest developed in evolutionary theory, and comparative embryology became the focal point of studies. Clues were sought for possible evolutionary relationships between organisms. The theory emerged that embryonic stages reflect the evolutionary past of an organism.

The twentieth century has seen the explosion of experimental embryology and multiplication of knowledge. Cleavage of the large fertilized egg was first observed in the eighteenth century, but not until the late twentieth century did the mechanics begin to be understood. With improved microscope techniques, a ring of microfilaments can be seen just below the egg cell surface. These protein filaments have contractile qualities, and it was thought perhaps they lined up around the equator to contract and squeeze the cell in two. To test this hypothesis, a drug which causes microfilament subunits to break down was added to the cell culture. It was found that cell division was inhibited, suggesting that microfilaments are involved in the division process. Removal of astral rays also hindered cleavage. Each new discovery answers some questions and raises more.

Embryologists have questioned how blastomeres all formed from the same cell could differentiate into many kinds of cells and tissues. Some of the earliest experiments in embryology involved separating the first two daughter cells to demonstrate that each could form two complete individuals. How and when cells differentiate continues to be a challenge to researchers. The substance in cells which predisposes them to differentiate between one another is still not understood.

It has been discovered that each part of the embryo surface is already divided into prospective organ areas by the blastula stage. Fate maps have been constructed by marking certain areas on the blastula with vital stains and observing the structures into which they develop.

Since the early days of experimental embryology, researchers have performed all kinds of operations on embryos, marking areas and observing their movement, transplanting cells from one area to another, exchanging cell nuclei and removing portions. These experiments have led to many discoveries and better understanding of the complicated developmental process. When one considers the multitude of complex events that must take place in the development of a new individual from a single cell, it might seem impossible that the entire developmental process could occur without a slip.

Malformation usually begins during early development. Deformities may arise from inherited mistakes in the genetic code or from the harmful influence of external factors such as radiation, poor nutrition, or infection. Studies of cell migration in the embryo have led to ideas for procedures to inhibit tumor cell migration. Knowledge of normal cell development is helping to find ways to prevent abnormal cell development.

—*Katherine H. Houp*

See also: Asexual reproduction; Birth; Brain; Cell types; Development: Evolutionary perspective; Embryology; Fertilization; Gametogenesis; Growth; Hormones and behavior; Hormones in mammals; Multicellularity; Mutations; Parthenogensis; Placental mammals; Pregnancy and prenatal development; Regeneration; Reproduction; Reproductive system of female mammals.

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CLINES, HYBRID ZONES, AND INTROGRESSION

Type of animal science: Evolution
Fields of study: Ecology, genetics, systematics (taxonomy), zoology

A cline is a genetic variation in the characteristics of populations of the same species that results from a variation in the geographical area that it occupies. Hybrid zones are areas where there are populations of a species composed of individuals with characteristics of one or more species that have interbred. Introgression is speciation that occurs when the genes of one species are incorporated into the gene pool of another as the result of successful hybridization.

Principal Terms

CLINE: a gradual, continuous variation from one population of a species to the next that is related to differences in geography

DEME: a local unit of the population of any one species

GENE: the unit of molecular information, a portion of a deoxyribonucleic acid (DNA) molecule that codes for some product, such as a protein, that governs inherited traits

GENE FLOW: the movement of genes from one part of a population to another part, or from one population to another, via gametes

GENE POOL: the sum total of all the genes of all the individuals in a population

HYBRID: the offspring of a mating between genetically differing individuals

INTROGRESSION: the assimilation of the genes of one species into the gene pool of another by successful hybridization

POPULATION: the members of a species that live in the same geographical area

SPECIES: a group of similar organisms whose members can reproduce with one another to produce fertile offspring

Gene flow among populations tends to increase the similarity of characters among all the demes (local populations) of a species. Natural selection has the opposite effect: It tends to make every deme uniquely specialized for its specific habitat. Clines are one possible result of these two opposing forces; a cline is a phenomenon in which a genetic variation occurs that is caused by a difference in geographical habitat. Each species is continuously adjusting its gene pool to ensure that the species survives in the face of an environment that is continuously changing.

Comparing the characteristics of the demes of a single species usually will reveal that they are not identical. The greater the distance between the demes, the greater the differences between them will be. The grass frogs in Wisconsin differ from the grass frogs in Texas more than they differ from those in Michigan. On the average, the song sparrows of Alaska are heavier and have darker coloration than those in California. These phenomena, in which a single character shows a gradient of change across a geographical area, are called clines.

North-South Clines

Many birds and mammals exhibit north-south clines in average body size and weight, being larger and heavier in the colder climate farther north and smaller and lighter in warmer climates to the south. In the same way, many mammalian species show north-south clines in the sizes of body extremities such as tails and ears, these parts being smaller in northern demes and larger in southern demes. Increase in average body size with increasing cold is such a common observation that it has been codified as Bergmann's rule. The tendency toward shorter and smaller extremities in colder climates and longer and larger ones in warmer climates is known as Allen's rule. The trend toward lighter colors in southern climates and darker shades in northern climates has been designated Gloger's rule. The zebra, for example, shows a cline in the amount of striping on the legs. The northernmost races are fully leg-striped, and the striping diminishes toward the southern latitudes of Africa; this appears to be an example of Gloger's rule. Another example of a cline, which does not fit any of the biogeographical rules mentioned, is the number of eggs laid per reproductive effort (the clutch size) by the European robin: This number is larger in northern Europe than it is for the same species in northern Africa. Other birds, such as the crossbill and raven, which have wide distribution in the Holarctic realm, show a clutch-size cline that reveals a larger clutch size in lower latitudes. The manifestation of such clines in clutch size is a consequence of the interplay of two different reproductive strategies that may give a species a competitive advantage in a given environment. The stability of the environment is what elicits the appropriate strategy.

In unstable environments, such as those in the temperate zone, where there may occur sudden variations in weather and extremes between seasons, a species needs to reproduce rapidly and build its numbers quickly to take advantage of the favorable warm seasons to ensure survival of the species during the harsh, unfavorable conditions of winter. This strategy is known as r strategy (r stands for the rate of increase). In the tropics, the climate is more equable throughout the year. The environment, however, can only support a limited number of individuals throughout the year. This number is called the carrying capacity. When carrying capacity is reached, competition for resources increases, and the reproductive effort is reduced to maintain the population at the carrying capacity. This is called K strategy, with K standing for carrying capacity.

In birds, clutch size tends to be inversely proportional to the climatic stability of the habitat: In temperate climates, more energy is directed to increase the reproductive rate. In the tropics, the carrying capacity is more important, resulting in a reduced reproductive rate. In the apparent contradiction of the crossbills and ravens, it may be the harshness of the habitat at higher latitudes that limits the resources available for successfully fledging a larger number of young.

Grass Frog Clines

The cline exhibited by the common grass frog is one of the best known of all the examples of this phenomenon. It has the greatest range, occupies the widest array of habitats, and possesses the greatest amount of morphological variability of any frog species. This variability and adaptation are not haphazard. The species includes a number of temperature-adapted demes, varying from north to south. These adaptations involve the departmental processes from egg to larva. The northernmost demes have larger eggs that develop faster at lower temperatures than those of the southernmost demes. These physiological differences are so marked that matings between individuals from the extreme ends of the cline result in abnormal larvae or offspring that are inviable (cannot survive) even at a temperature that is average for the cline region. Leopard frogs from Vermont can interbreed readily with ones from New Jersey. Those in New Jersey can hybridize readily with those in the Carolinas, and those in turn with those in Georgia. Yet hybrids of Vermont demes and Florida demes are usually abnormal and inviable. Thus, it appears that the Vermont gene pool has been selected for a rate of development that corresponds to a lower environmental temperature. The gene pool of the Florida race has a rate of development that is slower at a higher average temperature. The mixture of the genetic makeup of the northern and southern races is so discordant that it fails to regulate characteristic rates of development at any sublethal temperature, so the resulting embryo dies before it becomes a tadpole.

There are two primary reasons why characters within a species may show clinal variation. First, if gene flow occurs between nearby demes of a population, the gene pools of demes that are close to one another will share more alleles than the gene pools of populations that are far apart. Second, environmental factors, such as annual climate, vary along gradients that can be defined longitudinally, latitudinally, or altitudinally. Because these environmental components act as selective pressures, the phenotypic characters that are best adapted to such pressures will also vary in a gradient.

Hybridization

Hybridization is the process whereby individuals of different species produce offspring. A hybrid zone is an area occupied by interbreeding species. Partial species can and do develop on the way to becoming new species as products of hybridization. Natural hybridization and gene flow can take place between biological species no matter how sterile most of the hybrid offspring may be. As long as the mechanisms that prevent free exchange of genes between populations can be penetrated, there is the potential for a new species to develop. Because the parental species has a tendency to be replaced by the hybrid types if natural selection favors them, hybridization can be a threat to the integrity of the parental species as a distinct entity.

Hybridization between different species leads to various and unpredictable results. Any time that hybridization occurs, the isolation mechanisms of populations are overcome, forming bridging populations. Such connecting demes of hybrid origin fall into one of two general categories: hybrid swarms or introgressive demes. The formation of these types of demes reverses the process of speciation and changes the formerly distinct species into a complex mixture of highly variable individuals that are the products of the segregation and independent assortment of traits. This is the primary advantage of sexual reproduction: to produce variation in the population that is acted upon by natural selection over time. It cannot be overemphasized that hybrid swarms and introgressive demes are highly variable.

The environmental conditions that contour animal communities have endured for a very long time. In long-lived communities, every available niche has been filled by well-adapted species. When populations with new adaptive characteristics occur, there is no niche for them to occupy, so they usually die out. In contrast, when such communities are disturbed, the parity among their component species is upset, which gives new variants an opportunity to become established.

Hybrid swarms can be observed in nature by the careful investigator. The hybrid swarm forms in a disturbed habitat, where hybrid individuals backcross with the parental types to form a third population, which result from the migration of the genes of one population into the other. Such a population is designated an introgressive population. The progeny of such populations resembles the parent species, but the variations are in the direction of one parental species or the other. If introgression is extensive enough, it may eradicate the morphological and ecological distinctions of the parental types. The parental types become rarer and rarer, until they are no longer the representatives of the species.

There appear to be three reasons that first-generation hybrids occurring naturally are more likely to form offspring by backcrossing to one of the parental species than by mating with each other. Primarily, the hybrids are always rarer than the parents. Second, the parental individuals are so much more fertile than the hybrids that many more parental gametes are available than hybrid ones. Finally, backcross progeny, since they contain primarily parentally derived genes, are more likely to be well adapted to the habitat in which they originated than are the purely hybrid individuals.

Introgression

Thus, the most likely result of hybridization is backcrossing to one of the parental species. Genotypes containing the most parental genes usually have the selective advantage, and the fact that they contain a few chromosomal segments from another species gives them unique characteristics that may also be advantageous. This sequence of events—hybridization, backcrossing, and stabilization of backcross types—is known as introgression. Hybrid swarms are interesting phenomena, but they are unlikely to be of evolutionary significance except through introgression.

There are many examples of introgression among plants, but examples of introgression in animals are not common. Those that have been demonstrated are usually associated with the domestication of livestock. In the Himalayan region of Asia, there exists a relative of cattle, the yak, which is also domesticated. Many of the herds of cattle found along the western edge of the Himalayas, in central Asia, contain characteristics that clearly are derived from the gene pool of the yak. Many of these characteristics are manifested as adaptations to the harsh climatic conditions in this region.

In western Canada, there has been a modest introgression of the genes of the American bison into the gene pool of strains of range cattle. The bisonlike characters incorporated into beef cattle created a new breed called the beefalo, which exhibits such characteristics as greater body musculature, lower fat content of the flesh, and great efficiency in the utilization of range forage. A beefalo steer is ready for market in only eight months, while the same live weight is not obtained in the standard beef breed until eighteen months.

These examples serve to illustrate the concept that, as an evolutionary force, introgression is rather insignificant in natural biomes. It is almost always in the wake of human activity or the activities of their domesticated animals that the process of introgression can and does result in new combinations of gene pools from different species.

—Edward N. Nelson

See also: Adaptations and their mechanisms; Adaptive radiation; Biodiversity; Biogeography; Convergent and divergent evolution; Demographics; Ecological niches; Ecosystems; Evolution: Animal life; Evolution: Historical perspective; Extinction; Gene flow; Genetics; Isolating mechanisms in evolution; Mating; Migration; Mutations; Natural selection; Nonrandom mating, genetic drift, and mutation; Population analysis; Population genetics; Systematics; Wildlife management; Zoology.

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CLONING OF EXTINCT OR ENDANGERED SPECIES

Type of animal science: Scientific methods
Fields of study: Biochemistry, cell biology, conservation biology, developmental biology, embryology, genetics, reproduction science

Cloning involves the insertion of deoxyribonucleic acid (DNA) from a body cell into an egg cell from which the nucleus has been removed. This method may permit the reproduction of endangered or recently extinct species if the fertilized egg is then implanted into the uterus of a closely related, but nonendangered species. It provides a novel but controversial way of rescuing species headed for extinction.

Principal Terms

BIODIVERSITY: variety of plants, animals, and habitats, and the interactions among these species

BIOTECHNOLOGY: the use of the tools of recombinant DNA technology to study or modify biological systems

CLONING: the reproduction of an individual that is genetically identical to its parent

EXTINCTION: the dying off of all individuals of a species

GENE POOL: the collection of genes or genetic information in a population of individuals

NUCLEAR TRANSFER: the insertion of genetic material from a donor cell to a recipient cell; in reproductive technologies the recipient cell is an egg cell from which the nucleus has been removed

The threat of extinction to endangered animal species is of great concern to conservation biologists as well as to animal lovers everywhere. Extinction is the dying off of all members of a species. It occurs naturally as a process termed background extinction, part of evolution in response to global climatic changes and dynamic relationships within ecosystems that result in interspecies competition. Conservation biologists have noted that ever since the 1600's, the rate of animal species extinction has increased significantly, primarily due to the rapid growth of the human population and the resulting destruction of animal habitats. The global extinction rate is about twenty thousand species per year; moreover, conservation biologists have theorized that the planet is in the midst of the greatest period of animal extinction since the dinosaurs disappeared, sixty-five million years ago. Such wide-scale extinctions may have profound effects on ecosystem survival, as they culminate in the irretrievable loss of thousands of species of plants and animals, some of which have never even been identified. Some of the more recent extinctions of note include the great auk and the passenger pigeon, both of which disappeared in the nineteenth and early twentieth centuries. Other species, such as the California condor, are on the verge of extinction. Mammals are not exempt from this list; of particular concern are the 20 percent of the world's primates that may be lost to extinction in the next ten to twenty years. Due to recent advances in reproductive biotechnology, however, it has become apparent that the rise and decline of a species may no longer be determined solely by the forces of natural selection and the survival of the fittest, as proclaimed by the great evolutionary biologist Charles Darwin. Rather, the tools of recombinant DNA technology may afford humans a role in preventing the extinction of endangered species. On this rapidly evolving planet, where human civilization increasingly encroaches upon the domain of the natural world, the possibility of preserving endangered wildlife species by biotechnology approaches may be the last remaining hope for treasured animal species whose numbers had dwindled sharply by the end of the twentieth century.

Cloning Technology

The basic scientific procedure that has made this hope possible is a cloning technology termed nuclear transfer. This method involves the insertion of a body cell from an endangered animal into an egg cell obtained from a closely related species. First, the nucleus which contains the genetic material is removed from the egg cell, and then the body cell obtained from the endangered animal is inserted by a microinjection technique using a fine needle. An electric pulse then fuses the inserted body cell with the egg cell cytoplasm, the nucleus enters the egg cell cytoplasm, and cell division begins. Amazingly, the genetic material of a fully differentiated or mature body cell (such as a skin cell) becomes genetically reprogrammed once fused to the egg cell to generate all the cells that will ultimately make up the tissues and organ systems of the fetus. Because the donor body cell and egg cell originate from two different species, the procedure is termed interspecies nuclear transfer. This concept is critical to cloning endangered species, since often it is impossible to harvest egg cells from the threatened species and a related but thriving species must serve as the egg donor. Once the nuclear transfer has been accomplished, the embryonic cells are implanted into the uterus of a surrogate mother, also from a related species. The result is that an animal of one species participates in the reproduction of a cloned animal of a different species.

Image Not Available

Endangered Species on the Cloning List

The world's first successful cloning of an animal belonging to an endangered species by interspecies nuclear transfer was carried out by researchers at Advanced Cell Technology (ACT), in Worcester, Massachusetts, who cloned a baby gaur, an oxlike animal found in India, Indochina, and Southeast Asia. Using skin cells from the gaur as a source of genetic material, internuclear transfer by microinjection of an egg cell obtained from a cow and subsequent implantation into the uterus of a cow serving as a surrogate mother resulted in the birth of a cloned ox named Noah on January 8, 2001. Unfortunately, the cloned animal died just two days later from a common dysentery infection,

Cloning Extinct Animals

An intriguing question involves the cloning of animals that are extinct. In order to accomplish this feat, one must have access to preserved frozen animal cells as a source for the genetic material to be cloned. In 1999, a preserved frozen woolly mammoth was discovered in Siberia, giving rise to the hope that this great creature might one day live again. However, the animal's body had been subject to repeated cycles of freezing and thawing over many years, disrupting the structure of its genetic material so that it is unsuitable for interspecies nuclear transfer. Scientists at the Australian Museum have attempted to clone the Tasmanian tiger, which became extinct in the 1930's. The source of animal tissue in this case is a tiger that was preserved in alcohol in 1866; however, DNA analysis has shown that there was extensive damage to the genetic material of this specimen, making successful cloning unlikely. In Spain, the recently extinct bucardo, a mountain goat, has been the subject of cloning experiments. Scientists at the Agricultural Research Service in Zaragoza prepared frozen tissue from the last surviving animal of this species of mountain goat, which had been relegated to extinction due to loss of its natural habitat and poaching. In 1999, successful interspecies transfer of embryos of the bucardo using a domestic goat as a surrogate mother raised hopes that the bucardo might be cloned using this same surrogate species.

apparently unrelated to the cloning procedure or gestation in a different species. In November, 1999, the first successful transplantation of a frozen embryo from an African wildcat, an endangered animal species, into a surrogate mother of another species, the common housecat, was carried out by Betsy Dresser and colleagues of the Audubon Center for Research of Endangered Species (ACRES). Other interspecies embryo transfer successes include a mouflon sheep born to a domestic sheep, a red deer born to a white-tailed deer, and a bongo antelope born to a common African antelope called an eland.

Endangered species that could benefit from the new interspecies cloning technologies include the cheetah, which is close to extinction due to the loss of its natural habitat, and the panda, which has already been the subject of assisted reproductive technologies in captivity. In August, 1999, Hua Mei was born at the San Diego Zoo following successful artificial insemination. Research efforts on interspecies embryo transfer involving pandas have been largely focused on American black bears as egg donors and surrogate mothers. The first donor panda cells used in these experiments were frozen cells obtained from the late Hsing Hsing and Ling Ling.

Future Challenges

A broader question involves the potential role of cloning in maintaining species and genetic diversity. It has been argued that the selective cloning of individual members of a species will lead to a reduction in genetic diversity due to a streamlined gene pool. This may ultimately affect the survival and adaptability of a species. Moreover, cloning does not impact directly the conditions that led to the loss of species fitness, which are reflected in reproduction and survival rates. In many instances, species become endangered due to a loss of habitat; thus, survival of the species may require long-term existence in captivity. In certain cases, attempts have been made to return animals bred in captivity to their natural habitat; however, it is not clear that these efforts will be successful in general. The reproductive technologies and long-term effects of captivity may have serious consequences on the survival of the species once reintroduced to the wild. Some successes have been noted in this area; for example, the American peregrine falcon has been reintroduced into the wild in eastern North America, where it had become extinct.

Another problem associated with interspecies nuclear transfer and assisted reproductive technologies in general is their high cost and low success rate. It has been estimated that the success rate of same species nuclear transfer in cows is between 1 and 2 percent. The success rate for interspecies nuclear transfer is considerably less. For example, attempts by scientists at ACT at interspecies nuclear transfer involving the gaur required almost seven hundred cow eggs, about eighty of which developed as suitable donors for transplantation. About forty of these were implanted into cows, which resulted in eight pregnancies and ultimately one live birth.

Despite these concerns, zoological parks around America have collected sperm and eggs from many types of animals in the form of "frozen zoos," which may serve as genetic repositories for producing animals of the future. In addition, the San Diego Zoo's Center for Reproduction of Endangered Species and ACRES have sponsored animal tissue banks which could be the future source of cloned animals to safeguard species from extinction.

The death of a species by extinction engenders a sense of profound loss as it brings to a close a chapter of evolutionary and biological history. It may also disrupt the delicate balance of life, as species interdependence is a fundamental component of ecological systems. As efforts to save individual species from permanent extinction by the cloning of selected members are applauded, it is important to reflect upon the conditions and circumstances which have contributed to their loss.

—Sarah Crawford Martinelli

See also: Biodiversity; Cleavage, gastrulation, and neurulation; Determination and differentiation; Ecological niches; Embryology; Endangered species; Extinction; Fertilization; Gametogenesis; Genetics; Parthenogenesis; Population genetics; Pregnancy and prenatal development; Reproduction; Reproductive strategies; Zoos.

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COCKROACHES

Type of animal science: Classification
Field of study: Entomology

There are more than 3,700 species of cockroaches, also called roaches. They are among the oldest insects, having a fossil record that dates back about 340 million years.

Principal Terms

NOCTURNAL: active at night
VESTIGIAL: an organ that is no longer biologically useful

Cockroaches are one of the oldest and most primitive of insects. They flourished during the Carboniferous period of the earth's history, 350 to 320 million years ago, which has been nicknamed "The Age of Cockroaches" by paleontologists. The fossil evidence uncovered indicates that during this time, cockroaches made up about 40 percent of the world's insect population. Cockroaches from 340 million years ago looked much like roaches living today.

Cockroaches have a flattened, oval body, long, slender antennae, and a shiny black or brown exoskeleton. Most species also have wings that are held flat over the back. The exoskeleton, or shell, is made of chitin, which is about as thick as a human hair. The chitin covers the roach's entire body, even its eyes. Cockroaches range from about 0.5 to 2 inches in length, with the largest being found in the tropics. They have grasshopper-like mouth parts for chewing and feed on plants or animal matter, including dead insects and bedbugs or even cardboard, paper, books, glue, and other manufactured products. They are nocturnal insects and are rarely active or visible during the day. They live and hide in warm, damp, dark places, coming out at night to hunt for food.

The cockroach has three life stages: egg, nymph, and adult. Cockroach eggs are deposited in groups in a leathery case or capsule, the ootheca. There may be from thirty to forty-eight eggs in the capsules of some species, while others have only ten to twenty-eight. The newly hatched nymphs have no wings and shed their skins (molt) several times before becoming winged adults. Indoor roaches generally have several generations of young per year, but outdoor species may require a full year to develop from egg to adult.

Cockroach Classification

The German cockroach, *Blatella germanica*, also called the "water bug" in some places, is found throughout the world. It is commonly carried home in paper grocery bags and boxes (where it hides because it loves the taste of glue) and also likes to live around water pipes. Though it has only a 150-day life span, one adult female can produce as many as eight egg capsules, each filled with up to forty eggs. Thus, a female can produce more than 3,200 young in its lifetime. According to a bulletin from the U.S. Food and Drug Administration, one female could be the source of over ten million females in a single year, and over ten billion females in 1.5 years, assuming that all the babies survived and reproduced and food supplies were adequate.

The German roach is relatively small in size, about one-half inch long, compared to some of its Asian relatives. The Asiatic (or oriental) cockroach, *Blatta orientalis*, can be up to two inches in length and is considered one of the dirtiest household pests. It is oval in shape, with a shiny black exoskeleton. Males have short wings and can fly, unlike females, who have only vestigial wings. This species is found throughout the world, having been carried almost everywhere by ships, trucks, railroad cars, and airplanes.

The American cockroach, *Periplaneta americana*, is found in most warm climates throughout the world. It prefers to live indoors and is found in basements and furnace rooms. It has a life span of about 1.5 years and lays about sixteen eggs every forty-five days. It originally came from Central and South American rain forests. The American roach has a set of wings that enable it to fly long distances.

The American and German species are cannibals. Young nymphs eat their own kind if there is not enough food available. Mothers frequently eat their own egg capsules if food shortages develop. However, roaches can survive for more than a month without water or food. This feature has consequences for the food industry—for instance, roaches accidentally sealed in shipping crates can survive fairly comfortably even if shipped long distances with extremely limited resources.

Cockroaches are found in the desert as well as the forest. Desert roaches, *Arenivaga investigata*, burrow under the sand during the hottest part of the day, coming out to feed only at night. They can absorb water merely by sticking out their tongues. The brown-hooded wood cockroach, *Cryptocercus punctulatus*, lives in decaying logs in the forest along the Atlantic coast. Only three other species of this genus survive, one in China, one in Russia, and one in the western United States, because the forest habitat in which it thrives is disappearing. The common wood cockroach, *Parcolblatta pennsylvanica*, on the other hand, is found in abun-

Image Not Available

Cockroach Facts

Classification:
Kingdom: Animalia
Subkingdom: Eumetazoa
Phylum: Mandibulata
Subphylum: Arthropoda
Class: Insecta
Subclass: Exopterygota
Order: Dictyoptera
Suborder: Blatteria
Families: Blattidae, Blaberidae, Blattellidae, Polyphagidae, Cryptocercidae
Species: Over 3,700 species, about forty considered household pests

Geographical location: Every continent except Antarctica

Habitat: Land (forests, deserts, and grasslands)

Gestational period: Varies greatly, but typically forty to sixty days

Life span: Five months to 1.5 years, depending on species

Special anatomy: Oval body, brown or black; two pairs of wings in males; females usually wingless; eggs carried in an egg case (ootheca) dance under logs and stones in northern forests. This species eats wood, which it digests with the help of bacteria living in its stomach, and is not considered a household pest.

Cockroach Control

Closing spaces and cracks around pipes, doorframes, and baseboards can prevent cockroach infestations. Paper bags and cardboard boxes should be inspected for roaches when they are brought into the home. Store food in containers with tight fitting lids. Pet food should be served by placing the bowl in a second, shallow bowl filled with soapy water. Roaches cannot swim across this barrier. Leaking water attracts roaches, so plumbing leaks should be fixed quickly. Sink and bathtub drains without stoppers are also inviting homes for roaches. Garbage cans should have lids and be emptied frequently. Cool temperatures can also kill roaches; few survive temperatures below freezing.

—Leslie V. Tischauser

See also: Antennae; Arthropods; Exoskeletons; Insects.

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COEVOLUTION

Type of animal science: Evolution
Field of study: Ecology

Numerous stable and surprisingly complex relationships between various apparently unrelated organisms, such as plants and animals, have evolved over long periods of time. All these relationships, whether beneficial or harmful to one or more of the participants, represent adaptive interactions that can be used to understand ecological patterns and processes.

Principal Terms

ANTAGONISM: any type of interactive, interdependent relationship between two or more organisms that is destructive to one of the participants

COEVOLUTION: the interactive evolution of two or more species that results in a mutualistic or antagonistic relationship

COMMENSALISM: a type of coevolved relationship between different species that live intimately with one another without injury to any participant

PARASITISM: a type of coevolved relationship between different species in which one species exploits the other to its physical detriment

PHYTOPHAGOUS: animals, also referred to as herbivorous, that feed on plants

RECIPROCAL RELATIONSHIP: any type of coevolved, highly interdependent relationship between two or more species

SELECTIVE PRESSURE: evolutionary factors that favor or disfavor the genetic inheritance of various characteristics of a species

SYMBIOSIS: a type of coevolved relationship between two species in which both participants benefit; a type of mutualism

Coevolution is an extremely important and widespread phenomenon in the world of living things; it is a biological factor that is global in influence. When two or more different species experience a relationship in which any of the participating species' evolution directly affects the evolution of the other members, coevolution is taking place. This interactive type of evolution is characterized by the fact that the participant life-forms are acting as a strong selective pressure upon one another over a period of time.

The assumption of the interdependence of all organisms is today such a commonplace and fundamental concept that it is surprising that the phenomenon of coevolution has not always enjoyed a more prominent position in evolutionary thinking. Many scientists seem to have considered sets of coevolved organisms as relatively unimportant phenomena, almost on the level of biological "curiosities." The consensus appears to have been that while numerous examples of coevolution existed in both plant and animal kingdoms, on the whole it was of relatively minor importance in comparison with other evolutionary phenomena, such as competition. This opinion has begun to change as researchers increasingly recognize the intrinsic and ubiquitous role that coevolution has played, and continues to play, in the evolution of life at all levels throughout earth history.

Gaia

Organisms do not evolve in a biological vacuum. All organisms exist in, and have evolved within, the framework of one of a great number of delicately balanced and self-tuning biological systems or living communities termed ecosystems. Indeed, the entire planet can be regarded as one huge, incredibly complex ecosystem in which all the lesser ecosystems fit together and work together harmoniously. This planetary ecosystem has been called "Gaia" by some biologists, in reference to the ancient Greek earth goddess. In some respects, Gaia can be conceived of as actually one giant, worldwide organism. All the living communities in this huge ecosystem are products of coevolution. This phenomenon has been in effect over the vast expanses of geologic time and continues today. The only period in history when coevolution was probably not operating was at the dawn of life, billions of years ago, when the very first species of organisms appeared and had not yet established interactive communities. The importance of coevolution as a factor affecting life cannot be overstated.

Some biologists use the term coevolution in a more restricted sense to describe coevolved relationships that have developed between plants and animals, particularly between plants and animals that are herbivores or pollinators. The coevolution between plants and animals is one of the aspects of the field that has traditionally received the most attention, so this aspect of coevolution provides a useful departure point in describing the phenomenon.

Coevolutionary Warfare

The coevolution of plants and animals, whether animals are considered strictly in their plant-eating role or also as pollinators, is abundantly represented in every terrestrial ecosystem throughout the world where flora has established itself. Moreover, the overall history of some of the multitude of present and past plant and animal relationships is displayed (although fragmentally) in the fossil record found in the earth's crust. The most elemental relationship between plants and animals is that of plants as food source. This relationship has an extremely long history, beginning with the evolution of microscopic, unicellular plants that were the earth's first autotrophs (organisms that can produce their own food from basic ingredients derived from the environment). In conjunction with the appearance of autotrophs, microscopic, unicellular heterotrophs (organisms such as animals, which must derive food from organic sources such as autotrophs) evolved to exploit the simple plants. This ancient and basic relationship has resulted in uncounted numbers of plant and animal species evolving and coevolving over billions of years of earth's history.

As both plants and animals became multicellular and more complex, more elaborate defense mechanisms evolved among plants, as did more elaborate feeding apparatuses and behavior among animals. This biological "arms race" grew ever more intense as groups of plants and animals eventually adapted to the more rigorous demands of a terrestrial existence, leaving the marine environment behind. New ecosystems developed that culminated in the world's first swamps, jungles, and forests. The plant-animal arms race engendered increasingly more sophisticated strategies of botanical defense and animal offense, and this coevolved interrelationship has continued unabated. This coevolutionary "warfare" between plants and animals has expressed itself partly through the evolution of botanical structures and chemicals that attempt either to discourage or to prevent the attentions of herbivores. These include the development of spines, barbs, thorns, bristles, and hooks on plant leaf, stem, and trunk surfaces. Cacti, holly, and rose bushes illustrate this form of plant strategy.

Another type of deterrence evolved in the form of chemical compounds that can cause a wide spectrum of negative animal response. These compounds range in effect from producing a sensation of mild distaste, such as bitterness, to more extreme effects, such as actual poisoning of herbivore metabolisms. Plants that contain organic compounds such as tannin are examples of the chemical defensive strategy. Tannins produce several negative results in animals, including partially inactivating digestive juices and creating cumulative toxic effects that have been correlated with cancer. Plants containing tannin include trees, such as members of the oak group, and shrubs, such as those that produce the teas used as human beverages. Other plants have developed more lethal poisons that act more rapidly. Plants have also developed other strategies, such as possession of a high silica content (as found in grasses), that act to wear down the teeth of plant eaters. Animals have counteradapted to these plant defensive innovations by evolving a higher degree of resistance to plant toxins or by developing more efficient and tougher teeth with features such as harder enamel surfaces, or the capacity of grinding with batteries of teeth.

Coevolutionary Alliances

Not all coevolution is characterized by having an adversarial nature; mutually beneficial relationships are also very common. Sometime during the latter part of the Mesozoic era, angiosperms, the flowering plants, evolved and replaced most of the previously dominant land plants, such as the gymnosperms and the ferns. New species of herbivores evolved to exploit these new food sources. At some point, probably during the Cretaceous period of the late Mesozoic, animals became unintentional aids in the angiosperm pollination process. As this coevolution proceeded, the first animal pollinators became more and more indispensable as partners to the plants. Eventually, highly coevolved plants and animals developed relationships of extreme interdependence exemplified by the honeybees and their coevolved flowers. This angiosperm-insect relationship is thought to have arisen in the Mesozoic era by way of beetle predation, possibly on early, magnolia-like angiosperms. The fossil record gives some support to this theory. Whatever the exact route along which plant-animal pollination partnerships coevolved, the end result was a number of plant and animal species that gained mutual benefit from the new type of relationship. Such relationships are in general termed mutualisms.

Eventually some of these plant-animal mutualisms became so intertwined that one or both participants reached a point at which they could not exist without the aid of the other. These obligatory mutualisms ultimately involved other types of animal partners besides insects. Vertebrate partners such as birds, reptiles, and mammals also became involved in mutualisms with plants. Contemporary ecosystems, such as the United States' southwestern desert, include mutualisms between aerial mammals, such as bats, and plants, such as the agave and the saguaro cactus. The bats involved are nectar drinkers and pollen eaters. They have evolved specialized feeding structures such as erectile tongues similar to those found among moths and other insects with similar lifestyles. In turn, the plants involved with the pollinating bats have evolved either reciprocal morphologies or behavior patterns to accommodate their warm-blooded visitors. For example, angiosperms coevolutionarily involved with bats have developed such specializations as bat-attractive scents, flower structures that minimize the chance of injury to bats, and petal openings timed to the nocturnal activity of bats.

Symbioses, Commensalisms, and Parasitisms

Coevolved relationships are not restricted to beneficial or nonbeneficial relationships between plants and animals. They also include an immense number of relationships between animals and other animals, and even between plants and other plants. Among these various types of coevolved situations can be found subcategories such as symbioses, commensalisms, and parasitisms. The first two involve relationships beneficial to varying degrees that feature interactions of increasing physical intimacy between or among two or more species. Parasitism involves an intimate relationship produced through coevolution in which one participant, the host, experiences serious harm or even death through exploitation by the parasite. Predation is probably the most obvious form of coevolution among higher animals such as vertebrates. Modern carnivores such as the canines and felines and their prey are a dramatic example of coevolution at work. Animal hunters over time responded to the improved defenses of their prey by evolving better senses, such as stereoscopic, three-dimensional vision, hearing with expanded range of frequency response, and more effective body structures, such as multifunctional teeth. Such teeth are termed heterodont and represent a great improvement over the simple dental array of the more primitive vertebrates, such as fish and amphibians.

Beginning with the more advanced reptiles appearing in the late stages of the Paleozoic era, teeth began to differentiate into specialized components—incisors, canines, premolars, and molars—that enhanced food acquisition and improved mastication. This, in turn, improved digestion and allowed quicker energy acquisition from food. This evolutionary advantage has reached a zenith of adaptive success among the mammals. Mammalian predators evolved fangs and efficient claws, sometimes retractable, to minimize injury and wear. Along with improved hunting senses and better dentition came increased speed from the evolution of improvements in pelvic and limb arrangements. In response to this process, vertebrate herbivores also became generally swifter or better defended, more alert, attained higher metabolic rates, and were thus better able to elude or defend against predation. Advanced predators placed an intense selective pressure on their prey herbivores, spurring ever more efficient and acutely tuned responses among the herbivore populations. Herbivores evolved either as swift forms, such as deer, or became efficiently defended, walking fortresses, such as porcupines or armadillos. Because of the pervasive effect of coevolution, the overall relationship between predator and prey has been a reciprocal one in which all participants affect one another in an interactive manner.

Unraveling the Intricacies of Coevolution

Field research and laboratory research are pursued concurrently in the effort to unravel the intricacies of the subject of coevolution. Field research involves actual observation in nature of animals and plants, their behavior, and, especially, their interaction with other species. Special attention is given to useful clues that can be employed to establish evolutionary relationships, either presently existing or previously in effect. For example, cooperative behavior between or among several different species of animal or plant is often indicative of an established, coevolutionary relationship. If this behavior is consistent over time and can also be traced or inferred through the agency of the fossil record, more useful data are acquired concerning a possible, evolved, reciprocal relationship. Of particular importance is the confirmation of specialized physical structures that are unique to the members of the observed relationship. Examples are the specialized feeding apparatuses of pollinating animals and the specialized, accommodating flower structures of their angiosperm partners. Such physical structures are strong evidence for the handiwork of the coevolutionary process. Direct human observation is preferable in ascertaining coevolutionary behavior; however, this is not always possible because of the rapidity of the animals involved, their habitat, their extremely small size, their preference for nocturnal activity, or their determined avoidance of humans. Consequently, electronic and mechanical aids are sometimes indispensable. These include remote-controlled still and video cameras, microscopic or telephoto lenses, infrared or ultraviolet lighting units, sonar or radar sensors, trip wires and other mechanical triggering devices, and sound recording equipment with high-gain or long-range microphones.

Laboratory research in the field of coevolution involves investigations heavily reliant on modern, sophisticated laboratory equipment and techniques. High-powered conventional, optical microscopes are employed to determine tissue and cellular structures. Scanning electron microscopes (SEMs) are employed for study of extremely small unicellular animals or plants such as planktonic organisms or extremely small organic structures. In addition to these tools of laboratory specimen observation, there are the analytical equipment and techniques used to determine the genetic codes and blood protein complexes of animals and plants to establish the degree of relatedness or divergence between various species.

Maintaining Balances

Coevolutionary studies are increasingly important in the biological sciences. One of the aims is to determine the degree of interdependence between various species, whether the relationship is between animals and plants, animals and other animals, or plants and other plants. A key factor to be determined in all these coevolved relationships is that of the nature and degree of balance attained. Although most of the biological world is forever in a state of flux, some categorical, coevolved relationships have been of long duration and can be reasonably assessed as having been in existence for tens of millions of years, such as that of flowering plants and vertebrate and invertebrate pollinators, or even hundreds of millions of years, such as the oceanic, planktonic food chain.

The degree to which these large-scale, coevolved relationships, involving entire planetary ecologies, continue to enjoy their former degree of health and well-being is of the utmost importance to human society. The present depth of understanding of the biological sciences clearly indicates the interrelatedness of all nature. Many angles of study agree that the global life system is experiencing great stress from human intervention: industrialization, urbanization, and overpopulation. It becomes increasingly urgent to know with the utmost precision all facets of the way the global life system operates, and has operated with general stability, over geological expanses of time. Every detail that contributes to this knowledge—every coevolved relationship, no matter how seemingly insignificant—adds to the total effect. This information can be used as an important resource to help maintain the stability of the entire system for ourselves and future generations.

—Frederick M. Surowiec

See also: Adaptations and their mechanisms; Adaptive radiation; Bees; Biodiversity; Carnivores; Competition; Convergent and divergent evolution; Ecological niches; Ecology; Ecosystems; Evolution: Animal life; Evolution: Historical perspective; Habitats and biomes; Herbivores; Hippopotamuses; Lampreys and hagfish; Mimicry; Natural selection; Plant and animal interactions; Predation; Sharks and rays; Symbiosis; Wildlife management.

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COLD-BLOODED ANIMALS

Types of animal science: Anatomy, behavior, physiology
Fields of study: Anatomy, environmental science, physiology, zoology

Cold-blooded animals, which include all invertebrate animals, as well as fish, amphibians, and reptiles, maintain body temperature by exposure to environmental sources of heat and cold, rather than by the internal feedback mechanisms utilized by warm-blooded animals.

Principal Terms

CORE TEMPERATURE: internal body temperature around the heart, brain, and spinal cord

ECTOTHERM: an animal that depends on environmental heat sources, usually solar radiation, to maintain body temperature

HOMEOTHERM: an animal that maintains a constant, steady body temperature

METABOLIC RATE: the rate (expressed as calories per minute) at which an animal produces and consumes energy

METABOLISM: the conversion of carbohydrates, proteins, or fats into chemical energy that can be used to accomplish work and generate heat

POIKILOTHERM: an animal that has a changing body temperature

Cold-blooded animals include all the invertebrate animals. Insects, spiders, other "bugs," worms, and all animal sea life except fish are examples of invertebrates. Of the five classes of vertebrate animals, fish, amphibians, and reptiles are cold-blooded. Only birds and mammals are warm-blooded. The proper scientific term for cold-blooded animals is poikilotherms (or ectotherms), while the scientific term for warm-blooded animals is homeotherms (or endotherms).

The best way to understand and appreciate cold-blooded animals and how they adapt is to compare them with warm-blooded animals. While a few of the cold-blooded animals have some rudimentary abilities to achieve temperature control internally, only birds and mammals are truly homeothermic.

Both birds and mammals maintain quite high core (internal) body temperatures with a very narrow range of variability. Mammals maintain a temperature of about 37 degrees Celsius with only about one degree of variation. Birds' temperatures are about two degrees higher. Homeotherms control their high and constant temperatures with an elaborate system of neural and chemical feedback systems. Most homeotherms have highly developed systems of insulation (feathers, fur, or fat).

Mechanisms of Ectothermic Temperature Control

Poikilotherms have little or none of the internal mechanisms of the homeotherms and they usually have poor insulation or surfaces that enhance heat transfer. They maintain their temperature control primarily by external exposure to the environment. They have a much lower basal metabolism and most species maintain a much lower temperature range than homeotherms.

Some cold-blooded animals live in very constant environments and maintain their temperature range with little or no adjustment. For sea life and other organisms that live in the ocean or very large bodies of freshwater, this is especially true. The entire surface of the organism is in contact with water, which conducts heat at least five times as fast as air. Fish can easily adjust their thermal

Since they cannot generate their own body heat, cold-blooded animals such as this lizard often lie on rocks in the direct sun to warm themselves. (Corbis)

environment in lakes and estuaries by changing their depth, since water temperatures can vary greatly below the surface. Some fish have internal mechanisms to become somewhat dormant with extreme seasonal changes in lakes whose surfaces freeze during the winter.

Amphibians and reptiles have more complicated mechanisms and use more adaptations than fish. Amphibians and reptiles can operate within a much wider core body temperature range than mammals or birds. This is especially true of some amphibians. Some salamanders' body temperatures range from –2 degrees Celsius to 36 degrees Celsius (mean 27). The range of external temperatures that some amphibians can tolerate, at least for varying lengths of time, varies from 28 degrees Celsius (below freezing) to 38 degrees Celsius (about 100 degrees Fahrenheit).

Both amphibians and reptiles maintain their body temperatures primarily by changing their locations to gain or lose heat from the sun, shade, or substrate. Some species achieve control by moving in and out of the water. This is an especially effective method since water conducts heat so rapidly. Many of these animals change body positions to increase or decrease exposure to the sun or to decrease surface area to gain or lose heat more rapidly. Reptiles have scaly and often thin skins, while amphibians have moist secretory skins, both of which are very effective for heat transfer. A very interesting internal adaption that is present in some amphibians and reptiles is the ability to change the color of their skins. A darker skin color will absorb heat and lighter will reflect the heat.

Reptiles

Reptiles are the most interesting of the poikilotherms for several reasons. Lizards and snakes are very adept at changing their locations frequently to maintain temperature control. They may be in holes or in the shade, hidden in the grass, or among rocks and vegetation, quietly conserving energy and waiting for prey. They will bask in the sun or lay on warm surfaces in the evening as needed. Some lizards will actively generate heat by doing multiple push-ups.

Reptiles have a wider body temperature range than homeotherms, but usually not nearly as wide as amphibians. The crocodile is one of the more advanced reptiles. One species was found to have a mean body temperature of 25 degrees Celsius with a maximum range of six degrees above or below the mean. Being so large, the surface area to body ratio is not very great compared to smaller reptiles, and the surface exchange of heat takes much longer. Crocodiles sometimes spend long periods in the water and will be at their lower temperature range. Then they will lay for hours in the sun on warm sand or dirt. They have learned to use the water to cool down, and they may submerge or be partially in and out of the water. On hot days, they will open their huge jaws, not to pant like fur-bearing animals, but to expose the very large surface area of the mucous membranes in their mouths, which creates an effective evaporative cooling effect. When crocodiles or alligators have had their jaws tied shut for transport by their captors, many have died from overheating. They do have some ability to slow or speed up their metabolic rate. In severe drought conditions they will burrow into deep wet mud and sand and change their metabolic rate enough to survive.

—*C. Mervyn Rasmussen and Penny Rasmussen*

See also: Amphibians; Deep-sea animals; Dinosaurs; Fish; Invertebrates; Lizards; Marine biology; Reptiles; Thermoregulation; Warm-blooded animals.

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COMMUNICATION

Type of animal science: Ethology
Fields of study: Evolutionary science, invertebrate biology, systematics (taxonomy), zoology

In animal communication, information is exchanged through signals. Such signals are vital for survival, finding mates, and rearing young.

Principal Terms

DISCRETE SIGNALS: signals that are always given in the same way and indicate only the presence or absence of a particular condition or state

DISPLAY: a term used to indicate social signals, particularly visual signals

PHEROMONE: a chemical substance used in communication within a species

PRIMER PHEROMONE: a chemical substance that affects behavior by altering physiology and is therefore not rapid in its effects

RELEASER: a standard signal that elicits a standard response

TROPHALLAXIS: food exchange between organisms, particularly in social insects

A simple definition of animal communication is the transmission of information between animals by means of signals. Developing a more precise definition is difficult because of the broad array of behaviors that are considered messages or signals and the variety of contexts in which these behaviors may occur. Animal signals can be chemical, visual, auditory, tactile, or electrical. The primary means of communication used within a species will depend upon its sensory capacities and its ecology.

Pheromones

Of the modes of communication available, chemical signals, or pheromones, are assumed to have been the earliest signals used by animals. Transmission of chemical signals is not affected by darkness or by obstacles. One special advantage is that the sender of a chemical message can leave the message behind when it moves. The persistence of the signal may also be a disadvantage when it interferes with transmission of newer information. Another disadvantage is that the transmission is relatively slow.

The speed at which a chemical message affects the recipient varies. Some messages have an immediate effect on the behavior of recipients. Alarm and sex-attractant pheromones of many insects, aggregation pheromones in cockroaches, or trail substances in ants are examples. Other chemical messages, primers, affect recipients more slowly, through changes in their physiology. Examples of primers include pheromones that control social structure in hive insects such as termites. Reproductive members of the colony secrete a substance that inhibits the development of reproductive capacity in other hive members. The chemicals important for controlling the hive are spread through grooming and food sharing (trophallaxis). Chemical communication is important not only among social and semisocial insects but also among animals, both vertebrate and invertebrate. Particularly common is the use of a pheromone to indicate that an animal is sexually receptive.

Visual Signals

Visual communication holds forth the advantage of immediate transmission. A visual signal or display is also able to encode a large amount of information, including the location of the sender. Postures and movements of parts of an animal's body are typical elements of visual communication. Color and timing are additional means of providing information. Some visual signals are discrete; that is, the signal shows no significant variation from performance to performance. Other displays are graded so that the information content of the signal can be varied. An example of a graded display is found in many of the threat or aggressive postures of birds. Threat postures of the chaffinch vary between low-intensity and high-intensity postures. The elevation of the crest varies in ways that indicate the bird's relative readiness for combat. The song spreads of red-winged blackbirds and cowbirds show variation in intensity. In red-winged blackbirds, the red epaulets, or shoulder patches, are exposed to heighten the effect of the display. Discrete and graded signals may be used together to increase the information provided by the signal. In zebras, ears back indicates a threat and ears up indicates greeting. The intensity of either message is shown by the degree to which the mouth is held open. A widely open mouth indicates a heightened greeting or threat.

Visual displays depend upon the presence of light or the production of light. The ability to produce light, bioluminescence, is found most frequently in aquatic organisms, but its use in communication is probably best documented in fireflies, beetles belonging to the family Lampyridae. Firefly males advertise their presence by producing flashes of light in a species-specific pattern. Females respond with simple flashes, precisely timed, to indicate that they belong to the appropriate species. This communication system is used to advantage by females in a few predatory species of the genus *Photuris*. After females of predatory species have mated with males of their own species, they attract males of other species by mimicking the responses of the appropriate females. The males that are tricked are promptly eaten. The luminescence of fireflies does not attract a wide variety of nocturnal predators, because their bodies contain a chemical that makes them unpalatable.

Visual displays are limited in the distance over which they can be used and are easily blocked by obstacles. Visual communication is important in primates, birds, and some insects, but can be dispensed with by many species that do not have the necessary sensory capacities.

Auditory Communication

The limitation of visual communication is frequently offset by the coupling of visual displays with other modes of communication. Visual displays can be coupled with auditory communication, for example. There are many advantages to using sound: It can be used in the dark, and it can go around obstacles and provide directional information. Because pitch, volume, and temporal patterns of sound can be varied, extremely complex messages can be communicated. The auditory communication of many bird species has been studied intensively. Bird vocalizations are usually classified into two groups, calls and songs. Calls are usually brief sounds, whereas songs are longer, more complex, and often more suited to transmission over distances.

The call repertoire of a species serves a broad array of functions. Many young birds use both a visual signal, gaping, and calling in their food begging. Individuals that call more may receive more food. Begging calls and postures may also be used by females in some species to solicit food from mates. One call type that has been intensively studied is the alarm call. Alarm calls of many species are similar, and response is frequently interspecific (that is, interpretable by more than one species). Alarm calls are likely to be difficult to locate, a definite advantage to the individual giving the call. Calls used to gather individuals for mobbing predators are also similar in different species. Unlike alarm calls, mobbing calls provide good directional information, so that recruitment to the mobbing effort can be rapid.

Call repertoires serve birds in a great variety of contexts important for survival of the individual. Song, on the other hand, most often serves a reproductive function, that of helping a male hold a territory and attract a mate. Songs are species-

Karl von Frisch

Born: November 20, 1886; Vienna, Austria
Died: June 12, 1982; Munich, West Germany
Fields of study: Biology, ethology, zoology
Contribution: Frisch, founder of the science of ethology (animal behavior), was awarded a Nobel Prize in Physiology or Medicine in 1973 for his studies of sensory discrimination and communication in bees.

Karl von Frisch enrolled at the University of Vienna as a medical student in 1905. Although he excelled in the study of anatomy and physiology, he realized he had no interest in clinical medicine. In 1907, he transferred to the Zoological Institute in Munich. After studying zoology with Richard von Hertwig and experimental biology with Hans Przibaum in Vienna, Frisch studied marine biology at the Biological Institute for Marine Research in Trieste, Italy. He was awarded the Ph.D. in 1910 for his thesis on light and color perception in minnows. These studies led to experiments on color discrimination in bees. While serving as assistant to Richard Hertwig at the Zoological Institute at the University of Munich, he earned his University Teaching Certificate in Zoology and Comparative Anatomy. By 1914, Frisch had proved that food stimuli could be used to train bees to respond to different colors. His research was interrupted by World War I, during which he worked in a Vienna hospital.

Frisch returned to Munich as an assistant professor in 1919 and carried out research on the ability of bees to distinguish specific scents. Working from premises based on Darwinian theory, Frisch thought that there must be an evolutionary link between sensory discrimination in bees and the scents and colors found in flowers. While analyzing the ability of bees to distinguish between different scents, Frisch noted that when a bee discovered a new food source it was able to summon other bees to the exact location. His observations revealed that bees communicate information about food by means of a "round dance." He subsequently discovered that the round dance was used to direct bees to a source of sugar water, but a more vigorous "waggle dance" provided information about a source of flower pollen. According to Frisch, in the language of the bees the round dance was performed when a bee discovered a food source that was close to the hive. The waggle dance provided information about more distant food sources.

After accepting appointments at the University of Rostock (1921-23) and the University of Breslau (1923-25), Frisch returned to Munich as director of the Zoological Institute. Here he helped establish a new research facility for the study of insects. In addition to his continuing ethological research on the behavior of bees, he carried out pioneering investigations on the hearing abilities of fish. Frisch established that bees use the sun as a compass and that they possess an internal clock. His research had practical implications for apiculture (beekeeping) and plant pollination. Frisch retired in 1958, but continued his research and writing and served as director emeritus of the Zoological Institute of the University of Munich. Having deciphered what he called the Rosetta Stone of honeybee communication, Frisch published several books that made his work accessible to general readers. These books include *Aus dem Leben der Bienen* (1927; *The Dancing Bees: An Account of the Life and Senses of the Honeybee*, 1955), *Du und das Leben* (1936; *Man and the Living World*, 1963), *Erinnerungen eines Biologen* (1957; *A Biologist Remembers*, 1964), *Bees: Their Vision, Chemical Senses, and Language* (1950), and *Tiere als Baumeister* (1974; *Animal Architecture*, 1974). In 1973, at the age of eighty-six, Frisch shared the Nobel Prize with Konrad Lorenz and Nikolaas Tinbergen.

—*Lois N. Magner*

specific, like the distinctive markings of a species. In some cases, songs are more distinctive than physical appearance. The chiffchaff and willow warbler were not recognized as separate species until an English naturalist named Gilbert White discovered, by examining their distinctive songs, that they are separate. The North American wood and hermit thrushes can also be distinguished more readily by song than by appearance. Bird song can communicate not only the species of the individual singing but also information about motivational state. Most singing is done by males

Karl von Frisch founded the science of ethology as the result of his study in the communicative dances of honeybees. (Nobel Foundation)

during the breeding season. In many species, only the male sings. In some species, females sing as well. Their songs may be similar to the songs of the males of their species or they may be distinctive. If the songs are similar to those of the males, the female may sing songs infrequently and with less volume. In some instances, the female song serves to notify her mate of her location. An interesting phenomenon found in some species is duetting, in which the male and female develop a duet. Mates may sing in alternate and perfectly timed phrases, as is done by the African boubou shrike, *Laniarius aethiopicus*. An individual shrike can recall its mate by singing the entire song alone.

Individuals in some bird species have a single song, and individuals of other species have repertoires of songs. Average repertoire size of the individual is characteristic of a species. Whether songs in repertoires are shared with neighbors or unique to the individual is also characteristic of a species. Sharing songs with neighbors permits song matching in countersinging. Cardinals and tufted titmice are species that frequently match songs in countersinging. Possible uses for matching are facilitating the recognition of intruders and indicating which neighbor has the attention of a singer. Some species of birds have dialects. The species-specific songs of one geographic region can be differentiated from the song of another geographic region. The development of dialects may be useful in maintaining local adaptations within a species, provided that females select mates of the same dialect as their fathers.

Although auditory signals of birds have received a disproportionate share of attention in the study of animal communication, auditory communication is used by a broad spectrum of animals. Crickets have species-specific songs to attract females and courtship songs to encourage an approaching female. The ears of most insects can hear only one pitch, so the temporal pattern of sound pulses is the feature by which a species can be identified. Vervet monkeys use three different alarm calls, depending upon the kind of threat present; they respond to the calls appropriately by looking up, looking down, or climbing a tree, depending upon the kind of call given.

Tactile and Electrical Communication

Tactile communication differs significantly from other forms of communication in that it cannot occur over a distance. This form of communication is important in many insects, equipped as they are with antennae rich in receptors. Shortly after a termite molts, for example, it strokes the end of the abdomen of another individual with its antennae and mouthparts. The individual receiving this signal responds by extruding a fluid from its hindgut. Tactile signals are frequently used in eliciting trophallaxis (food sharing) in social insects. Tactile signals are also important in the copulatory activity of a number of vertebrates.

Additional channels of communication available in animals are electrical and surface vibration. Many modes of communication are used in combination with other modes. The channels used will depend in part on the sensory equipment of the species, its ecology, and the particular context. Most messages will be important either for the survival of the individual or the group or for the individual's ability to transmit its genes to the next generation.

Communication Studies

Early study in animal communication depended primarily on careful observation of animals. This technique has been supplemented by a number of tools. The motion-picture or videotape camera permits the observer to analyze visual displays more completely. The tape recorder is a particularly versatile tool; acoustical communication can be recorded and the result used in playback experiments, in which the ethologist plays the recording in the field in order to test hypotheses about communication. Playbacks have helped scientists determine that some species of birds can discriminate between songs of neighbors and songs of strangers. Taped songs have been cut and spliced in various sequences to find out which features of a song's structure are important in species recognition.

The development of song in some species has been studied by means of isolation experiments. Birds that have been hatched and reared in the laboratory have been isolated from their species-specific song to determine whether the song needs to be learned. Some isolates are exposed to tutors (either tape recordings or living birds) at various intervals to examine the possibility of critical periods for song learning.

Sound spectrographs make it possible to produce pictures of calls and songs. Spectrographs represent song frequency on one axis and time on the other. These graphs have revealed the intricate structures of many auditory communication signals.

Information about sensory reception and about neural control of signals is an important research area. Some information in this area has come from ingenious but simple experiments. Bees have been trained to respond to color clues in association with a sugar source to determine which colors they are able to discriminate. Important knowledge in sensory research comes from determining the specific stimuli that will elicit a response in specific neurons. By using microelectrodes placed in or near the neuron, scientists can detect the presence of a response. Another technique used to determine the function of a presumed sense organ is to block or remove either the organ or the neural connections to the organ. One of the earliest experiments of this type was done in 1793 by Lazzaro Spallanzani. He found that flying bats could not avoid obstacles when their ears were tightly plugged but that the bats were able to avoid obstacles when they were blinded. In 1938, the use of an ultrasonic recorder made it possible for Donald Griffin to discover the bat's use of ultrasonic sound.

Synthetic pheromones can be produced that have the same effects on behavior as natural pheromones. Scientists can also determine at what dilution a pheromone will still evoke response. Hence, the sophisticated tools of chemistry have important applications in ethology.

Talking to Animals

Animal communication provides a fascinating frontier for exploration. Some of the knowledge acquired has had practical applications as well. Pheromones have been used to bait traps for insect pests. In some cases, this technique is used directly as a control measure; in other instances, the traps are used to estimate population size, and other control measures are used when pest populations are high. A key advantage of pheromone use is its specificity.

Recognizing the communication signals of pets and domestic animals is often useful in their care. Knowledge of releasers, standard signals that receive standard responses from animals, is important for survival in some contexts. Knowing which signals are perceived by animals as threats allows humans to avoid triggering an attack. This knowledge also allows control of animals in less destructive ways. Recordings of alarm signals of birds are used to disperse flocks that are creating problems.

Knowledge of a species' communication repertoire is critical in the training of animals for useful work or for entertainment. Also, knowledge of their sensory capacities makes it possible for appropriate signals to be selected—particularly important as it applies to human nonverbal communication. Knowing which signals of our nonverbal communication repertoire are characteristic of the whole species is both useful and interesting.

—Donna Janet Schroeder

See also: Antennae; Bioluminescence; Communities; Courtship; Displays; Ethology; Grooming; Groups; Habituation and sensitization; Hierarchies; Hormones and behavior; Imprinting; Insect societies; Instincts; Language; Learning; Mammalian social systems; Mimicry; Pheromones; Reproductive strategies; Rhythms and behavior; Sense organs; Smell; Territoriality and aggression; Tool use; Vision; Vocalizations.

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COMMUNITIES

Type of animal science: Ecology
Fields of study: Conservation biology, ecology, population biology, wildlife ecology, zoology

Each ecological community has a characteristic structure and function that determines its ability to withstand and recover from disturbance. Since so many of the disturbances experienced by communities are caused by human activities, ecologists seek to understand why some communities are susceptible and why some disturbances cause irreversible damage.

Principal Terms

ECOSYSTEM: a community together with its physical environment

FOOD CHAIN: a pathway through which energy travels in a community

FOOD WEB: the interconnections among all food chains in a community

FREQUENCY-DEPENDENT PREDATION: predation on whichever species is most common in a community

GLOBAL EXTINCTION: the loss of all members of a species

KEYSTONE SPECIES: a species that determines the structure of a community, usually by predation on its dominant competitor

LOCAL EXTINCTION: the loss of one or more populations of a species, but with at least one population of the species remaining

RESILIENCE STABILITY: stability exhibited by a community that changes its structure when disturbed but returns to its original structure when the disturbance ends

RESISTANCE STABILITY: stability exhibited by a community that absorbs the effects of a disturbance until it can no longer do so; then, it typically shifts permanently to an alternate structure

TROPHIC LEVEL: a single link in a food chain; all species that obtain energy in the same way are said to be at the same trophic level

An ecological community is the assemblage of species found in a given time and place. The populations that form a community interact through the processes of competition, predation, parasitism, and mutualism. The structure and function of communities are determined by the nature and strength of the population interactions within it, but these interactions are affected by the environment in which a community exists. An ecological community together with its physical environment is called an ecosystem. No ecological system can be studied apart from its physical environment; the structure and function of every community are determined in part by its interactions with its environment.

The species constituting a community occupy different functional roles. The most common way to characterize a community functionally is by describing the flow of energy through it. Correspondingly, communities usually contain three groups of species: those that obtain energy through photosynthesis (called producers), those that obtain energy by consuming other organisms (consumers), and those that decompose dead organisms (decomposers). The pathway through which energy travels from producer through one or more consumers and finally to decomposer is called a food chain. Each link in a food chain is called a trophic level. Interconnected food chains in a community constitute a food web. Food webs have no analogy in populations.

Very few communities are so simple that they can be readily described by a food web. Most communities are compartmentalized: A given set of producers tends to be consumed by a limited number of consumers, which in turn are preyed upon by only a few predators, and so on. Alternatively, consumers may obtain energy by specializing on one part of their prey (for example, some birds may eat only seeds of plants) but utilize a wide range of prey species. Compartmentalization is an important feature of community structure; it influences the formation, organization, and persistence of a community.

Dominant and Keystone Species

Some species, called dominant species, can exert powerful control over the abundance of other species because of the dominant species' large size, extended life span, or ability to monopolize energy or other resources. Communities are named according to their dominant species: for example, oak-hickory forest, redwood forest, sagebrush desert, and tallgrass prairie. Some species, called keystone species, have a disproportionately large effect on community structure by preventing dominant species from monopolizing the community. Keystone species usually exert their effects through predation, while dominant species are good competitors (that is, better at obtaining and holding resources than other species).

The species that make up a community are seldom distributed uniformly across the landscape; rather, some degree of patchiness is characteristic of virtually all species. There has been conflicting evidence as to the nature of this patchiness. As one moves across an environmental gradient (for example, from wet to dry conditions or from low to high elevations), there is a corresponding change in species observed and in the type of community present. Some studies have suggested that changes in species composition usually occur along relatively sharp boundaries and that these boundaries mark the boundaries between adjacent communities. Other studies have indicated that species tend to respond individually to environmental gradients and that community boundaries are not sharply defined; rather, most communities broadly intergrade into one another.

The Nature of Community

These conflicting results have fueled a continuing debate as to the underlying nature of the community. Some communities seem to behave in a coordinated manner; for example, if a prairie is consumed by fire, it regenerates in a predictable sequence, ultimately returning to the same structure and composition it had before the fire. This coordinated response is to be expected if the species in a community have evolved together with one another. In this case, the community behaves analogously to an organism, maintaining its structure and function in the face of environmental disturbances and fluctuations (as long as the disturbances and fluctuations are not too extreme). The existence of relatively sharp boundaries between adjacent communities supports this explanation of the nature of the community.

In other communities, it appears that the response to environmental fluctuation or disturbance is determined by the evolved adaptations of the species available. There is no coordinated community response, but rather a coincidental assembly of community structure over time. Some sets of species interact together so strongly that they enter a community together, but there is no evidence of an evolved community tendency to resist or accommodate environmental change. Data support this explanation of the community as an entity formed primarily of species that happen to share similar environmental requirements.

Mechanisms of Community Structure

Disagreement as to the underlying nature of communities usually reflects disagreement as to the relative importance of the underlying mechanisms that determine community structure. Interspecific competition has long been invoked as the primary agent structuring communities. Competition is certainly important in some communities, but there is insufficient evidence to indicate how widespread and important it is in determining community structure. Much of the difficulty occurs because ecologists must infer the existence of past competition from present patterns in communities. It appears that competition has been important in many vertebrate communities and in communities dominated by sessile organisms, such as plants; it does not appear to have been important in structuring communities of plant-eating insects. Furthermore, the effects of competition typically affect individuals that use identical resources, so that only a small percentage of species in a community may be experiencing significant competition at any time.

The effects of predation on community structure depend on the nature of the predation. Keystone species usually exert their influence by selectively preying on species that are competitively dominant. Predators that do not specialize on one or a few species may also have a major effect on community structure, if they attack prey in proportion to their abundance; this frequency-dependent predation prevents any prey species from achieving dominance. If a predator is too efficient, it can drive its prey to extinction, which may cause a selective predator to become extinct as well. Predation appears to be most important in determining community structure in environments that are predictable or unchanging.

Natural Disturbances

A variable or unpredictable environment influences the structure of a community. No environment is completely uniform; longer-term or seasonal environmental fluctuations affect community structure by limiting opportunities for colonization, by causing direct mortality, and by hindering or exacerbating the effects of competition and predation. Furthermore, all communities experience at least occasional disturbance: unpredictable, seemingly random environmental changes that may be quite severe. It is useful in this regard to distinguish between disasters and catastrophes. A disaster is an event that occurs so frequently in the life of a population that adaptation is possible; for example, fire occurs so often in tallgrass prairies that most of the plant species have become fire-adapted—they have become efficient at acquiring nutrients left in the ash and at sprouting or germinating quickly following a fire. In comparison, a catastrophe is so intense, widespread, or infrequent that a population cannot adapt to it; the eruption of Mount St. Helens in 1980, for example, was so violent and so unpredictable that the species affected could not evolve adequate responses to it.

Natural disturbances occur at a variety of scales. Small-scale disturbances may simply create small openings in a community that are filled in by other species suited to thrive in such spaces. Large disturbances are qualitatively different from small disturbances, in that large portions of a community may be destroyed, including some of the ability to recover from the disturbance. Early ecologists almost always saw disturbances as destructive and disruptive for communities. Under this assumption, most mathematical models portrayed communities as generally being in some stable state, at equilibrium; if a disturbance occurred, the community inevitably returned to the same (or some alternative) equilibrium. It later became clear, however, that natural disturbance is a part of almost all natural communities. Ecologists now recognize that few communities exhibit a stable equilibrium; instead, communities are dynamic, always responding to the last disturbance, always adjusting to the most recent environmental fluctuation.

The Long-Term Dynamics of Communities

The evidence suggests that three conclusions can be drawn with regard to the long-term dynamics of communities. First, it can no longer be assumed that communities remain at equilibrium until changed by outside forces. Disturbances are so common, they occur at so many different scales and frequencies, and they so readily affect the processes of competition and predation that the community must be viewed as an entity that is constantly changing as its constituent species readjust to disturbance and to one another.

Second, communities exhibit several types of stability in the face of disturbance. A community may absorb disturbance without markedly changing, until it reaches a threshold and suddenly and rapidly shifts to a new state, called resistance stability. Alternatively, a community may change easily when disturbed but quickly return to its former state; this characteristic is called resilience stability. Resilience stability may occur over a wide range of conditions and scales of disturbance; such a system is said to be dynamically robust. On the other hand, a community that exhibits resilience only within a narrow range of conditions is said to be dynamically fragile.

Finally, there is no simple way to predict the stability of a community. At the end of the 1970's, it appeared that complex communities were generally more stable than simple communities. It appeared that stability was conferred by more intricate food webs, by more structural complexity, and by higher species diversity. On the basis of numerous field studies and theoretical models, ecologists now conclude that no such relationship exists. Both very complex communities, such as tropical rain forests, and very simple communities, such as Arctic tundra, may be very fragile when disturbed.

Complex Systems

Most communities consist of thousands of species, and their complexity makes them very difficult to study. Most community ecologists specialize in taxonomically restricted subsets of communities (such as plant communities, bird communities, insect communities, or moss communities) or in functionally restricted subsets of communities (such as soil communities, tree-hole communities, pond communities, or detrivore communities).

The type of community under investigation and the questions of interest determine the appropriate methods of study. The central questions in most community studies are how many species are present and what is the abundance of each. The answers to these questions can be estimated using mark-recapture methods or any other enumeration method.

Often the aim is to compare communities (or to compare the same community at different times). A specialized parameter called similarity is used to compare and classify communities; more than two dozen measures of similarity are available. Measures of similarity are typically subjected to cluster analysis, a set of techniques that groups communities on the basis of their similarity.

Many multivariate techniques are used to search for patterns in community data. Direct gradient analysis is the simplest of these techniques; it is used to study the distribution of species along an environmental gradient. Ordination includes several methods for collapsing community data for many species in many communities along several environmental gradients onto a single graph that summarizes their relationships and patterns.

Patterns of Community Responses to Disturbance

At the most basic level, destruction of a community eliminates the species comprising the community. If the community is restricted in its extent, and if its constituent species are found nowhere else, those species become extinct. If the community covers a large area or is found in several areas, local extinction of species may occur without causing global extinction.

Destruction of a community can cause unexpected changes in environmental conditions that were modified by the intact community. Even partial destruction of an extensive community can eliminate species. For example, the checkerboard pattern of clear-cutting in Douglas fir forests of the Pacific Northwest threatens the survival of the northern spotted owl, the marbled murrelet, Vaux's swift, and the red tree vole, even though fragments of the community remain. Many fragments are simply too small to support these species. A Douglas fir forest is regenerated following cutting, but this young, even-aged stand is so different from an old, mixed-age forest that it functions as a different type of community.

Altering the population of one species can affect others in a community. The black-footed ferret was once found widely throughout central North America as a predator of prairie dogs. As prairie dogs were poisoned, drowned, and shot throughout their range, the number of black-footed ferrets also declined. As of 1989, fewer than one hundred black-footed ferrets were in a captive breeding program in Wyoming in a final attempt to preserve the species.

Introducing a new species into a community can severely alter the interactions in the community. The introduction of the European rabbit into Australia led to a population explosion of rabbits, excessive predation on vegetation, and resulting declines in many native marsupials.

Finally, it appears that many communities exhibit stability thresholds; if a community is disturbed beyond its threshold, its structure is permanently changed. For example, acid deposition in lakes is initially buffered by natural processes. As acid deposition exceeds the buffering capacity of a lake, it causes insoluble aluminum in the lake bottom to become soluble, and this soluble aluminum kills aquatic organisms directly or by making them more susceptible to disease. The lesson is clear: It is far easier to disrupt or destroy natural systems (even accidentally) than it is to restore or reconstruct them.

—*Alan D. Copsey*

See also: Coevolution; Competition; Demographics; Ecological niches; Ecology; Ecosystems; Food chains and food webs; Groups; Herds; Insect societies; Mammalian social systems; Mark, release, and recapture methods; Pair-bonding; Population analysis; Population fluctuations; Population genetics; Predation; Rain forests; Symbiosis; Wildlife management.

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Pielou, E. C. *The Interpretation of Ecological Data: A Primer on Classification and Ordination*. New York: John Wiley & Sons, 1984. The definitive book for those interested in cluster analysis and ordination, and in the classification of communities. Although it is an introductory textbook, the reader with a knowledge of matrix algebra and previous instruction would benefit most.

COMPETITION

Type of animal science: Ecology
Fields of study: Evolutionary science, zoology

Competition is the conflict between different organisms for control of food, natural resources, territories, mates, and other aspects of survival. Competition can occur between individuals of the same species or between individuals of different species. In either case, it is natural selection for the fittest organisms and species; therefore, it is a major driving force in evolution.

Principal Terms

EVOLUTION: gradual changes in organisms over time, caused by mutation and selected by the environment, resulting in better adapted organisms and new species

HABITAT: the type of environment in which a particular organism prefers to live, based upon various physical and chemical conditions

NATURAL SELECTION: the ability of an organism or species to survive, compete, and reproduce in its habitat; success is dictated by the alleles (traits) that it possesses

NICHE: an organism's role in its habitat environment

PREDATION: a situation in which one animal species hunts and eats another species (examples: lynx versus hare; cheetah versus gazelle)

TERRITORIALITY: a phenomenon in animal behavior whereby individual organisms occupy and defend an area from other individuals of the same or different species

THREAT DISPLAY: a territorial behavior exhibited by animals during defense of a territory, such as charging, showing bright colors, and exaggerating body size

Competition is the struggle between individuals of different species (interspecific competition) or between individuals of the same species (intraspecific competition) for food, territories, and mates in order to survive. It is a major driving force in evolution, the process by which living organisms change over time, with better-adapted species surviving and less well-adapted species dying. Evolution begins with mutation, changes in the nucleotide sequence of a gene or genes, resulting in the production of slightly altered genes called alleles which encode slightly different proteins. These altered proteins are the expressed traits of an organism and may give the organism an advantage over its competitors. The organism outcompetes its rivals in the environment, and hence the environment favors the better-adapted, fitter organism, a process called natural selection. A mutation may help an organism in one environment but may hurt the same organism in a different environment (for example, an albino squirrel may flourish in snowy regions but may not do as well in warm regions). Mutations can be caused by chemicals called mutagens or by ionizing radiation such as ultraviolet light, X rays, and gamma radiation.

The Struggle to Survive

The science of ecology can best be defined as the experimental analysis of the distribution and abundance of organisms. Natural selection influences the distribution and abundance of organisms from place to place. The possible selecting factors include physical factors (temperature and light, for example), chemical factors such as water and salt, and species interactions. Any of these factors can influence the survivability of organisms in any particular environment. According to ecologist Charles Krebs, species interactions include four principal types: mutualism, which is the living together of two species that benefit each other (for example, humans and their pets); commensalism, which is the living together of two species that results in a distinct benefit (or number of benefits) to one species while the other remains unhurt (commensalism is shown in the relationship of birds and trees); predation, which is the hunting, killing, and eating of one species by another (examples: cats and mice; dogs and deer); and competition, which is defined as an active struggle for survival among all the species in a given environment.

This struggle involves the acquisition of various resources: food, territory, and mates. Food is an obvious target of competition. All organisms must have energy in order to conduct the cellular chemical reactions (such as respiration) that keep them alive. Photoautotrophic organisms (plants, phytoplankton, photobacteria) obtain this energy by converting sunlight, carbon dioxide, and water into sugar, a process called photosynthesis. Photoautotrophs, also called producers, compete for light and water. For example, oak and hickory trees grow taller than most pines, thereby shading out smaller species and eventually dominating a forest. All other organisms—animals, zooplankton, and fungi—are heterotrophs; they must consume other organisms to obtain energy. Heterotrophs include herbivores, carnivores, omnivores, and saprotrophs. Herbivores (plant eaters such as rabbits and cattle) obtain the sugar manufactured by plants. Carnivores (meat eaters such as cats and dogs) eat other heterotrophs in order to get the sugar that these heterotrophs received from other organisms. Omnivores, such as humans, eat plants and animals for the same reason. Saprotrophs (such as fungi and bacteria) decompose dead organisms for the same reason. Life on earth functions by intricately complex food chains in which organisms consume other organisms in order to obtain energy. Each human being is composed of molecules that were once part of other living organisms, even other humans. Ultimately, the earth's energy comes from the sun.

Competition Between and Within Species

Territoriality is equally important for two reasons: An organism needs a place to live, and this place must contain adequate food and water reserves. A strong, well-adapted organism will fight and drive away weaker individuals of the same or different species in order to maintain exclusive rights to an area containing a large food and water supply. Species that are less well-adapted will be relegated to areas where food and water are scarce. The stronger species will have more food and will tend to produce more offspring, since they will easily attract mates. Being stronger or more adapted does not necessarily mean being physically stronger. A physically strong organism can be overwhelmed easily by numerous weak individuals. In general, adaptability is defined by an organism's ability to prosper in a hostile environment and leave many viable offspring.

Within a species, males attempt to attract females to their territory, or vice versa, by courtship dances and displays, often including bright colors such as red and blue and exaggerated body size. Mating displays are very similar to the threat displays used to drive away competitors, although there is no hostility involved. Generally, females are attracted to dominant males having the best, not necessarily the largest, territories.

Competition for food and territory is interspecific and intraspecific. Competition for mates is intraspecific. In an environment, the place where an organism lives (such as a eucalyptus tree or in rotting logs) is referred to as its habitat. Simultaneously, each species has its own unique niche, or occupation, in the environment (such as decomposer or carnivore). More than one species can occupy a habitat if they have different ecological niches. When two or more different species occupy the same habitat and niche, competition arises. One species will outcompete and dominate, while the losing competitors may become reduced in numbers and may be driven away from the habitat.

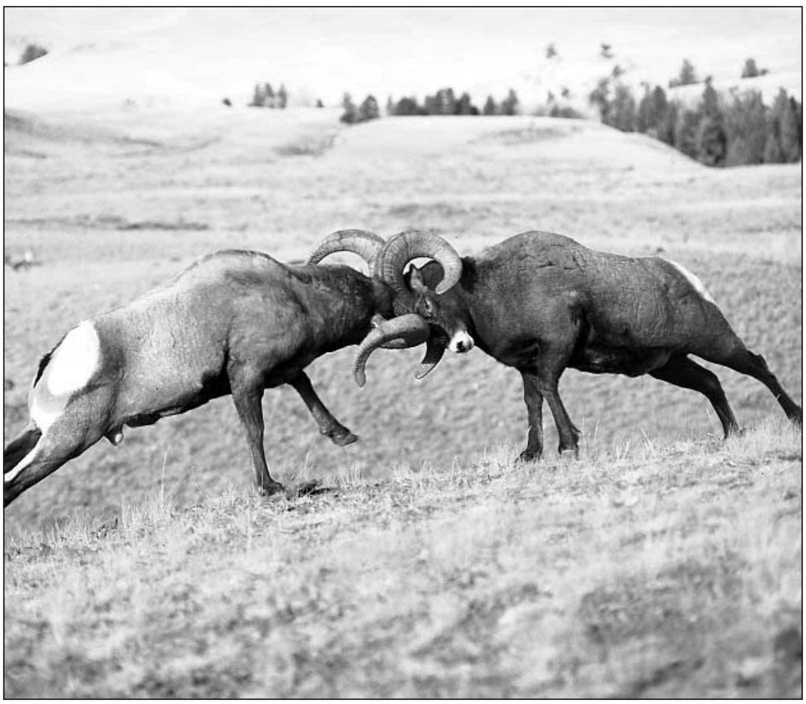
Pecking Orders

In vertebrate organisms, intraspecific competition occurs between males as a group and between females as a group. Rarely is there male-versus-female competition, except in species having high social bonding—primates, for example. Competition begins when individuals are young. During play fighting, individuals nip or peck at each other while exhibiting threat displays. Dominant individuals exert their authority, while weaker individuals submit. The net result is a very ordered ranking of individuals from top to bottom, called a dominance hierarchy or pecking order. The top individual can threaten and force into submission any individual below it. The number two individual can threaten anyone except number one, and so on. The lowest-ranked individual can threaten no one and must submit to everyone. The lowest individual will have the least food, worst territory, and fewest (if any) mates. The number one individual will have the most food, best territory, and most mates. The pecking order changes over time because of continued group competition that is shown by challenges, aging, and accidents.

Pecking orders are evident in hens. A very dominant individual will peck other hens many times but will rarely be pecked. A less dominant individual will peck less but be pecked more. A correct ranking can be obtained easily by counting the pecking rate for each hen.

In The Netherlands, male black grouse contend with one another in an area called a "lek," which may be occupied by as many as twenty males. The males establish their territories by pecking, wing-beating, and threat displays. The most dominant males occupy small territories (several hundred meters) at the center of the lek, where the food supply is greatest. Less dominant males occupy larger territories with less food reserves to the exterior of the lek. Established territories are maintained at measurable distances by crowing and flutter-jumping, with the home territory owner nearly always winning. Females, which nest in an adjoining meadow, are attracted to dominant males in the heavily contested small central territories.

A baboon troop can range in size from ten to two hundred members, but usually averages about forty. Larger, dominant males and their many female mates move centrally within the troop. Less dominant males, with fewer females, lie toward the outside of the troop. Weak individuals at the troop periphery are more susceptible to predator attacks. Dominant males exert their au-



Animals compete for territory, social status, food, and access to mates. Although the competition may be violent and painful, as when these rams butt heads at high speeds, animals rarely compete to the death. (Corbis) thority by threat displays, such as the baring of the teeth or charging; weaker males submit by presenting their hindquarters. Conflicts are usually peacefully resolved.

Female lions maintain an organized pride with a single ruling male. Young males are expelled and wander alone in the wilderness. Upon reaching adulthood, males attempt to take over a pride in order to gain access to females. If a male is successful in capturing a pride and expelling his rival, he will often kill the cubs of the pride, simultaneously eliminating his rival's descendants and stimulating the females to enter estrus for mating.

Competition Within Niches

Interspecific competition occurs between different species over food and water reserves and territories. Two or more species occupying the same niche and habitat will struggle for the available resources until either one species dominates and the others are excluded from the habitat or the different species evolve into separate niches by targeting different food reserves, thus enabling all to survive in the same habitat. Numerous interspecific studies have been conducted, including crossbills, warblers, blackbirds, and insects, to mention a few.

Crossbills are small birds that live in Europe and Asia. Three crossbill species inhabit similar habitats and nearly similar niches. Each species has evolved a slightly modified beak, however, for retrieving and eating seeds from three different cone-bearing (coniferous) trees. The white-winged crossbill has a slender beak for feeding from small larch cones, the common crossbill has a thicker beak for feeding from larger spruce cones, and the parrot crossbill appropriately has a very thick beak for feeding from pine cones. The evolution of different niches has enabled these three competitors to survive.

Another example of this phenomenon is shown by five species of warblers that inhabit the coniferous forests of the American northeast. The myrtle warbler eats insects from all parts of trees up to seven meters high. The bay-breasted warbler eats insects from tree trunks six to twelve meters above the ground. The black-throated green, blackburnian, and Cape May warblers all feed near the treetops, according to elaborate studies by Robert H. MacArthur. The coexistence of five different species is probably the result of the warblers occupying different parts of the trees, with some warblers developing different feeding habits so that all survive.

G. H. Orians and G. Collier studied competitive exclusion between redwing and tricolored blackbirds. Introduction of tricolored blackbirds into redwing territories results in heavy redwing aggression, although the tricolored blackbirds nearly always prevail.

Two species of African ants, *Anoplolepis longipes* and *Oecophylla longinoda*, fight aggressively for territorial space. M. J. Way found that *Anoplolepis* prevails in sandy environments, whereas *Oecophylla* dominates in areas having thick vegetation.

Interspecific competition therefore results in the evolution of new traits and niches and the exclusion of certain species. Mathematical models of competition are based upon the work of A. J. Lotka and V. Volterra. The Lotka-Volterra equations attempt to measure competition between species for food and territory based upon the population size of each species, the density of each species within the defined area, the rate of population increase of each species, and time.

Observing Competiton

Studies of competition between individuals of the same or different species generally follow one basic method: observation. Interactions between organisms are observed and carefully measured to determine if the situation is competition, predation, parasitism, or mutualism. More detailed analyses of environmental chemical and physical conditions are used to determine the existence of additional influences. Observations of competition between organisms involve direct visual contact in the wild, mark-recapture experiments, transplant experiments, measurements of population sizes in given areas, and competition experiments in artificial environments.

Direct visual contact involves the scientist entering the field, finding a neutral, nonthreatening position, and watching and recording the actions of the subject organisms. The observer must be familiar with the habits of the subject organism and must be keen to detect subtle cues such as facial gestures, vocalizations, colors, and patterns of movement from individual to individual. Useful instruments include binoculars, telescopes, cameras, and sound recorders. The observer must be capable of tracking individuals over long distances so that territorial boundaries and all relevant actions are recorded. The observer may have to endure long periods of time in the field under uncomfortable conditions.

Mark-recapture experiments involve the capture of many organisms, tagging them, releasing them into an area, and then recapturing them (both tagged and untagged) at a later time. Repeated collections (recaptures) over time can give the experimenter an estimate of how well the species is faring in a particular environment. This technique is used in conjunction with other experiments, including transplants and population size measurements.

In transplant experiments, individuals of a given species are marked and released into a specific environmental situation, such as a new habitat or another species' territory. The objective of the experiment is to see how well the introduced species fares in the new situation, as well as the responses of the various species which normally inhabit the area. The tricolored blackbird takeover of redwing blackbird territories is a prime example. Another example is the red wolf, a species that was extinct in the wild until several dozen captive wolves were released at the Alligator River Wildlife Refuge in eastern North Carolina. Their survival is uncertain. Accidental transplants have had disastrous results for certain species; for example, the African honeybee poses a threat to the honey industry in Latin America and the southern United States because it is aggressive and produces poorly.

Measurements of population sizes rely upon the point-quarter technique, in which numerous rectangular areas of equal size are marked in the field. The number of organisms of each species in the habitat is counted for a given area; an averaging of all areas is then made to obtain a relatively accurate measure of each population's size. In combination with mark-recapture experiments, population measurements can provide information for birthrates, death rates, immigration, and emigration over time for a given habitat.

Laboratory experiments involve confrontations between different species or individuals of the same species within an artificial environment. For example, male mouse (*Mus musculus*) territoriality can be studied by introducing an intruder into another male's home territory. Generally, the winner of the confrontation is the individual that nips its opponent more times. Usually, home court advantage prevails; the intruder is driven away. Similar studies have been performed with other mammalian, reptile, fish, insect, and bird species.

Interactions between different species are subtle and intricate. Seeing how organisms associate enables scientists to understand evolution and to model various environments. Competition is a major driving force in evolution. The stronger species outcompete weaker species for the available ecological niches. Mutations in organisms create new traits and, therefore, new organisms (more species), which are selected by the environment for adaptability.

All environments consist of a complex array of species, each dependent on the others for survival. The area in which they live is their habitat. Each species' contribution to the habitat is that species' niche. More than one species in a given habitat causes competition. Two species will struggle for available territory and food resources until either one species drives the other away or they adapt to each other and evolve different feeding habits and living arrangements. Competition can be interspecific (between individuals of different species) or intraspecific (between individuals of the same species). The environment benefits because the most adapted species survive, whereas weaker species are excluded.

—David Wason Hollar, Jr.

See also: Adaptations and their mechanisms; Coevolution; Courtship; Demographics; Displays; Ecological niches; Ecology; Ethology; Food chains and food webs; Habitats and biomes; Hierarchies; Mammalian social systems; Mark, release, and recapture methods; Mating; Predation; Reproductive strategies; Sex differences: Evolutionary origins; Territoriality and aggression.

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CONVERGENT AND DIVERGENT EVOLUTION

Type of animal science: Evolution
Fields of study: Ecology, invertebrate biology, zoology

The phenomena of convergent and divergent evolution have produced a number of good examples of natural selection at work. Thus, they provide results which can be studied in detail of interactions between environment and species which solidly validate aspects of basic evolutionary theory. Examples abound in the earth's fossil record as well as in a number of living species.

Principal Terms

ADAPTIVE RADIATION: the successful invasion by a species into a number of previously unavailable ecological niches

ANALOGUE: an individual structure shared by two or more species that is of only superficial similarity; thus, it is not indicative of a common ancestor

CLADE: a type of grouping of living or extinct species along lines of shared, unique structures, or homologues, indicative of a common ancestor; helpful in establishing evolutionary relationships

CONVERGENCE: the evolution of a similar morphology by unrelated or only distantly related species caused by both having adapted to similar lifestyles in similar environments

DIVERGENCE: the evolution of increasing morphological differences between an ancestral species and offshoot species caused by differing adaptive pressures

ENVIRONMENTAL CONSTRAINTS (PRESSURES): the physical demands placed upon any species by its surroudings that ultimately determine the success or failure of its adaptations and consequently its success as a species

HOMOLOGUE: an individual structure shared by two or more different species that is indicative of a common ancestor

Biological species have been defined as populations of organisms that are capable of successfully interbreeding (producing fertile offspring) only with other members of the same species. Members of any species possess unique sets of biological characteristics, termed "characters." These characters are physical expressions of a genetic code unique to members of that species. The code represents an extremely complex and thorough set of instructions for equipping an individual organism with the body and the behavioral knowledge it requires for success in the particular environment to which its species has adapted.

Thus, because of natural selection acting upon many past generations of that species, living members are fine-tuned to a specific ecological niche, or econiche, of the greater ecosystem of which the species is a member. When conditions within the ecosystem change (a general climatic change, for example) or when other scenarios occur, such as when a smaller subpopulation of the species migrates into new, ecologically different territory or becomes isolated in some way, selective pressure is brought to bear upon members of the group or subgroup. Random mutation is a mechanism by which selective pressure is thought to be brought about. Such mutations are changes in the genetic code that occur spontaneously in some individuals within the species in an ongoing manner. Most random mutations are insignificant phenomena with regard to the species as a whole, because most have either a neutral or negative survival value: Either they do not help the individual possessing them to survive or they are counteradaptive to an extreme degree and prove fatal. Consequently, mutations in general are not usually transmitted beyond the generation in which they occur or beyond the affected member or members. In certain scenarios, however, mutations that have a positive survival value can spread throughout the population. This is believed to be especially true when a smaller, isolated subgroup of the population is dealing with a changed or new environmental situation. Such processes are thought, for example, to have been instrumental in the evolution of groups of closely related but now morphologically distinct species found in isolated, mid-ocean island groups. These adaptive radiations of species that are monophyletic and thus share a relatively recent common ancestor are good examples of the process of evolutionary divergence at work.

The Case of the Galápagos Finches

In one of the best-known cases, studies have traced the presumed paths of divergence among a set of island bird species. This particular radiation produced a number of new species possessing novel adaptive morphologies evolved to exploit new econiches. This is the classic example of Darwin's finches. Darwin's finches are a group of closely related birds, numbering about fourteen species, found on the various islands of the Galápagos Archipelago, which straddles the equator. The islands are remote from any large body of land that would typically harbor similar birds: South America lies about 960 kilometers to the east across an unbroken stretch of the Pacific Ocean. In 1835, Charles Darwin, author of the highly influential work on organic evolution, *On the Origin of Species* (1859), visited the islands while employed as a naturalist on a British scientific voyage. His studies of the flora and fauna of these islands provided him with many observations that directly influenced his later writings.

Darwin's studies of the Galápagos finches convinced him, and generations of subsequent scientists, that the finches are a clear example of divergent evolution in operation. The scenario he deduced is that probably only one ancestral species arrived from South America by ocean currents or winds, established itself, and began to exploit the numerous, as yet unoccupied, econiches that the volcanic islands provided. In the relative ecological vacuum that the original finch species found among the islands, adaptive radiation occurred, resulting in the present, diverse species. The species of Darwin's finches found today on the islands exhibit a great variety of beak types, many of which are atypical of finch-type birds in general but rather are typical of birds found among totally different avian family classifications. Typical finches are noted for beaks adapted for the crushing of seeds—the diet of the usual members of the finch family, such as the familiar North American cardinal. Among the dozen or so Galápagos finches can be found a wide assortment of beaks adapted for obtaining or processing a much greater variety of diets. Darwin's finches include species with beaks and behaviors adapted for diets of insects, seeds, cacti, and other vegetal matter. The adaptive radiation in the case of the Galápagos finches was relatively easy to work out because of the obvious environmental factors involved (the islands' remoteness and general barrenness) and the unusual variety of adaptations that the finches had made. Establishing the details of evolutionary divergence in other living ecosystems can be confusing because the numbers and types of econiches and interacting species are often far more numerous and diverse—for example, the lush and intricate ecosystem of a large, tropical rain forest such as the Amazon.

Tracing the Fossil Record

Myriad examples of evolutionary divergence exist between both living plant and animal species throughout existing ecosystems in the modern world. The fossil record, however, also can be studied, to examine the phenomenon between extinct animal groups. This record of past life-forms preserved in the crustal rocks of the earth provides numerous examples of diverging species as organisms adapted to changing general conditions or spread into novel environments. An ex-

An example of convergent evolution is the way that sharks (left), which are fish, and dolphins (right), which are mammals, have evolved similar body shapes to adapt to their marine ecological niches. (Digital Stock)

ample is the many species of ceratopsian dinosaurs found in the latter part of the Cretaceous period of the Mesozoic era of the earth's history. Although the earlier ancestral forms appear to be bipedal and possess no significant armor, the later radiation of ceratopsians is well known by way of such impressive animals as *Triceratops*, a typical ceratopsian: a heavy, quadrapedal herbivore with a large, horned and beaked skull with a defensive, bony frill. Many variations on the basic late ceratopsian body architecture evolved through divergence. Varieties included such forms as *Pentaceratops*, *Torosaurus*, *Styracosaurus*, *Chasmosaurus*, and *Centrosaurus*, among many others. In all these later animals, the basic morphology regarding body, tail, and limbs remained the same. All forms also retained the typical massive, beaked head. What diverged were such morphological features as number and length of facial horns and length and degree of ornamentation of the frill. One of the important things that study of such fossil forms shows is that such past examples of evolutionary divergence eloquently underscore the continuity of the evolutionary process through time down to the present living world. This continuity further reinforces the validity of basic evolutionary theory in general.

Evolutionary Convergence

A related phenomenon concerning adaptive evolution is the phenomenon of evolutionary convergence. This process can be described briefly as the evolution of similar body structures in two or more species that are only quite distantly related; they therefore come to resemble each other, sometimes to a startling degree of at least outward sameness. These sets of similar-looking but polyphyletic species frequently even display similar behavioral characteristics. All similarities found in convergence cases are believed to be attributable to the fact that the various species involved have adapted to a similar econiche within a similar ecosystem. Because in nature, form follows function and the morphology of an animal or plant is the product of environmental pressures that continuously favor the better-adapted organism, it is easy to understand how convergence can take place. Like divergence, the evidence for convergence can be traced not only among the many participants in contemporary biospace but also over the course of vast stretches of past time.

One of the classic examples of convergence is a threefold example that, conveniently, not only includes representatives from three different classes of vertebrates but also spans many millions of years of time and includes an extinct group. This is the textbook example that compares and contrasts the morphology of sharks, a type of cartilaginous fish; ichthyosaurs, an extinct type of marine reptile; and dolphins, marine mammals like whales. All three groups possess numerous member species, both fossil and alive (except for ichthyosaurs), which resemble each other in body plan and lifestyle. All three groups include species which lead (or led) an open ocean, fish-eating existence. Consequently, the forms of their bodies came to follow the functions dictated by their environment—sometimes termed their environmental constraints. All three groups' general body plan began to approach a hydrodynamic ideal for a water-living animal: a streamlined fusiform, or spindle shape, efficient in passing through an aqueous medium. Besides this feature, pelagic, or open ocean-living, sharks, ichthyosaurs, and dolphins all evolved a dorsal fin to act as a vertical stabilizer for water travel. In addition, each group evolved a propulsive tail and a pectoral fin necessary for the demands of constant swimming and steering in water. Even more remarkable in this comprehensive example, dolphins' and ichthyosaurs' ancestors were both originally land-dwelling vertebrates that returned to the marine environment. This case presents an inclusive and persuasive argument for the reality of the phenomenon of convergent evolution.

As with the use of both living and extinct examples in the discussion of divergent evolution, the existence of fossil as well as contemporary species that display convergent morphology is convincing evidence for the process of adaptive evolution. Again, a continuity across vast stretches of time exists that connects evolutionary phenomena in a continuum.

Observation, Comparison, and Classification

Research in the field of adaptive evolution, especially the phenomena of divergence and convergence of species, began centuries ago with the simple process of recognizing relationships in the surrounding environment between living plants and animals. The search for a unifying order to tie the complex web of animal and plant life together in some meaningful manner was for a long time a part of natural science. The modern theory of organic evolution fulfills this goal admirably in many respects. The methods used to illuminate the intricacies of evolution still encompass the type of keen, analytical observation of phenomena and reflection on their causes and effects that characterized Darwin's studies on the voyage of HMS *Beagle*. Observation, collection of specimens for comparison, classification of specimens according to a meaningful scheme, and, finally, an attempt to sort out the processes involved in a way that agrees with the dictates of strict logic are hallmarks of the scientific method at work.

Researchers investigating evolutionary divergence and convergence have powerful aids in the form of increasingly sophisticated technology. The main focus of their work is the correct interpretation of the path that various lineages took over time to arrive at known, living forms or extinct forms. In the case of living forms, technology originally developed in the field of medicine has been pressed into service to help establish relationships. For example, detailed analyses of various body tissues and fluids have been employed. Blood types have been traced with varying degrees of success, as have various proteins. Powerful optical microscopes are employed to analyze various tissue types and their structures. Since the invention of scanning electron microscopes, these more powerful instruments have further aided in probing the compositions and textures of animal and plant tissues to determine affinities among various species. In addition to these methods, very sophisticated laboratory techniques are now used to unravel and analyze deoxyribonucleic acid (DNA) strands and to try to determine the actual genetic encoding possessed by a particular organism. All these methods help establish more clearly the picture of biological relationships in regard to ancestries.

This physiological approach is obviously of limited utility with regard to fossil species. Except for such instances as the various ice age animals that were frozen in such environments as the tundra, extinct life-forms cannot be analyzed by medical means, as the original tissue has been transformed or destroyed by geological processes. In the case of most fossil forms, hard body parts such as bones and teeth (for vertebrates) and exoskeletons (in the case of invertebrates) must be analyzed in a more structural way to determine possible evolutionary relationships.

The clarification of the paths that various animal and plant lineages took during the process of their evolution further confirms the validity of basic organic evolutionary theory such as natural selection and adaptation. Study of divergent and convergent species is part of the ongoing study of living organisms that make up the functional ecosystems of which humankind is also a part. Learning more about these ecosystems and the parts that all the member species play within them is extremely important in the light of the contemporary world picture of pollution, overpopulation, and industrialization. The increased insight into how ecosystems operate from the species interaction approach is one of the positive by-products that studies of divergent and convergent evolution among species provide.

—Frederick M. Surowiec

See also: Adaptations and their mechanisms; Adaptive radiation; Birds; Competition; Development: Evolutionary perspective; Ecological niches; Ecology; Evolution: Historical perspective; Extinction; Fauna: Galápagos Islands; Fossils; Habitats and Biomes; Invertebrates; Isolating mechanisms in evolution; Mammals; Natural selection; Paleontology; Phylogeny; Predation; Reptiles; Systematics; Vertebrates.

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COPULATION

Type of animal science: Reproduction
Fields of study: Anatomy, developmental biology, embryology, reproduction science

Copulation, also called coitus or sexual intercourse, is the process by which sperm are placed directly into the female reproductive system by the male reproductive system, thus assuring that sperm and ova are in close contact for fertilization. It is also a critical adaptation for land-based reproduction, since on land, unlike in the water, sperm released into the environment cannot swim to ova that have also been released. The behaviors leading up to copulation are also important in assuring that gametes of the same species meet for fertilization.

Principal Terms

AMPLEXUS: a form of pseudocopulation seen in amphibians, where the male mounts and grasps the female so that their cloacae are aligned, and eggs and sperm are released into the water in close proximity and at the same time

CLOACA: a common opening for the reproductive, urinary, and digestive systems

HEAT: that part of the estral cycle when the female is receptive to male copulatory behavior

SEMEN: fluid produced by the male reproductive system that contains the sperm

Animals have many diverse strategies to ensure that eggs and sperm are in close enough proximity for fertilization to take place. One widespread process that is seen in many different phyla is copulation. Copulation is seen in many aquatic phyla and is the rule in terrestrial phyla. In most forms of copulation, the male reproductive system has an intromittent organ, often called a penis, which deposits sperm into the female reproductive system. Once there, sperm can travel the short distance to the eggs.

In some organisms, pseudocopulation is seen. In hermaphroditic oligochaetes, such as earthworms (*Lumbricus terrestris*), two worms align in opposite directions so that their genital pores are applied to the openings of the seminal receptacles of their partners. Semen released by the genital pores flows into the seminal receptacles where it is stored. Fertilization, however, is actually external. The worms build cocoons where they lay their eggs and then deposit the stored sperm. Amphibian amplexus is also a form of pseudocopulation. Here, the male frog clasps the female in such a way that their cloacae are in close proximity. Sperm are not deposited in the female's cloaca, however. Instead, both sperm and eggs are released into the aquatic environment for external fertilization.

Copulatory Organs

True copulation takes many forms. In several invertebrates, such as a few flatworms (some Acoela, Rhabdocoela, and Polycladida) and the bedbugs (Cimicidae), hypodermic injection is sometimes seen. In this form of copulation, the female has no external gonopore and the intromittent organ punctures the epidermis and deposits sperm in the underlying body tissue. This sperm must then migrate through the intercellular spaces to the female reproductive organs for fertilization of the eggs to occur. In most organisms, however, the male does not have to pierce the female's epidermis, but instead deposits sperm in an already-present opening of the female's reproductive system.

In birds and some reptiles (such as the tuatara, *Sphenodon punctatus*), the male does not have a true intromittent organ. Instead, the male must manipulate the female during mounting so that their cloacae are pressed against each other. During this "cloacal kiss," the male ejaculates sperm into the female's cloaca. In some bird species, a false penis is present in the male. These organs are not connected to the ducts of the male reproductive system and thus do not serve as intromittent organs. There is speculation that they may provide a necessary stimulation to the female during copulation.

In some fish, fins are modified for semen delivery. In guppies and their allies (Poeciliidae), gonopodia, modified anal fins, are used for insemination. Each gonopodium is a hollow, tube-like structure formed from the paired anal fins of the male. When mating, the male inserts his gonopodium directly into the female's gonopore. Usually, not all the sperm are used to fertilize this batch of eggs, and the rest is stored in the oviduct walls for future fertilizations. Other fish (such as the Coodeidae) have the anal fins modified into andropodia, which are cup-shaped structures that direct the flow of semen into the female without the andropodia actually entering the female's gonopore. Sharks (Elasmobranchii) have modified pelvic fins called claspers, which the male directs into the female's cloaca for insemination. Each shark has two claspers and, depending on species, either the one closer to the female or both are inserted for copulation.

Males of mammals, some reptiles, and many arthropods also have intromittent organs that deposit sperm directly into the female reproductive tract. In these copulations, by either female behavior or male manipulation, the opening of the female reproductive tract must be exposed. In many organisms, the male mounts a squatting or otherwise stationary female. Male snakes and lizards (Squamata) have two intromittent organs called hemipenes. Males and females line up side by side and the male uses the hemipenis closer to the female to inseminate her. Many arthropods often go through intricate body contortions to bring the male's penis in proper position for mating. This may be the common rear-mounting pattern, but can also be face-to-face or tail-to-tail. In many animal species, insertion of the penis is followed by one or more thrusting movements that lead to ejaculation.

Copulatory Behaviors

Among animals, both the lengths of time per copulation and the frequencies of copulation vary widely. When a female lion comes into heat, the male will remain near her, copulating up to one hundred times a day for periods up to ten days. Each copulation, however, lasts for just a few seconds. Other animals may copulate only once, but the copulation may be prolonged. Canid females do not usually remain stationary for mating. To remedy this, once the male mounts, his penis becomes further engorged and this effectively locks him to the female long enough to ejaculate even if she tries to get away. Other animals have hooks and barbs on their penises that may also help to lock them to a female for prolonged copulation. In some animals, prolonged copulation can last sev-

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Echidna Mating

The female echidna, or spiny anteater (*Tachyglossus aculeata*), an Australian monotreme mammal, makes it rather difficult for the male to access her cloaca. As a female comes into heat, she is followed closely by one or more males that will try to mate with her. When she is ready to mate, she lies flat on the ground on her abdomen, often grabbing a tree or other support with her forelegs. This directs her cloaca toward the ground, certainly not exposed toward the male. If there are no other males present, the single enterprising male must dig a ditch on one side of the female. When it is deep enough, he can descend into the ditch, turn on his back and insert his tail beneath the female's tail. This positions his penis to enter her cloaca and deposit semen. When more than one male is present, they dig a semicircular rut on both sides of the female's tail, in which rut the males jostle for position until one finally maneuvers his tail under the female's. If all goes well the female lays a single small egg a few weeks later that she incubates in an abdominal pouch until hatching.

eral hours. This may be a mechanism to prevent other males from fertilizing the same female. Females can also play a role in prolonging copulation. In some water mites (*Arrenerus* sp.), the female gonopore can be opened or closed by means of chitinous plates. The smaller male inserts his intromittent organ into the female's gonopore, which then closes, trapping the male. Although sperm transfer is thought to occur in the first few minutes, the female may swim off dragging the male with her for several hours.

Copulation can be dangerous to males. In the domestic honeybee (*Apis mellifera*), a swarm of drones pursue the unmated queen. In-air copulation occurs as a drone inserts his endophallus into the queen's sting chamber. After ejaculation, a small part of the drone's phallus remains inside the queen and the drone falls to the ground and soon dies. Several more drones mate and die until the queen's spermatheca is filled. Male spiders have to be very careful when copulating. If a male does not leave the female's web immediately after depositing his sperm, the female may envenomate and then eat him. The female praying mantis (*Stagmomantis carolina*) have also been known to begin feeding on the heads of males with which they are copulating. Luckily, the headless male can continue to deposit sperm.

—Richard W. Cheney, Jr.

See also: Asexual reproduction; Breeding programs; Cloning of extinct or endangered species; Courtship; Estrus; Fertilization; Hydrostatic skeletons; Mating; Parthenogenesis; Reproduction; Reproductive strategies; Reproductive system of female mammals; Reproductive system of male mammals.

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CORAL

Types of animal science: Anatomy, classification
Fields of study: Anatomy, invertebrate biology, marine biology

Coral refers to a large group of marine invertebrates, class Anthozoa, in the phylum Coelenterata. Anthozoa form reefs, gorgeous coral bushes, and precious coral.

Principal Terms

BUDDING: development of asexually produced protuberances that become complete organisms

EXOSKELETON: an external skeleton

HORN: hard, smooth, keratinous material forming an external covering

LIMESTONE: the insoluble calcium-containing substance, calcium carbonate

PLANKTON: microscopic plants and animals that float in huge numbers in oceans

RADIAL SYMMETRY: symmetry around a central axis

Coral refers to a large group of marine invertebrates, class Anthozoa, in the phylum Coelenterata. Anthozoa form reefs, gorgeous coral bushes, and precious coral, used for jewelry. The individual organisms involved are coral polyps. They have protective calcium carbonate (limestone) or horn skeletons.

Stony corals of the order Scleractinia, also called true corals, form reefs. The reefs are limestone formations in oceans, made by billions of polyps. The polyps have saclike shapes, with a mouth at the upper end, surrounded by tentacles. Coral polyps form reefs from calcium taken from ocean water and deposited around their bodies.

Besides reef-building corals, their relatives, gorgonians, have skeletons of flexible, horny material. Gorgonians make coral bushes and lacy-looking coral fans. These formations are covered with live polyps, which are yellow, pink, purple, brown, and even black. Wherever they occur, such as in West Indian waters, the forms produced look like parts of underwater gardens.

Precious coral is used to make jewelry. It is produced by polyps closely related to gorgonians. This hard coral polishes into beautiful red, rose, or pink material that can be made into jewelry beads. Most precious coral grows as small "bushes" in the Sea of Japan and the Mediterranean.

Physical Characteristics of Coral Polyps

There are two colonial anthazoan subclasses, differing in radial symmetry. The first, Octocorallia, is composed of eight-tentacled animals. Included are gorgonians and red precious coral. Members of the second subclass, Hexacorallia, have six tentacles (or multiples of six tentacles). Hexacorallia include true corals (Scleractinia).

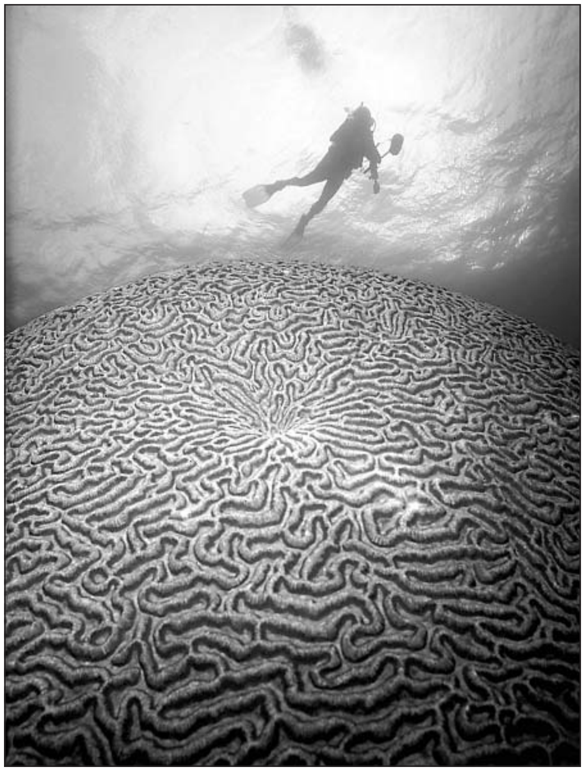
Most scleractinians are colonial. Their polyps have diameters of about 0.1 inches and are interconnected. The shapes of coral colonies, such as branched forms, depend on the coral species. Colonial corals can grow in deep waters, but reef-building corals occur only in warm, shallow ocean regions. The true corals secrete calcium carbonate from the bottom of each polyp, forming skeleton cups in which each polyp is anchored and into which it withdraws for safety. In an oral apparatus atop the stalk is an opening with tentacles and cilia. It serves as both mouth and anus. At night, the tentacles catch plankton and carry them to the mouth. Stinging cells on the tentacles paralyze prey.

Life Cycles of Coral Polyps

Each coral colony grows by asexual polyp budding. Live polyps build on limestone or horn deposits of past generations. In this way, they make new reefs or other coral masses. The polyps remain associated in colonies. The combined limestone- or horn-forming activity of a colony yields huge masses of coral. They may be dome-shaped or towering and branched.

Live polyps cover the outside of each mass and create its gorgeous colors, ranging among tans, browns, oranges, yellows, pinks, purples, and greens. When reef coral is removed from the ocean, the polyps die and wash off, leaving behind white skeletons. These corals build foundations for tropical atolls and barrier reefs.

Reef corals must live at depths where light penetrates, because symbiont algae (zooxanthellae) that live in their tissues require sun light for photosynthesis, and polyps cannot exist without the algae. The algae produce most of the carbon compounds that polyps use to make energy and protoplasm. The plankton caught by polyps provides the algae with nitrogen, phosphorus, and other nutrients otherwise unavailable. The coral's dependence on the algae varies with coral species and habitat.



This hard coral is composed of the fused, calcified exoskeletons of thousands of individual corals. (Digital Stock)

Coral Facts

Classification:
Kingdom: Animalia
Phylum: Coelenterata
Class: Anthozoa
Subclass: Hexacorallia (six-tentacled or six-tentacle multiples), Octocorallia (eight-tentacled)
Orders: Include Gorgonia (bush or fan corals), Scleractinia (true corals, Hexacorallia)
Geographical location: Mediterranean, Sea of Japan; east coast of the Americas from Brazil, through the West Indies, and along Florida coast; the Bahamas and Bermuda; South Pacific islands; East Indies; Indian Ocean; around Australia
Habitat: Marine, warm to tropical waters
Gestational period: None; reproduction uses asexual budding of indeterminate duration
Life span: Coral colonies can live indefinitely as living polyps grow on the skeletons of dead ones
Special anatomy: Tentacles, exoskeletons

Coral Reefs and Atolls

Coral reefs, elevated parts of shallow ocean floors, form by accumulation of calcium-containing exoskeletons of scleractinian polyps. The tropical reefs extend to 30 degrees north and south of the equator. They form only in shallow waters, at temperatures of 65 degrees Fahrenheit or warmer.

The three reef types are fringing reefs, barrier reefs, and atolls. Fringing reefs extend from the shore, with no body of water between reef and land. Barrier reefs are farther offshore, follow shorelines, and are separated from them by lagoons. They form barriers between the shore and the open ocean. Atolls are coral islands that have narrow, horse-shoe reefs and shallow lagoons. Many South Pacific islands are atolls.

Reefs are especially abundant on the east coast of the Americas from Brazil to the West Indies, along Florida's coast, and through the Bahamas and Bermuda. Very beautiful reefs occur in the South Pacific islands, the East Indies, and near Madagascar. The most magnificent coral reef is the Great Barrier Reef of Australia, over 1,200 miles long.

Polyps that build reefs have diameters from 0.05 inches to 1 foot. Constant battering by the ocean breaks up the reefs. The pieces accumulate over time, and eventually reach above the ocean surface. Soil deposited by ocean water lodges on them, and seeds wash up and become vegetation. Then the pile of coral debris becomes a coral island or atoll.

—Sanford S. Singer

See also: Asexual reproduction; Communities; Ecological niches; Ecology; Ecosystems; Exoskeletons; Fauna: Caribbean; Fauna: Madagascar; Fauna: Pacific Islands; Marine biology; Reefs; Shells; Symbiosis.

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COURTSHIP

Type of animal science: Behavior
Fields of study: Ethology, invertebrate biology, zoology

Courtship is a set of behaviors that function to bring males and females of the same species together for the purpose of mating and reproduction. Courtship usually is quite similar among individuals within a species but is usually quite distinctive among individuals of different species. The behavior increases the likelihood that males and females are brought together at a time when mating is most likely to be successful.

Principal Terms

ARACHNID: a class of arthropods with jointed legs and hard external skeleton that includes mites, scorpions, spiders, and ticks

ESTRUS: the period during a female's sexual cycle when she is sexually receptive

LEK: a territory used by certain animals for mating

MONOGAMY: a mating system in which one male pairs with one female

PHEROMONE: a chemical produced by one animal that influences another animal of the same species

POLYGAMY: a mating system is which an individual of one sex pairs with several of another sex

Courtship is the ritualistic behavior animals carry out preceding mating. The courtship process allows the male and the female of the species to attract each other and choose a mate for reproduction. This behavior varies greatly among the species. Courtship rituals for mating can be as simple as sign stimuli, such as the emission of pheromones by certain female moths, to the complex dance of the stickleback or the bowerbird.

In nature, most animals are solitary except when courting and rearing their young. For each animal the signals used to communicate with and attract a mate must be clear and unambiguous. This is to avoid any confusion in identifying the sex and species of an animal's potential mate, as the ultimate goal of nature is to encourage reproduction and survival of all species.

The procreation process in most multicellular plants and animals involves a complex form of sexual reproduction. Here unique and differentiated male and female reproductive cells called gametes unite to form a single cell known as the zygote. The zygote undergoes successive divisions to form a new multicellular organism where half the genes in the zygote come from one parent and half from the other, creating a singularly different living creature.

The sexual reproduction process requires a pair of distinct partners of opposite sexes to mate, hence the need for courtship, so that animals can find and attract prospective mates for producing offspring. It is the sexual interest of the opposite sexes that leads to mating; therefore, copulation in most animals is preceded by a period of courtship. The mating of most lower animals is governed by endocrine secretions specific to certain seasons. In female mammals, receptivity to mating is called estrus, which is operative only for short periods during the year. Cows have several such periods of estrus during the year; dogs have one or two.

As courtship is always a precursor to mating, which leads to the proliferation of the species, it is often intermixed with both greeting and aggression. Often the aggression is directed toward a rival that might wander into marked territory. What is fascinating is that quite often it is difficult to distinguish between greeting and aggression. There are many different types of courtship be-

Pseudoscorpions: Unusual Courtship in Invertebrates

Pseudoscorpions are arthropods in the order of Pseudoscorpinadea. These are a group of small arachnids, such as spiders, mites, and ticks, that look like scorpions but do not have the scorpion's tail and sting. Even though the sexes in these creatures look very similar, they have complex courtship displays. The male in some of these species will drop a sperm bundle or spermatophore, which is often in the shape of a stalk, onto the ground. The female is attracted to this either by some chemical in the deposit or by a strand of silk left by the male. The female situates herself on top of the spermatophore and admits it into her own body through her genital opening. There are other species where the male steers the female to the spermatophore and helps her to position herself above it. He does this by grabbing her pedipalps. These are small appendages that resemble pincers with poison glands at their tips. The male pushes and vibrates against her to help in the reception of the sperm into her body. After the successful transmission of the sperm into her body, the female is ready to produce eggs. At this point, the female in several species of spiders will devour the male simply for nourishment. Although this is quite a common practice in spiders, the black widow is renowned for it, hence the name. This carnivorous mating behavior is not uncommon in nature. The female praying mantis, which is not an arachnid, does the same with its mate.

havior, including shoaling, nest building, mouth or pouch brooding, parasitic mates, carnivorous mates, marking territory, pair bonding, domination, female dominance, bower building and gift offerings, communal display, exotic pirouettes, group breeding, monotremes, odor marking, color signals, sounds, and migration.

Fish Courtship

The male stickleback, a fish similar to the minnow, orchestrates its mating by changing its color. During breeding season the underside of the male turns bright red. The bright red not only attracts females but also instigates attacks from other males. In fact, studies have shown that during this time, just about any red object can provoke male stickleback aggression. The female's response to the red signal of the male stickleback is to advance in a posture that clearly exhibits her swollen, egg-filled underbelly. This stimulates the male to carry out a zigzag dance that in turn seduces the female into following him to the tunnel-like nest he has built. The male waits until the female struggles into the nest and immediately touches her tail with his nose and starts quivering. The vibration causes the female to release her eggs so that the male stickleback can externally fertilize them. If for some reason the male is unsuccessful in executing the last part of this intricately choreographed dance, the female will not lay her eggs. However, it is extremely interesting to note that vibrating the female with some arbitrary object, which she may even realize is not a male stickleback, works just as well to induce the release of the eggs, although, as the male did not complete the last step of the courtship ritual, he does not fertilize the eggs, but rather eats them.

Amphibian and Reptile Courtship

Amphibians have varied and interesting courtship rituals. Generally the tailless amphibians breed communally. Amphibians such as frogs or toads will use sound to attract their mates, whereas male newts use odor to attract the females. The American tree frog (*Hyla crucifer*) sings in trios. Only the males have vocal sacs that can make sounds; the females are silent. The sounds of the males among the different species are distinctly different and versatile. The notes are delivered in different speeds and frequencies. The female has her own features of recognition. The way a female frog advertises her sex and readiness for mating is that she develops a series of granulations on her thighs, which is clearly visible to a male frog. During courtship many amphibians use their heads in different ways to rub their partners. For most frogs, the male climbing onto the female's back and aiding in the discharge of her eggs accomplishes mating. The male in turn releases his sperm after being excited by the female's movements.

In reptiles, even though the courtship behavior is not very complex, bobbing, circling, and marking of territory is noticed. Snakes such as the crotalids, including vipers and rattlesnakes, have a mutual dancelike ritual for courtship. As the snakes circle each other, they rear up facing one another and intertwine together for copulation. Most snakes of the Crotalidea family give birth to living young from eggs that hatched inside the mother's body. The colubrids, such as the boomslangs and kingsnakes, and elapids, such as the cobras, have a nuptial procedure where the male rubs his lower jaw along the back of the female in an attempt to stimulate her. It is conjectured that perhaps this behavior also stimulates him and all the other males in the matrix group. A male snake copulates by throwing coils round the female and bringing their cloacas into juxtaposition. However, sometimes they simply lie close without the retaining coils. They may use a branch or similar object to maintain a grip to hold them close together. Even though most snakes are more aggressive during mating season, few males fight among themselves. Other than among the elapids there does not seem to be much competition among the males.

This is contrary to what is noticed in crocodiles and alligators. In these reptiles, the breeding season for the males is a loud and contentious time. They will battle and resist any potential competitor with ritual gaping, lunging, and hissing. Yet the courtship behavior is serene. The male marks his territory using a secretion from his musk glands. This not only warns off unwelcome male rivals, it also attracts females. Male crocodiles and alligators confidently bellow their love calls to make their presence and location known to the females. Once a female gets paired with a male, they swim together. They progressively increase their speed and the male rubs his throat against the female's snout to mark her with his odor, and vocalizes without encumbrance before he copulates with her. The male leaves to find his own area after mating. The female goes on to build a nest above flood level using mud and vegetational debris. She covers her eggs with mud and decaying vegetation so that the sun's heat will incubate her eggs. She guards her eggs until they are hatched. She may aid the young ones to get to the water's edge by carrying them in her mouth. It has been observed that some female alligators may even stay with their young for a year or more. A female alligator is quite protective of her young and responds quickly to the sharp croaks of a young one in distress.

Bird Courtship

Birds in general have engaging and quite elaborate courtship rituals. Usually birds do not stay with the same mate all year round or from year to year. Sometimes the same pair may be together for several years, but nonetheless the pair bond, that is, the relationship of the couple, must be renewed or reinforced at the onset of each breeding season. Birds use auditory, visual, or both kinds of display in order to conclude their courtship ritual. Peacocks use intricate visual displays that involve specialized plumes. In the barbets and wrens, duetting is used for courtship and attracting the mate. The male and the female alternate their calls in such exact synchronization that it seems as though the sound is coming from one bird. This is an example of an auditory display. Some birds, such as ducks, follow an extremely stereotyped movement pattern. However, both birds must respond with the correct display or the sequence is broken. There are certain birds where a pair bond does not exist at all. The male birds gather together and display against each other, contending for the right to mate with the maximum number of females possible. This type of a gathering of males is called a lek. The bird of paradise is well known for this particular type of courtship behavior. Other examples would be manakins, sandpipers, and grouse.

The different types of bowerbirds are renowned for their extraordinary courtship behavior. These birds are commonly found in New Guinea and Australia. It is believed that the bowerbirds are close relatives of the birds of paradise of this area. For the most part, the males and females live apart from each other during the course of the year. Only during mating season do the males gather together and compete for females. Each male bird creates a clearing on the forest floor that becomes his "playing field." This is where he tries to entice and lure the females. The bird will arrange rocks, shells, colorful fruits and berries, flowers, and inanimate articles such as pieces of glass or other interesting manmade items. In some species, the males will construct different types of forms and structures. Some of these birds erect what look like upright poles of sticks around a tree trunk that are embellished with colorful flowers, mushrooms, lichens, and other objects.

The Australian male satin bowerbird is a silky blue-black bird that is approximately 20 centimeters (about 7.8 inches) long, with bright blue eyes. The male bird builds a stick mat. He then places two walls of vertical sticks down the middle. These walls may reach a height of thirty-eight centimeters (sixteen inches). The bird then mixes his own saliva with a blue or green fruit juice to form a "paint." He uses a tree bark to paint the bower, and tries to attract the grayish-green female into the bedecked bower to mate. This is one of the few known instances of birds using tools.

Another species known as the gardener or Vogelkop bowerbird makes a tentlike structure that resembles a teepee. The bird is only about 25 centimeters (10 inches) long, but the teepee can be as extensive as 1.6 meters (63 inches) across. This little teepee comes complete with a low entranceway overlooking a "garden," consisting of brightly colored flowers and objects that are diligently replenished as soon as they fade. There are about nineteen species of bowerbirds and they all have similarly elaborate courtship displays.

Mammal Courtship

Mammals have evolved to have the most sophisticated sexual apparatus of all animals, yet in general mammals do not spend as much time in courtship as birds do. Mammals also have the most highly evolved manner of parenting. Therefore, the relationships between mates are diverse. Lower mammals, such as some rodents, practice promiscuous polygamy without any particular selection process by the female. The females are left to rear the young on their own. In bears, both the male and female are promiscuous. There are others where the male appears to have a harem. The California sea lion may have up to forty females, the Pribilof seal from forty-five to a hundred. Many deer and antelope have harems, too. Even the sedate koala may monopolize several females. These are also examples of dominance. Dominance can also extend toward other males, so that the dominant male can have all the females to himself.

Monogamy is rarer in mammals. A few canines are monogamous, but only for a particular season. Some monkeys and apes, not including chimpanzees, follow this rule. Foxes may be monogamous, and the American beaver is one rare mammal that practices monogamy for life. Even in the higher mammals, including humans, monogamy causes a decline in sexual interest for the partner and eventually sexual relations may cease if there is no stimulus of novelty. There is also the other extreme, where the animals are solitary and only meet for copulation, such as the titi monkey.

Most mammals tend to be complacent in their efforts at enticement, and rely on simpler stimuli such as secretions, color changes, and odors. For mammals, arctic foxes have an elaborate and rather graceful courtship dance. They rear up on their hind legs and face each other as though they are playing. The elephant has a most gentle approach to courtship. The female is attracted to the male by the strong scent of the two glands near his ears, which start to secrete during rut. Once the male and female have found each other, they caress one another with their trunks and intertwine these sensitive organs. They express their affection and confidence by placing the tips of their trunks in each other's mouths.

In some species, the female takes the initiative for mating. A small number of primates will do so. When the female is ready she entices the male to attend to her. The female hedgehog will lift her tail up and lay all her spines down to solicit the male for mating.

Odor marking is very common in placental mammals. Most male mammals, even the pack animals, will mark out their territory by odor glands, urine, or feces. Some will mark the female as a sign of ownership. There are others that display color, signaling a potential partner of the opposite sex of its interest in mating. The female gelada baboon, which mostly spends her time sitting, develops a red patch on her chest similar to the one in her genitals, so that both markings can be easily observed by other baboons.

In many different animals, migration is required as part of the courtship and breeding process. Migratory rituals exist in just about all types of animals: fish, birds, and mammals. Some fish, such as the salmon or sturgeon, will travel thousands of miles in order to return to their ancestral waters to spawn. The urge is so strong that the fish will die trying to reach this place rather than give up.

Ultimately, nature's most primordial instinct is to continue the species. Every living organism feels the irrepressible compulsion to perpetuate its genes. This necessitates sexual selection, Darwin's other type of natural selection. The consequence is sexual dimorphism, including different size, color, and traits in the sexes. There are two types of sexual selection: intrasexual selection, where males contend among themselves through contests and displays for the favor of a female; and epigamic selection, where the females accept males with certain characteristics. The male may monopolize the females by practicing polygamy and thereby effecting a much more intense sexual selection for procreation purposes. Courtship behavior is about sexual selection, which eventually leads to the proliferation of the species.

—Donald J. Nash

See also: Asexual reproduction; Breeding programs; Cloning of extinct or endangered species; Copulation; Estrus; Fertilization; Hydrostatic skeletons; Mating; Parthenogenesis; Reproduction; Reproductive strategies; Reproductive system of female mammals; Reproductive system of male mammals.

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CRABS AND LOBSTERS

Types of animal science: Anatomy, classification
Fields of study: Anatomy, invertebrate biology, marine biology

Crabs and lobsters are joint-legged crustaceans of the phylum Arthropoda. Phylum characteristics include a chitinous exoskeleton, jointed appendages, a ventral nervous system, and a dorsal brain.

Principal Terms

ABDOMEN: posterior portion of a crustacean

CEPHALOTHORAX: combined head and thorax

CHELICERAE: also called pincers, claws, or chelipeds, these are the enlarged first and sometimes second pairs of walking legs, which are used for feeding, defense, or sexual recognition

DECAPODS: animals with ten appendages (from Greek *deca*, "ten," plus *poda*, "foot or leg")

THORACIC: related to the middle section of the body of arthropods, which are generally subdivided into a head, thorax, and abdomen; both thorax and abdomen may have several segments

Crabs and lobsters are joint-legged animals that belong to the phylum Arthropoda. This diverse phylum of animals also includes the insects, spiders, ticks, mites, millipedes and centipedes. Phylum characteristics include a chitinous exoskeleton, jointed appendages, a ventral nervous system, and a dorsal brain. Both crabs and lobsters are crustaceans, which are placed in the class Malacostraca along with the shrimp. Crabs differ from lobsters in having a broad upper shell or carapace and an abdomen that is shorter and either tapered or tucked forward beneath the carapace.

Because they have five pairs of legs, crabs and lobsters belong to the order Decapoda. The first one or two pairs of legs are typically enlarged and modified as chelicera, which are variously used for feeding or defense. In some decapods they may also have a sexual function. The remaining three or four pairs of legs are used for walking, or, in some species, swimming or climbing.

Crabs

There are two kinds of crabs. The irregular-tailed crabs, or Anomurans, include the hermit, porcelain, and mole crabs. Some have a small, tapered abdomen, and others, especially the hermit crabs, have a somewhat coiled abdomen that is tucked into a discarded snail shell. The true crabs, or Brachyurans (short-tailed crabs), have a greatly reduced abdomen that is tucked forward beneath the carapace.

Contrary to popular belief, crabs do not always scuttle sideways; they can walk forward or backward with equal facility. A few of the fast moving crabs seem to use two pairs of legs when running. The blue crab (*Callinectes sapidus*) family, which also includes the familiar lady crab (*Ovalipes ocellatus*) have a paddlelike last pair of appendages and are fast and agile swimmers.

Crabs vary greatly in size and shape. The smallest are pea crabs, which measure only a few millimeters across the carapace, while the legs of a Japanese spider crab can span up to four meters. The differences in size and shape have allowed crabs to colonize a wide range of habitats. Most of the 4,500 species of true crabs are marine, inhabiting the rocky intertidal zone or burrowing in sand and mud. Some species are benthic and others invade freshwater, especially in the tropics. Still others are terrestrial or semiterrestrial, often ranging far away from water, although they generally prefer moist places. A tree-dwelling tropical species feeds on coconuts.

Ecologically, almost all crabs function as scavengers, feeding on dead or dying animals or organic debris of any kind. Many species are also active predators, capable of killing small fish and breaking open the shells of different mollusks. Porcelain crabs, for example, have one of their mouthparts equipped with long, feathery setae that are swept through the water. They catch small particles and transfer them to other parts of the mouth, where they are eaten. Organic matter is dismembered by the pincers and conveyed to the mouth by a series of appendages called maxillipeds and maxillae. A pair of comblike mandibles guard the mouth and chop the food into tiny pieces, which are then swallowed. A short esophagus leads to a gastric mill analogous to the gizzard of other animals, where food is ground up.

Crab Reproduction

Reproductive behaviors vary, but during courtship males may use various chemical, visual, or acoustic signals including pheromones, waving chelipeds back and forth, or drumming at the entrance to the female's burrow. Other males build pyramid-shaped mounds to attract females. Following courtship the male transfers sperm to her in a packet called a spermatophore. The eggs are attached to the female's abdominal appendages and form an egg mass between the abdomen and the thorax. The abdomen is therefore out of place and hangs downward when the female is carrying eggs. The eggs are usually brightly colored with carotenoid pigments, and can be red, yellow, blue, brown, or green. They range in size and number between species, but a large marine crab can lay up to a million eggs at a time. The tiny larvae are called zoea and are very common summer components of marine plankton. It takes one or two

Image Not Available

Crab and Lobster Facts

Classification:
Kingdom: Animalia
Phylum: Arthropoda
Subphylum: Crustacea
Class: Malacostraca
Order: Decapoda
Families: Homaridae or Nephropsidae (true lobsters), Palinuridae (spiny lobsters or sea crayfish), Scyllaridae (slipper, Spanish, or shovel lobsters), Polychelidae (deep-sea lobsters); Brachyryncha (true crabs), Anomura (irregular-tailed crabs)
Geographical location: All the earth's oceans, except at the poles
Habitat: Mostly marine, although some crab species live much of their lives on land near salt water
Gestational period: Lobsters, eggs hatch in one year
Life span: Lobsters, up to fifty years
Special anatomy: Segmented exoskeleton; large claws on front pair of legs (one often larger than the other); eyes on the ends of stalks

more molts before the crablike form is evident. Many of the semiterrestrial and freshwater species develop directly into miniature crabs.

Lobsters

Millions of American lobsters (*Homarus americanus*) are harvested for food each year, making them possibly the most commercially important of all crustaceans. Lobsters differ from crabs in having an extended thorax. Most are large: up to sixty centimeters in length and twenty-two kilograms in weight. The first pair of walking legs is modified into large claws or chelipeds. The European lobster (*Homarus gammarus*) is similar in shape but somewhat smaller. Lobsters walk forward using their walking legs, but when threatened swim rapidly backward using their broad tail segment or telson.

Ecologically, lobsters are creatures of rocky subtidal zones that rarely extend activities shoreward. Eggs are laid in late summer, generally July and August of every other year, and are glued to the female's abdominal appendages. They hatch in about a year and the young remain attached for some time before drifting free and becoming part of the plankton.

The spiny and slippery lobsters of the tropics and pantropics are not closely related to the American lobster. Some reach the size of American lobsters, but lack pincers. Spiny lobsters are noted for their mass migrations during fall, in which up to fifty individuals march together, heads-to-tails, in long queues. Females are capable of producing four million eggs during the spring reproductive season. The transparent juveniles attach to jellyfish and undergo a series of molts for about a year, gradually transforming into a five-centimeter lobster. Lobsters actively forage for live prey, including worms, mollusks, crabs, and small fishes, as well as organic debris.

Crustaceans as Food

Crabs are food for a variety of other animals, including fish and larger invertebrates. To protect themselves, some species carefully place sea anemones on their carapace, while others, such as the decorator crab, glue pieces of shell all over their carapace. Still other species, such as the pea crab, take refuge inside oysters and other shellfish, while boring crabs dig burrows into mud substrates or soft limestone rocks.

Both crabs and lobsters are important food for humans as well. Crabs are caught in traps or by crab dredges. The most highly prized are soft-shelled crabs, which are really the ordinary species of crabs that are caught just after molting and before they have had time to secrete a new shell. Both American and European lobsters are the centers of a fisheries industry measured in the billions of dollars annually. They are caught in baited lobster pots. Coastal pollution and over-fishing coupled with an apparent die-off of the American lobster population in the Northeast has spawned millions of federal dollars in research to determine causes and provide restoration protocols. With the demise of the American lobster population, most of the frozen lobster tails shipped to market are the spiny or slippery lobsters, which are caught in tropical and subtropical waters of the world.

—*Dwight G. Smith*

See also: Antennae; Claws, nails, and hooves; Crustaceans; Marine animals; Marine biology; Molting and shedding; Regeneration; Shells; Tidepools and beaches.

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CRANES

Type of animal science: Classification
Fields of study: Anatomy, conservation biology, physiology, population biology, wildlife ecology

Cranes are among the oldest of living bird groups, dating back sixty million years. Their interesting appearance, majestic flight, and unusual behavior characteristics have made them the subject of reverence and folklore around the world.

Principal Terms

FLYWAY: an established route that migratory birds take between their wintering and nesting grounds
MOLTING: the process whereby a bird loses its feathers and replaces them with new ones
OMNIVORE: an animal that feeds on both plants and animals
PREENING: a bird's act of grooming itself by cleaning and straightening its feathers
WETLAND: habitats that have an abundance of shallow waters, such as marshes and salt flats

Cranes are large wading birds that live in open wetland and meadow habitats. There are fifteen species of cranes in the world. North America is home to two species, the sandhill and the whooping crane. Sandhills are the most numerous of all cranes, and whoopers the least. Cranes are omnivores, though food preferences vary among species. As opportunistic feeders, they dine on numerous animal foods, such as fish, crustaceans, worms, insects, and small animals, and many plant foods, including berries, acorns, grains, and seeds.

Physical Characteristics of Cranes

Cranes vary in size from 2.5 to 6 feet tall, and weigh from five to twenty-five pounds. Their wingspan can measure up to 7.5 feet. Males and females look alike, though the male is usually larger. Plumage ranges from pure white to gray to brown. Many cranes have a red, featherless patch of skin on the head. Crowned cranes also have a golden ornamental tuft.

Cranes have long, slender legs and unwebbed feet, features that allow them to wade in shallow water and walk through mud. Their three large toes and a tiny back toe keep them from sinking. Cranes have long necks, and the length of the trachea correlates to the volume and resonance of vocalization among species. They also have pointed, powerful bills, which they use for obtaining food by fishing, digging, or foraging. They are also used for defense.

Crane Behavior

Most cranes are migratory, spending spring and summer in northern locations and wintering in more southerly habitats. A few species stay in the same location year round. The same flyway is always used. Unlike other birds, cranes learn the flyway through visual memorization rather than by instinct. Flock size varies from a single family to between fifty and one hundred birds. Cranes fly with their necks stretched out and their legs extended out straight behind them, distinguishing them from other large wading birds. They glide on thermal air currents to conserve energy. They are quite vocal during takeoff and landing.

Mating occurs in the spring, when the birds reach their northern nesting grounds. Cranes do not reproduce until they are about four years old. They mate for life and tenaciously nest in the same location from year to year. Nests are mounds of plant material, usually built in shallow water. Most species lay two eggs, and male and female share incubation. Generally only one chick survives to adulthood. The fledgling period lasts from two to five months, during which time the chick grows its feathers and the adults molt. Brooding parents are very protective. The young bird returns to the wintering grounds with its parents, but separates the following spring after migration.

Cranes have a distinctive, buglelike call and can be heard from up to three miles away. The most notable of the crane's vocal repertoire is the unison call between male and female, performed when mating or when defending their territory. It consists of a series of responsive, coordinated calls of differing length and pitch while the two birds stand in an erect, stylized position.

Cranes engage in many colorful behaviors, such as preening, defense posturing, stretching, feather ruffling, and head scratching. They are famous for their spectacular dance. One bird will lower its head and flap its wings, then leap upward with stiff legs, throwing its head upward. Another bird will respond with similar movements, and this may continue for several minutes. Although its function is not fully understood, it seems to correlate with a state of excitement. Dancing is exhibited throughout the year, often between bonded pairs, but also singly and in large groups.

Conservation

Changes to wetland habitats caused by building, farming, leisure pursuits, and pollution have threatened many crane species. The diminishing number of suitable habitats has interfered with their migration patterns and nesting habits. In 2000, the Siberian, Japanese, and whooping crane were listed as endangered by the International Union for Conservation of Nature and Natural Resources. Six additional species are considered vulnerable.

Around the world, efforts are being made to protect wetland ecosystems and reestablish dwindling species. In North America, biologists have been attempting to establish new migratory and nonmigratory flocks of whooping cranes. In the 1990's, a program was launched to establish new migration routes by imprinting chicks to follow an ultralight aircraft.

—Barbara C. Beattie

See also: Beaks and bills; Birds; Domestication; Feathers; Flight; Molting and shedding; Nesting; Respiration in birds; Wildlife management; Wings.

Cranes have slender, flexible necks and powerful bills for digging food out of the mud. Many species are "crowned" with a tuft of feathers on the tops of their heads. (Corbis)

Crane Facts

Classification:
Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Class: Aves
Order: Gruiformes (cranes, rails, and allies)
Suborder: Grues (cranes, rails, limpkins)
Family: Gruidae (cranes)
Subfamilies: Gruinae (true cranes), Balearicinae (crowned cranes)
Genus and species: Four genera and nineteen species, including *Balearica pavonina* (black-crowned crane), *B. regulorum* (gray-crowned crane); *Anthropoides virgo* (Demoiselle crane), *A. paradisea* (blue crane); *Bugeranus leucogeranus* (Siberian crane), *B. carunculatus* (wattled crane); *Grus grus* (Eurasian crane), *G. canadensis* (sandhill crane), *G. vipio* (white-naped crane), *G. monachus* (hooded crane), *G. antigone* (sarus crane), *G. nigricollis* (black-necked crane), *G. rubicundus* (Australian crane), *G. japonensis* (Japanese crane), *G. americana alba* (whooping crane)
Geographical location: Every continent except South America and Antarctica
Habitat: Wetlands, meadows, steppes
Gestational period: One breeding cycle per year; incubation averages thirty-two days
Life span: Twenty-five years in the wild; up to forty years or more in captivity
Special anatomy: Long slender legs; unwebbed feet; long neck with elongated trachea; straight, pointed bill

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CROCODILES

Types of animal science: Anatomy, behavior, classification, ecology, evolution, geography, physiology, reproduction

Fields of study: Anatomy, conservation biology, ecology, herpetology, paleontology, physiology, reproduction science, systematics (taxonomy), zoology

The Crocodilia, comprising twenty-three endangered species, are the last surviving reptilian group of the subclass Archosauria, which also includes the extinct dinosaurs, pterosaurs, and the stem group Thecodontia. Crocodilians are the closest living relatives of birds, and most species are highly endangered due to hunting and habitat destruction.

Principal Terms

BISERIAL DERMAL ARMOR: bony plates running along side of the vertebral column

EUSUCHIA: the living Crocodilia

MEOSUCHIA: the first aquatic crocodilians of the Mesozoic

PROTOSUCHIA: the first crocodilians of the Triassic

SECONDARY PALATE: the palate forming a shelf in the mouth that places the internal nares far back in the throat

Classically, the order Crocodilia is divided into six suborders: Protosuchia, Archaeosuchia, Mesosuchia, Thalattosuchia, Sebecosuchia, and the Eusuchia. Today, Crocodilia are familiar inhabitants of rivers, swamps, and lakes, distributed in the tropical and subtropical regions of North and South America, the Caribbean, Africa, Asia, and Australia. However, crocodilians did not begin their evolution as amphibious reptiles. The earliest recognizable crocodilians arose in the Upper Triassic and appear to have been terrestrial in nature. Protosuchians are small, averaging below two meters in length. They have terminal nostrils, a single row of dermal armor on either side of the vertebral column, and elongated carpal bones and hindlimbs. They show other classic morphological features of crocodilians in that the pubic bone does not contribute to the formation of the hip socket as in all other reptiles. Before apparently giving rise to the Mesosuchia, the first amphibious crocodilians, the protosuchids, gave rise to another side group, the Notosuchia. The Mesosuchia appear to be the ancestors of the living Eusuchia. The Thalattosuchia are Mesozoic marine crocodilians, most of which have longirostrine (having long, thin jaws) mandibles adapted for fish eating. Some Thalattosuchia, the geosaurs, apparently were well adapted to the marine environment, having reevolved a tail fin for aquatic locomotion.

The living Crocodilia are all placed within the suborder Eusuchia. They are divided into three families, the Gavailidae, Alligatoridae, and Crocodylidae, the latter with its two subfamilies, the Crocodylinae, and the Tomistominae. The gharials or gavials of Nepal and India comprise the family Gavialidae. They are longirostrine crocodilians specialized for fish eating. They attain large size, growing to nearly nine meters. Their limbs are reduced more than in most crocodilians and they are unable to climb over obstacles of more than a half meter high. The Crocodylidae are divided into alligatorines, which include the American and Chinese alligator and the caimans, and the Crocodylinae, which include members of the genus *Crocodilus*, *Osteolaemis*, and *Tomistoma*. The placement of the fourth mandibular tooth in crocodilians has often been cited as the difference between these families, in that in alligatorines the

Crocodile Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Craniata
Class: Reptilia
Subclass: Archosauria
Order: Crocodyla
Suborder: Eusuchia
Families: Alligatoridae (alligators and caimans, four genera, seven species), Crocodilidae (crocodiles, three genera, fourteen species), Gavialidae (garials, two genera, two species)

Geographical location: Every continent except Antarctica and Europe

Habitat: Variable depending on species; freshwater lakes, rivers, streams and swamps, estuaries, and oceans

Gestational period: Approximately three months

Life span: Up to seventy years

Special anatomy: Quadrupedal; biserial dermal armor consisting of two rows of osteoderms running on either side of the vertebral column; secondary palate with fleshy valve; ear flap; verticalized braincase; elongated carpals; pubic bone is excluded from the acetabulum; extensive air sinus systems extending from the Eustachian tubes to the middle-ear cavity and skull bones

fourth mandibular tooth resides in a socket in the upper jaw when the mouth is closed. Within the crocodiles this tooth fits in a groove in the upper jaw and thus is visible when the jaw is closed. The longirostrine crocodilians, such as gharials, tomistomines, and *Crocodilus johnstoni*, have longirostrine jaws and have interdigitating teeth. Thus, the tooth character is equivocal in these taxa. Another method of dividing the living forms into the subfamilies has to do with salt tolerance. With one exception alligatorines are salt intolerant. Crocodiles are often found in brackish waters and some, such as *Crocodilus porosus*, have been found hundreds of miles off the coast of Australia. Unlike alligatorines, crocodiles have well-developed salt glands in the tongue. Gharials, although not marine, have salt glands in the tongue as well as an orbital salt gland. This trait may indicate an oceanic origin for gharials.

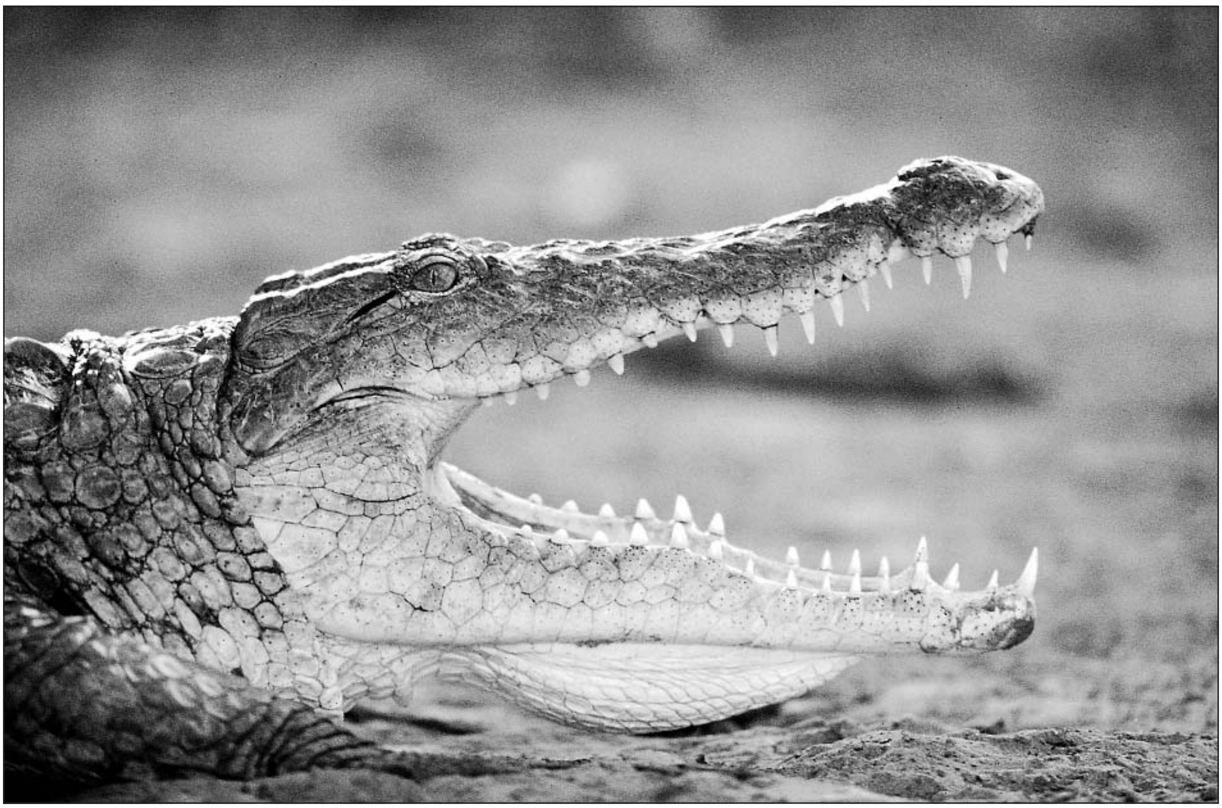
Aquatic Adaptations

Eusuchians are better adapted to the aquatic environment than their mesosuchian ancestors. The secondary palate is well developed, extending the internal nostrils back to the pharynx. The external nostrils face dorsally so the crocodiles can stay hidden in the water. Here a fleshy valve separates off the mouth from the pharynx and the internal nostril openings. Eusuchians also have an earflap or *Ohr Klappe* that closes off the external ear from the water during dives. The Eusuchia have enhanced the dermal armor and have a biserial or double row of osteoderms running on either side of the vertebral column. This dermal armor was once thought to be evolved for protection but this system is tied to back muscles that aid the crocodilians in bending the vertebral column for locomotion. Dermal armor was widespread in early archosaurs but is best-developed in eusuchian crocodilians. All crocodilians have a strong bite. Although crocodilians have jaw adductor muscles in the temporal region of the skull, the largest jaw adductor originates on the palate. Except for fish-eating species that have sharp, curved, conical teeth, most crocodilians have more squat-shaped teeth in the rear of the jaw for crushing. Crocodilians will often position turtles in the posterior region of the jaw in order to crush the shells of those they cannot swallow whole.

Crocodiles as Social Organisms

Crocodilians have complex mating rituals with both male and female mating displays. Both sexes engage in bellowing behavior, although male bellowing is of a deeper tone, as well as head splashing to announce their presence to potential mates. Moreover, males will create subaudible vibrations in the water above their backs, vibrating the water so that it "dances" above the animal's back, as a sexual display. Males may use bellowing to define territories during the mating season. Males will fight over territory and may not tolerate the presence of other sexually mature males in their territory during the breeding season. Females may approach males and by a series of rubbing moves indicate their intention to mate. Musk glands located under the lower jaws are used as a sexual perfume to arouse the male. The male also has musk glands that are used in response to the female scent. Mating occurs in the water, with the male on top of the female. Males have a copulatory organ, a grooved penis that is inserted into the cloaca of the female.

Many crocodilians, such as the American alligator and saltwater crocodile (*Crocodylus porosus*), build aboveground nests using foliage, while others, such as gharials, may dig nests in the sand. Temperature-dependent sex determination occurs in crocodilians. Low nest temperatures, below 30 degrees Celsius, produce females, whereas higher temperatures, above 33 degrees Celsius, produce males. Intermediate temperatures may produce males or females depending upon species. Thus, both sexes are found in a nest, since the temperature at the top of nest may differ from the temperature at the bottom. While egg numbers vary, many crocodilians lay forty eggs or more. In populations studied, only 2 percent of the hatchlings survived to maturity. When hatching occurs, crocodilians use an egg tooth to break the eggshell. Hatchlings inside the nest will bark or grunt to signal to the mother, who may defend the nest and may be nearby to come and help dig out the hatchlings. Female crocodiles may defend the hatchlings from predators that include other crocodiles. In some species, she will carry the hatchlings to the river in her mouth.



Crocodiles are the last surviving relatives of the dinosaurs. (Digital Stock)

The Gharial

The Indian crocodile, the gharial, is perhaps the most unusual living crocodile. It has an extreme longirostrine condition, where the elongated jaws are markedly set off from the skull. Below its skin, the gharial is different from all other crocodiles in the back and hindlimb muscles and the skull construction. It is worth noting that crocodiles as well as most other archosaurian reptiles have a verticalized floor of the braincase. Thus, in most crocodilians, the floor of the braincase is high and narrow. This feature of the braincase comes about only after the crocodile hatches. The function of this feature is to extend the space for the size of the jaw adductor muscles, thus increasing the crocodile's biting power. The gharial braincase is quite elongated and not high. They make up for some of this lost space for the jaw adductor muscles by elongating the back of the jaw and thus increasing the size of the pterygoideus muscle that helps close the jaws. The point of these differences in morphology as compared to other crocodilians suggests that gharials may represent a different lineage of crocodilians, apart from the Alligatoridae-Crocodylidae clade.

Diet and Locomotion

Diet is dependent upon the stage of life and the adult size. When crocodiles are juveniles they may eat insects, arachnids, small frogs, and snakes. Adults may eat snails, fish, turtles, small mammals, and birds. The larger species, such as *Crocodylus niloticus*, may take large prey such as wildebeest. Crocodiles may hunt cooperatively in bringing down large prey that a single individual cannot handle alone. Others species, such as caimans, may chase fish into the paths of waiting members of the population, or may herd fish to the shore for easy capture. Crocodilians are quite adept at stealthy behavior. They remain submerged and will slowly approach prey until they can leap or lunge to grab the prey in their viselike jaws. It is not the teeth that kill a prey but rather the crushing power of the jaws. If the prey is too large to kill outright, crocodiles will usually drown the prey animal and then tear it apart by rolling movements of the body. In this way two or more crocodiles can cooperate by holding on to the same prey animal and tearing it apart by combined rolling actions.

Aquatic locomotion is accomplished by undulations of the tail. There is a double row of elongated scutes running down the length of tail that may aid in swimming. The limbs are normally held against the body during swimming. Crocodiles show versatility in their terrestrial locomotion. Crocodiles are mainly quadrupedal in stance and gait; the limbs can be held at about 70 degrees under the body. Some of the smaller species, such as *Crocodylus johnstoni*, can gallop, while the saltwater crocodile, *C. porosus*, has been observed to run bipedally. All crocodilians are capable of leaping to capture prey. They appear to be fond of belly sliding as a means of locomotion over short distances, especially in entering the water.

Physiology and Size

Crocodilians are cold-blooded animals and must thermoregulate by means of evaporative cooling, using the mouth, and basking and shade usage behaviors. Crocodilians, like most reptiles, lack sweat glands. Despite the fact that crocodilians essentially have a four-chambered heart, there remains a small opening between the ventricles persisting as the foramen of Panizza at the base of the systemic and pulmonary trunks. Nonetheless, the crocodile heart is too small for the body to maintain a high metabolic rate. The stroke volume of the heart and the heart versus body mass ratio determines whether the animal may maintain high activity levels. Crocodiles have a metabolic rate that is about 4 percent that of an adult human. However, small crocodilians have higher metabolic rates than do larger species.

Crocodilians come in all sizes. Some of the caimans are small species, such as *Paleosuchus*, which may reach little more than five feet in length. However, other caimans, such as *Melanosuchus*, the black caiman, may reach up to twenty feet. Crocodiles also vary in length. The dwarf crocodiles of Africa, *Osteolaemis tetraspis*, may reach over six feet in length. The largest crocodilians are crocodiles. *Crocodylus niloticus* may reach over twenty-one feet in length, and specimens of *Crocodylus porosus* have been known to reach lengths of nearly thirty feet. Despite their size, some species of crocodilians, such as the gharials that are over twenty feet in length, are relatively harmless to humans because they are specialized for fish catching and cannot open their mouths very wide.

—Samuel F. Tarsitano

See also: Cold-blooded animals; Fauna: Africa; Fauna: Asia; Fauna: Australia; Fauna: North America; Fauna: South America; Lakes and rivers; Predation; Reptiles; Teeth, fangs, and tusks; Thermoregulation.

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CRUSTACEANS

Types of animal science: Anatomy, classification, ecology, reproduction
Fields of study: Anatomy, ecology, invertebrate biology, marine biology, zoology

The twenty-five thousand species of crustaceans make up the class Crustacea. They are mainly aquatic arthropod animals which have jaws and two pairs of antennae. Examples are crabs, lobsters, and shrimp. Crustaceans are food for humans and whales and have useful ecological functions.

Principal Terms

CARAPACE: a hard, chitinous outer covering, such as a crustacean shell or insect exoskeleton

CEPHALOTHORAX: the anterior (front) section of a crustacean, consisting of a fused head and thorax

CHITIN: a semitransparent, hard, horny substance forming much of crustacean shells and insect exoskeletons

DECAPOD: any crustacean having five pairs of locomotor appendages (legs)

DORSAL: at the hind (posterior) end of a living organism

HERMAPHRODITE: an organism having both male and female reproductive systems

MOLTING: shedding part of or all of a crustacean carapace (shell)

The majority of animals in the oceans are crustaceans. The name indicates their class, Crustacea, which consists of aquatic arthropods having jaws and two pairs of antennae, such as crabs, lobsters, and shrimps. Crustaceans are among the most successful of animals, dominating the oceans as the insects dominate the land. They also live in freshwater, and some even live in moist land habitats. Most crustaceans are small, but they can differ widely in body form, size, and habits. The twenty-five thousand crustacean species include lobsters up to two feet long and giant spider crabs with leg spans of over ten feet.

Physical Characteristics of Crustaceans

All crustaceans are covered by hard chitin coats (carapaces) acting as external skeletons (or exoskeletons), which grow as backward extensions of their heads. Carapace texture varies from bone-like to tough and leathery. The hardness of the covering depends on the amount of calcium salts in the chitin. The exoskeleton acts like armor, to protect the animal. Crustacean bodies are made up of several segments and divided into sections. Each section usually has one pair of jointed legs.

Crustacean heads are fused with several segments just behind them, forming the cephalothorax. This is followed by the abdomen. The head holds two pairs of sensory organs, jaws (mandibles), and antennae. Behind the mandibles are two other pairs of mouth parts, the maxillae. These limbs, which evolved under and in front of the mouth, are used to hold, tear, and taste food. Antennae provide the sense of touch. Each crustacean head also holds a pair of compound eyes, an unpaired eye, or both. Each eye is on a movable stalk and can be turned in any direction.

The cephalothorax also holds limbs used in locomotion and others used as gills in respiration. Special legs under the body are used for walking. Large legs called pincers or claws are used to catch fish, crack mollusks, dig burrows, and fight. Slow-swimming legs under the tail can be used to hold eggs. The legs at the end of the tail are flattened into a fan-shaped fin, also used in swimming.

The main body cavity is a blood circulatory system, pumped by a dorsally located heart. The crustacean intestine is a straight tube containing

Crabs and lobsters must periodically shed their hard exoskeletons in order to accommodate growth. (Adobe)

glands that secrete digestive fluid and absorb food. All crustaceans also have at least rudimentary brains, composed of ganglia near sense organs and below the intestine.

Shrimp, Lobsters, and Crabs

Shrimp make up two thousand crustacean species. Structurally similar to lobsters and crayfish but flattened laterally, they are green or brown. They range from insect size to ten inches long, inhabiting salt water and freshwater (mostly on shallow ocean floors) and eat smaller animals and plants. Some species, krill, live deep in the oceans and are eaten by whales. Shrimps have eight pairs of appendages; the first three are used for eating and the rear five are for walking. The shrimp abdomen also contains five pairs of swimming legs and a fanlike tail.

Lobsters are marine decapods, with five pairs of thoracic locomotor appendages. They belong to the crustacean suborder Reptantia and are related to freshwater crayfishes. Their narrow, dark green bodies are up to two feet long and weigh two to fifteen pounds. In each lobster, two large, body-length claws stretch forward to grasp prey, and a fan-shaped tail is used for propulsion. The three true lobster species are very important foods in North America and Europe. American and European lobsters (*Homarus americanus* and *Homarus vulgaris*) have enlarged claws. Norway lobsters (*Nephrops norvegicus*) have longer, thinner claws. In these true lobsters, one claw is heavy and has blunt teeth to crush prey. The other is smaller and has sharp teeth to tear prey up. Not all lobsters have the heavy claw on the same side. They are "right clawed" or "left clawed."

The lobster head has two pairs of antennae and its eyes are compound, on the ends of mobile stalks. A female lobster lays 5,000 to 160,000 eggs every two years, and carries them under her tail

Crustacean Cuisine

The terms “shrimp,” “lobster,” and “crab” are catchalls that do not definitively classify decapod crustacean groups. Rather, they are popular or slangy terms. “Shrimp” somewhat arbitrarily indicates smaller crustaceans. In the same vein, “lobster” generically indicates large crustaceans, and “crayfish” indicates freshwater lobsters. For example, the suborder Reptantia consists of crawling forms, including elongated species called lobsters and shorter ones called crabs. True lobsters are classified together with crayfish.

Many crustaceans provide food for humans. The well-muscled abdomens of shrimps provide shrimp meat. The tails and claws of lobsters are luxury food items, as are crab claws and legs. Millions of pounds of crabs, shrimps, and lobsters are eaten every year. This has led to an increasing scarcity of the most prized crustaceans. For example, at one time a hundred million lobsters were caught per year, some weighing fifteen pounds or more. This sort of fishing has made larger lobsters rare, and the average lobster sold now weighs two pounds or less.

Lobsters might have died out completely from overfishing, but laws were passed to protect them, and young lobsters were raised in areas where lobster fishing was forbidden. Most crustaceans have very sweet-tasting flesh, even though their diet includes dead, decaying matter. Because of their eating habits, they help keep the ocean and its beaches clean. Other crustaceans are eaten by fish that humans use as food.

for up to eleven months, until the young hatch. The young, initially 0.3 inches long, drift and swim for a month before settling on the bottom, at 1 inch long. Survivors of the next few months on the dangerous ocean bottom dig shallow burrows beneath rocks, or inhabit crevices in the ocean bed. During the day, a lobster stays inside its burrow waiting for prey. At night it comes out to search for dead or live food. Lobsters grow by molting and may live up to fifteen years. All are primarily scavengers.

American lobsters occur only off eastern North America, from Labrador to North Carolina. Most live on the ocean bottom, at depths of ten to one hundred feet. Caught in baited lobster pots, they average lengths of ten inches and weigh up to five pounds. Norway lobsters are most abundant near France and Spain. European lobsters are caught off Great Britain, France, Italy, Norway, and Portugal. Rock lobsters, lacking the enlarged claws of the true lobsters, are found off South Africa, Australia, New Zealand, Japan, Brazil, the United States, Mexico, and the Bahamas.

Crabs, related to lobsters and shrimp, can move sideways, burrow, and swim. They are decapods, whose smallest members, tiny pea crabs, consist of females which live in the shells of live oysters and males who live in the outside world and visit them to mate. The giant spider crabs of Japan are the largest crabs, often ten feet in circumference (including legs). Many kinds of crabs are used as human food. For example, the blue crab is the common food crab in eastern America. Two important groups, 1,500 species of Anomura (hermit crabs) and 4,500 species of Brachyura (true crabs), have similar body shapes, with small abdomens and large, broad anterior bodies, though hermit crabs have fewer walking legs. Seen most as ocean-bottom dwellers, crabs also inhabit freshwater, and some live on land.

The crab body is covered by a chitin carapace. The small abdomen under the body is most often a brood pouch. A crab has five pairs of walking legs, two sense antennae, and front legs which are pincers (claws) for feeding and defense. Crabs also have complex nervous systems, with keen compound eyes and the ability to smell and taste food. They enjoy complex mating rituals and communicate by pincer waving. Crabs often mate just after a female molts, when its shell is soft. Eggs are kept in the brood pouch and may pass through two larval stages: the initial form, zoea, does not resemble adults; the later form, megalops, does. Each time a crab molts after birth, it increases in size. Crabs may live for three to twelve years.

There are many different crab species. Some interesting crabs are the lobsterlike anomurans, called squat lobsters; sand crabs, which burrow into sand and filter suspended matter from the water; large spider crabs with long legs and slender bodies; swimming crabs (blue crabs) with paddlelike legs; and fiddler crabs, whose males each have a huge claw that they use in mating and combat. There are even land crabs, omnivores found in the tropics, that release larvae into oceans.

Life Cycle of Crustaceans

Crustaceans reproduce via eggs, which usually hatch underwater. Some crustaceans, such as lobsters, carry their eggs and young on the hairs of swimming legs. The eggs of different crustaceans hatch at different stages of development. Young lobsters and crayfish look like their parents; young crabs do not. After hatching, young crustaceans grow until their shells become too tight. Then the crustacean sheds its old shell for a larger new one. The process of changing shells (molting) takes place several times during growth. The new shell is formed inside the old one, and is soft and wrinkled until exposed to the environment. When a lobster molts, its shell splits along the back and the lobster leaves through the opening. Sometimes molting accidents will occur. For example, a leg or a feeler often breaks off in the process of leaving the old shell. When the animal molts again, it grows a replacement limb. The new limb is small at first, but becomes full-sized after several molts.

Some crustaceans, such as barnacles, are hermaphrodites. All barnacles live in oceans. Their larvae are free-swimming, but adults attach to foreign objects, such as ship bottoms, wharf piles, rocks, and whales. There are five orders of barnacles. Four are parasites of shellfish. The fifth order includes stalked barnacles, originally found in warm waters. However, because barnacles attach to ships, they are found worldwide.

—Sanford S. Singer

See also: Antennae; Arthropods; Claws, nails, and hooves; Crabs and lobsters; Exoskeletons; Marine animals; Marine biology; Molting and shedding; Regeneration; Shells; Tidepools and beaches.

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DEATH AND DYING

Types of animal science: Behavior, development, ecology, physiology
Fields of study: Cell biology, ethology, genetics, marine biology, population biology, physiology, wildlife ecology, zoology

Animals die from old age, disease, their encounters with predators, starvation, human use, human-made disasters, and pollution created by industrial and agricultural chemicals. Some nonhuman animals appear to have a concept of dying.

Principal Terms

CETACEANS: plant-eating marine mammals, such as whales, dolphins, and porpoises
MARINE MAMMALS: part of the class of mammals that adapted to life in the sea
MYOCARDITUS: inflammation of the heart muscle
PERSISTENT ORGANIC POLLUTANTS (POPs): chemicals that remain in the environment for a very long time and can be found at long distances from where they are used or released; they are nearly all of human origin
PINNIPEDS: flipper-footed marine mammals, such as sea lions, fur seals, true seals, walruses
SIRENIANS: plant-eating dugongs and manatees

The life span of all species in the animal kingdom depends upon genetic composition, environmental conditions, and the amount of energy expended throughout their lifetime. The natural life span varies from one species to another. Insects generally have the shortest lives; the adult mayfly lives only a few hours, the fruit fly lives from thirty to forty days. At the other extreme, a giant tortoise may live up to 177 years and the quahog clam can live up to 220 years. Human life expectancy has increased substantially since the beginning of the twentieth century. In 1998, it ranged from seventy-five to eighty years in the United States, Canada, Western Europe and Australia, to fifty-five years in most African countries.

Environmental conditions affecting the genetically determined life span and hastening death include the number and ferocity of predators, viral, bacterial and fungal disease, poisons and pollutants, changing climate, and the rise of carbon dioxide in the air. Humans have contributed to the annihilation of many species and placed others close to extinction by either deliberately or accidentally destroying animal habitats and by overhunting wildlife. In 1973, the United States Congress passed the Endangered Species Act, to protect endangered animals and their habitats. The Environmental Protection Agency (EPA) monitors the fate of endangered species. If pesticide use adversely affects the habitat of an endangered species, the EPA can prohibit it.

Pollutants

Maritime oil spills, which kill huge numbers of marine life and birds, affect wildlife species differently. Birds especially are sensitive internally and externally to the effects of crude oil and its refined products. If they become coated with oil and their feathers collapse and mat, the insulating properties of their feathers and down change, making them vulnerable to hypothermia. They become vulnerable to predators and can suffer from dehydration, drowning, and starvation.

Cetaceans, sirenians, and pinnipeds, who depend on air and have amphibious habits, are all susceptible to the effects of oil spills. Like birds, they can suffer from hypothermia. Due to ingesting the oil during grooming and feeding, they suffer from organ dysfunction, congested airways, damaged lungs, gastrointestinal ulceration and hemorrhaging, and eye and skin lesions. Sea turtles are particularly vulnerable during their breeding season, as their nesting sites are on beaches and their eggs may become contaminated by the oil. Newly hatched turtles would have to move over the oiled beach to the water. Among the most deadly oil spills was the wreck in Alaska of the supertanker *Exxon Valdez*, in March 1989, which resulted in more than thirty thousand sea birds dying.

Persistent organic pollutants (POPs) have been related to many behavioral problems in birds, marine mammals, and fish, as well as in humans. Studies of humans exposed through food to POPs show a possible relationship to disruptions of the immune system. This finding has been used to explain why more seals and whales are dying and getting stranded. High levels of cancers in fish have been attributed to another class of potential POPs. Environment Canada reported that when POP levels were reduced, population declines in some birds reversed.

Viral and Bacterial Disease

Nonhuman animals, like humans, are vulnerable to viruses. Livestock contract highly contagious and serious diseases. Among the more commonly known are foot and mouth disease, which affects hoofed animals; scrapie, which affects sheep; and bovine spongiform encephalopathy (BSE), known also as mad cow disease, which occurs in cattle. BSE appears to jump species; humans who contract BSE can develop Creutzfeldt-Jacob disease, a fatal brain disorder. Pigs contract swine fever. Capripox occurs in sheep. In Africa, Rift Valley fever kills livestock and humans. Poultry can contract avian influenza and Newcastle disease, both of which spread rapidly, killing more than 90 percent of infected birds. Because rabies is fatal in animals and humans, many countries require a quarantine period for animals entering the country. In wildlife, trapping has been used to prevent the spread of rabies. However, usually the healthier animals are caught in traps and not the sick, who are less active, are symptomatic, and debilitated, and who are more likely to deviate from their normal behavior.

Organized Animal Fighting, Animal Farming, and Sport Hunting

Humans are voracious predators of other species, killing nonhuman animals for food, clothing, sport, scientific experimentation, and financial gain. Many animals meet their death through organized fighting: bull fighting in Spain and Mexico, and cock fighting in the United States and several Asian cultures, which usually results in the death of one or both roosters. Dog fighting, although banned in most of the United States, is still held clandestinely.

Animal agriculture is the largest food industry in the United States. Animals reared for slaughter are frequently housed in crowded conditions in large buildings, which are ideal for disease. Under natural conditions, chickens can live for as long as fifteen to twenty years. In a modern egg factory hens live about a year and a half. Each year in the United States, about two-thirds of the eighty million pigs raised for slaughter live their lives in a confinement system, as do about half of the ten million milking cows and heifers raised. When birds are debeaked and calves and pigs weaned prematurely, they can die from the shock. Slaughtering is sometimes undertaken without safeguards in place to prevent unnecessary pain.

About 7 percent of the United States' population legally hunt animals. Sport hunting of polar bears in areas of Canada eventually led to such a substantial loss of bears that the local government banned hunting in 2002. In 2001, the government of British Columbia placed a moratorium on the hunting of grizzly bears. The whale population initially decreased because of hunting. The blue whale, which once numbered 200,000, was estimated to be 10,000 in 2001. Marine mammals also become accidentally entangled in fishing nets and

Foot and Mouth Disease

Foot and mouth disease (FMD—also known as hoof and mouth disease), an acute viral disease, is one of the most contagious animal diseases, affecting ungulates: cattle, sheep, pigs, and goats, wild and domestic cloven hoofed animals, elephants, hedgehogs and rats. It causes fever, followed by the development of blisters and sores on the feet and in the mouth. Pigs and sheep may suddenly become lame. There is a high mortality rate in young animals due to myocarditis.

The virus thrives in moist conditions, is airborne and endemic in parts of Asia, Africa, the Middle East, and North America. Transmission occurs directly or indirectly from contact with an infected animal, contaminated foodstuffs, or from a human who has attended an infected animal. It may be picked up on contaminated roads by the wheels of vehicles. Until they are disinfected, vehicles and implements from places where infected animals may have been present are sources of infection.

Prevention and control involves protecting disease-free zones with border animal movement control and surveillance, slaughtering infected, recovered, and FMD-susceptible contact animals, disinfecting premises, cars, clothes, and implements, destroying cadavers, litter, and susceptible animal products in the infected area, and introducing quarantine measures. After two initial vaccinations, one month apart, of an inactivated virus vaccine, immunity is provided for six months, depending on the antigenic relationship between the vaccine and outbreak strains.

An outbreak in 2001 in Great Britain was vastly different from a previous outbreak in 1967 due to the speed and geographical scale of the spread of the infection and the species involved. The outbreak necessitated slaughtering thousands of cattle. Despite the strenuous measures employed, the disease spread from Britain to parts of Europe and Ireland. Experts agreed the outbreak was unprecedented internationally.

collide with boats. Dolphins died at a considerable rate due to tuna fishing methods until U.S. legislation prohibited the method and the number caught in nets was reduced dramatically. Manatees, who move slowly and sometimes sleep near the surface of the water, are particularly vulnerable to being fatally hit by motor boats.

Scientific Experimentation

Using animals in scientific experiments has been widely sanctioned throughout the world for testing consumer products, disease prevention and/or progression techniques, the effects of noxious agents, and psychological theories of behavior. An animal rights movement developed in the late 1970's and early 1980's to protest this use of animals, who not only died during and following the experimental procedures but were also subjected to extreme pain and injury. Industrial manufacturers and scientists were urged to find alternate methods of safety testing and conducting experiments. The Johns Hopkins Center for Alternatives to Animal Testing was founded in 1981, while In Defense of Animals (http://www.idausa.org) grew out of challenges to the University of California's research. It grew into one of the foremost animal advocacy organizations in the United States. The ethical question raised by animal rights groups is whether nonhuman animals should be treated as independent sentient beings and not as a means to human ends.

Beyond the ethical issues raised by philosophers, such as Tom Regan and Peter Singer, are the questions concerning the emotional life of animals and whether animals experience grief and have a concept of death. Marc Hauser, an animal-cognition researcher, maintains that animals, lacking a capacity for empathy, sympathy, shame, guilt, and loyalty, are without self-awareness or an awareness of what another of their species experiences, and therefore are incapable of having a deep understanding of death.

Researcher Cynthia Moss, at the Amboseli Elephant Research Project in southern Kenya, takes a different view. From her field observations, she maintains that elephants have a concept of death. They recognize one of their own carcasses or skeletons, always react to the body of a dead elephant, and have been seen putting dirt on a dead elephant's body and covering it with branches and palm fronds. Healthy elephant mothers whose young calves have died look lethargic for many days afterward, trailing behind their family. Wild animals and birds, as well as animals in captivity and animal pets, have been seen reacting to the loss of a mate or companion that can be interpreted as mourning behavior and grief.

—Susan E. Hamilton

See also: Aging; Birth; Cannibalism; Demographics; Diseases; Emotions; Endangered species; Ethology; Extinction; Immune system; Infanticide; Life spans; Mating; Pollution effects; Population analysis; Predation; Veterinary medicine; Wildlife management.

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DEEP-SEA ANIMALS

Types of animal science: Anatomy, ecology
Fields of study: Ecology, marine biology

The great depths of the sea, below about 150 feet, had always been considered azoic (without animal life). Oceanographic research has shown the ocean supports a large number and diversity of animals in all areas, from the surface to the bottom of the deepest parts, nearly six miles down.

Principal Terms

BIOLUMINESCENCE: production of visible light by living organisms
DEEP SEA: water depths below six hundred feet, also below penetration of light
GULPER: a fish that captures and ingests its prey in one swallow
PLANKTON: marine organisms, usually small, that are free-floating
SUBMERSIBLE: a vessel, like a submarine, that can operate with or without occupants

Early in the nineteenth century, an English naturalist, Edward Forbes, theorized that there was an azoic or lifeless environment in the ocean deeper than about two thousand feet. However, as technology advanced, broken submarine cables recovered from depths greater than five thousand feet were found to be teeming with living organisms, many of which were new to science. In the 1950's and later, collections from deep-water zones, made both with collecting devices and through explorations by scientists aboard submersibles, revealed fishes, snails, and other animals in the deepest part of the world ocean, the Mariana Trench in the southwest Pacific Ocean. This trench, at 6.8 miles deep, with crushing pressure, near-freezing temperature, and complete absence of light, supports life.

Deep-Sea Exploration

Scientists exploring in submersibles such as *Trieste* and *Alvin* watched in wonder as bizarre-looking fishes swam past the viewing ports. Many of the fishes were brightly colored—red and orange—and most of them featured light organs on their skin, glowing or flashing a bioluminescent light in the otherwise total darkness. Some of the fishes were equipped with body parts which resembled fishing rods and lures.

The advent of submersibles offered the promise that someday soon, scientists might actually see one of the mythical sea monsters. This was not to be. Most of the strange-looking fishes were in many cases only a few inches long.

Gulpers and Anglers

In the lightless depths of the sea there is no primary production of food from plants as there is in the surface waters. Thus, the deep-sea fishes depend for food on whatever may descend from surface waters. A dead whale drifting down is a bonanza of nutrition to the organisms below. However, many of the deep-water fishes are unable to handle such large matter and are reduced to eating each other: their own kind or even a larger neighbor. The gulpers are remarkably adapted to the necessity of seizing and swallowing whatever comes along. The gulper, or pelican eel, has a huge mouth, jaws that open fantastically wide, and a belly that can contain a fish larger than itself. Some gulpers are about two feet long but one remarkable species reaches a length of six feet. Most of its length consists of a long, whiplike tail,

Hydrothermal vents in the ocean floor create temporary ecosystems that attract animal life, such as these tubeworms, during the relatively short life of the vent. (OAR/National Undersea Research Program)

with the mouth making up the rest of the body. The feeding action of the gulpers has been described as not swallowing their prey, but instead drawing themselves over it like a snake consuming a mouse.

Many deep-sea fishes are anglers; that is, they are fishes that fish. Most of them bear a long, flexible appendage dangling from the top of the head. A light organ at the tip of the rod is dangled provocatively. Any fish that comes closer to investigate the glowing, wormlike bait is rapidly taken in to the angler's mouth and swallowed. Most anglers are jet black with enormous heads and mouths. The mouth is fitted with long, sharp, curved teeth that effectively trap the prey.

A bizarre variation of the angler is the bottom-dwelling, deep-sea fish that has a lighted appendage hanging from the roof of its mouth. It rests on the bottom, mouth agape, with the glowing "worm" wiggling in the dark. Any fish that is attracted into the angler's maw by an apparent bit of live food is quickly swallowed with little effort on the angler's part.

Sea Monsters

Most scientists discount stories of sea monsters in the sense of serpentine animals that resemble the mythical dragon. None has ever been seen or examined by a reputable biologist. There are, however, denizens of the sea that are monstrous. Except for the whales (which are mammals, not fish), the three largest fishes are sharks. The megamouth shark (only discovered in 1976) is up to seventeen feet long. The basking shark reaches a length of forty feet. The giant of all fishes is the whale shark, reaching lengths of more than fifty feet. All three species are docile and feed on tiny plankton near the surface at night, but each day descend into the dark depths. Probably the source of most sea-monster stories is the giant squid. Related to the six- to eight-inch squid eaten as calimari or used as fishing bait, the giant squid truly lives up to its name. It grows to a length of sixty feet, has eyes the size of automobile hubcaps, and bears eight arms. It feeds on fishes and any other marine creature it can capture in its natural domain, three thousand feet down. It frequently is attacked and eaten by sperm whales. The squid is not a fish, but is a member of the same group of sea organisms that includes oysters and clams.

—*Albert C. Jensen*

See also: Bioluminescence; Dolphins, porpoises, and toothed whales; Eels; Fish; Food chains and food webs; Marine animals; Marine biology; Octopuses and squid; Sharks and rays; Whale sharks; Whales, baleen; White sharks; Zooplankton.

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DEER

Type of animal science: Classification
Fields of study: Anatomy, zoology

Deer are hoofed, artiodactyl mammals of the family Cervidae, having bony antlers, which are shed and regenerated annually.

Principal Terms

ANTLER: temporary horn made of solid bone, grown and shed each year

ARTIODACTYL: herbivorous, hoofed mammal that walks on two toes of each foot

FRONTAL BONE: bone comprising the forehead; important in forming the top (roof) of the orbital and nasal cavities

PEDICLE: small bone from which an antler grows

RUMINANT: hoofed animal, with a stomach divided into four parts; it chews a cud of regurgitated, partly digested food

SOLITARY: animal that lives alone

Deer are hoofed, artiodactyl mammals of family Cervidae. They have bony, branching antlers, which are shed and regrown annually. The family contains sixteen genera and approximately forty species, and inhabits the Americas, Europe, Asia, and North Africa. Deer live in woods, prairies, swamps, mountains, and tundra. Common species are the white-tailed and mule deer in the United States; wapiti in the United States, Canada, Europe, and Asia; moose in North America and Europe; reindeer in Russia, Finland, and Alaska; and caribou in northern North America.

The four deer subfamilies are the Cervinae (true deer), Moschinae (musk deer), Muntiacinae (muntjacs), and Odocoileinae (hollow-toothed deer). They are hunted worldwide for their meat, hides, and antlers. Deer meat (venison) tastes beeflike. Tanned deerhide makes soft leather. Reindeer, which are domesticated in Scandinavia and Russia, are sources of meat, leather, and milk, and serve as draft animals.

Physical Characteristics of Deer

Deer have gray, brown, red, or yellow upper bodies with lighter colored bellies. Their stiff fur is smooth looking in the summer and longer and shaggier in cold weather. Deer shed fur in spring and fall, a process called molting. They range in size from seven feet at the shoulder and a ton in weight for moose, to one foot at the shoulder and a weight of around twenty pounds for the tiny pudu. All deer have lithe, compact bodies, short tails, large, narrow ears, long, slender legs, and paired hooves on each foot. Their eyes are large, placed on the sides of the head, and yield a wide visual range. Deer also have keen senses of smell and hearing. They run quite quickly to escape danger.

Males of most species have antlers, as do female reindeer and caribou. Antlers are solid bone growths arising from the frontal bone. In moose, the largest deer, they reach widths of six feet and weigh nearly fifty pounds. Antlers are shed and regrown each year, arising from pedicles on the frontal bone. The pedicles and the growing antlers are covered with soft skin called velvet. Antlers grow rapidly. When the antlers have reached their maximum growth, bone deposition at the antler's base cuts off the velvet's blood supply. This makes the velvet dry up, and the itchiness of the dry velvet leads the deer to rub it off. The shape and complexity of branched antlers is species dependent. Antler shedding in late fall is due to bone resorption at the antler bases. This annoys deer and they rub their antlers against trees, weakening them and causing them to come off. Antlers are important protection for individual deer and their family groups. Males use antlers to fight other males and to protect their herds from predators. The protective function may explain why, most often, it is the males who have horns. Horns of females are much smaller than those of males of a species.

Deer are herbivorous, and their lower molars have ridges which enable them to grind vegetable foods. They are ruminants (cud chewers) and have four-chambered stomachs. Nearly all deer have facial glands in front of each eye. These make strongly scented musk, which is used to mark their territories.

Deer Life

Deer are solitary or live in small to large groups. Often males and females are solitary except when mating. Deer are polygamous, with males collecting harems and battling others for them. Deer can be gregarious at special times, when they live in herds ranging from extended families to thousands. In warm climates deer breed at any time, while in cold climates they breed from autumn to winter. Their gestation periods are between five and eleven months, depending on species. One or two young are born and are at first hidden, camouflaged by dappled body markings. Young deer mate at five to six years old.

All deer eat twigs, leaves, bark, buds of bushes and saplings, and grasses or other plants. They are diurnal (active during daylight), and feed most at twilight. They are also ruminants, who chew and swallow food several times. Rumination helps deer get all nutrients and vitamins they can from their food.

In many countries, especially the United States, deer have few natural predators. Many of

Deer are herbivores, eating grasses and the tender buds, shoots, bark, and twigs of trees. The boundary between forest and field offers them the widest range of food choices. (PhotoDisc)

Deer Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Artiodactyla
Family: Cervidae (deer)
Subfamilies: Cervinae (true deer), Moschinae (musk deer), Muntiacinae (muntjacs), Odocoileinae (hollow-toothed deer)
Geographical location: The Americas, Europe, Asia, and North Africa
Habitat: Forests, grasslands, deserts, tundra, swamps, mountains
Gestational period: Five to ten months
Life span: Eight to twenty years, depending on species
Special anatomy: Antlers, ruminant stomach

their predators, such as wolves and mountain lions, have been driven to endangerment or extinction as a result of their perceived threat to livestock, and the deer have benefited by this. If they become too plentiful, deer overbrowse and die of starvation during winter. This is managed through adjusting the hunting season, based on population estimates made by the U.S. Fish and Wildlife Service. Deer are one of the few wild animals that still provide a real contribution to the diet of humans in some parts of the United States, where some families rely on a deer or two in the freezer to provide their meat throughout the winter.

Deerskin is also used for shoes, boots, and gloves, and antlers are made into buttons and other decorative items. Scandinavian and Russian Lapps and North Asian nomads use reindeer for food, clothing, and transportation. Caribou, a reindeer variant, are equally important to North America's Inuit. Deer were brought to New Zealand from Europe, and are currently raised on deer farms. Most commercial venison used in the United States is imported from New Zealand.

—Sanford S. Singer

See also: American pronghorns; Antelope; Cattle, buffalo, and bison; Elk; Herds; Horns and antlers; Moose; Reindeer; Ruminants; Ungulates; Wildlife management.

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DEFENSE MECHANISMS

Types of animal science: Behavior, ecology, evolution
Fields of study: Biochemistry, ecology, entomology, ethology, invertebrate biology, marine biology

All organisms represent a potential resource for their predators. Several have evolved ingenious ways to prevent themselves from becoming their predator's next meal.

Principal Terms

APOSEMATIC COLORATION: brightly colored warning coloration that toxic species use to advertise their distastefulness to would-be predators

AUTOTOMY: the self-induced release of a body part

MIMICRY: a type of defense in which an organism gains protection from predators by looking like a dangerous or distasteful species

PREDATION: broadly defined, any interaction in which one organism consumes another living organism, including herbivory (predation on plants), parasitism (predation by small organisms), and familiar predation (where one animal kills and eats another animal)

SECONDARY METABOLITE: a biochemical that is not involved in basic metabolism, often of unique chemical structure and capable of serving a defensive role for the organism

SEQUESTER: to store a material derived from elsewhere. In defenses, some predators sequester defensive properties from their prey to defend themselves from their own predators

SYMBIOSIS: "living together"; a term that describes the association between two species in which one species typically lives in or on the other species. Parasitism is a common type.

All organisms are composed of fixed carbon, biomolecules, and mineral nutrients, and therefore represent energy and nutrient resources for consumers. To be successful in life, animals must avoid, tolerate, or defend themselves against natural enemies such as predators, parasites, and competitors. The term "defense" can be attributed to any trait that reduces the likelihood that an organism, or part of an organism, will be consumed by a predator. There are several categories of defenses that have evolved in animals, including structural defenses, chemical defenses, associational defenses, behavioral defenses, autotomy, and nutritional defenses. Animals often possess more than one type of defense, thereby having backup plans in case the first line of defense fails. The number of defenses devised by organisms is a reflection of the strong selective pressure exerted by predators.

Structural Defenses: Being Hard and Sharp

Structures that defend animals can act as external shields: sharp spines located externally or internally, skeletal materials that make tissues too hard to bite easily, or weaponry such as horns, teeth, and claws. External structures that protect vulnerable soft tissues include the chitonous exoskeleton of crustaceans, the calcareous shells of corals, mollusks, and barnacles, the tests (skeletal plates) of echinoderms, the tough tunic of ascidians, and the hard plates of armadillos. The pretty shells that tourists collect along beaches were once used to protect a soft, delicate animal that lived inside the shell. Hard, protective shells remain after the animal dies and can be used by other animals for pro-

Sequestration

The production of chemical defenses is often assumed to be expensive because it requires resources that might otherwise have been used for growth and reproduction. One way for a species to avoid such cost is to sequester compounds produced by its prey.

Sequestration was first discovered in the monarch butterfly. Monarch caterpillars feed on milkweeds and sequester the plant's cardenolides. Milkweeds produce toxic cardenolides that deter most vertebrate herbivores, but monarchs have evolved the ability to tolerate and sequester these compounds. When blue jays were fed monarchs, the birds soon regurgitated and learned to associate this unpleasant response with eating monarchs. To help advertise their chemical nastiness and perhaps to increase the learning response of birds, monarchs evolved aposematic coloration. Other species of butterflies, such as the viceroy and the queen butterflies, mimic monarchs, affording them protection from predators that have already learned to avoid orange and black butterflies.

Nudibranchs are a class of sea slugs that lack the protective shell that most of their gastropod relatives possess. Because they lack the physical defense of a shell, they must protect themselves from other mechanisms, and have ingenious ways of doing so. Most nudibranchs do not produce their own defenses. Rather, they sequester the defenses of their prey. For example, aeolid nudibranchs are famous for sequestering functional nematocysts from their cnidarian prey. They transfer nondischarged nematocysts from their gut to their skin, thereby protecting themselves from predators such as fish. Nudibranchs also sequester secondary metabolites from their invertebrate prey, which effectively protect them from predatory fishes.

tection. For example, small fishes will retreat into empty conch shells when they feel threatened by predators, and hermit crabs live inside empty snail shells to protect their soft, vulnerable abdomens.

Some animals cover their bodies with sharp structures that puncture predators that try to bite them. The porcupine is a good example of a mammal that uses this defensive strategy. Porcupines are covered with tens of thousands of long, pointed spines, or quills, growing from their back and sides. The quills have needle-sharp ends containing hundreds of barbs that make the quills difficult to remove. Sea urchins are also covered with long, sharp spines that deter would-be predators. Urchins can move their spines, and will direct them toward anything that comes in contact with them, such as a predator. While porcupines and urchins are covered with multiple spines, stingrays defend themselves from enemies by inflicting a wound with a single barbed spine. The wound is extremely painful, giving these rays their common name.

Predators have sharp claws and teeth that help them grasp, subdue, and consume their prey. These same structures, used offensively in hunting, can also be used to protect themselves from their own predators. Small predators such as badgers, raccoons, and foxes can fend off larger predators such as wolves and mountain lions with their weaponry. Rather than risk injury, the larger predators will avoid a fight with the smaller predator and seek a less risky meal, such as a rabbit or mouse.

Chemical Defenses: Poor Taste, Bad Smell, or Toxic Chemicals

Both plants and animals defend themselves by using compounds that are distasteful, toxic, or otherwise repulsive to consumers. Most defensive compounds are secondary metabolites of unique structures, but can also include more generic compounds such as sulfuric acid or calcium carbonate. Secondary metabolites get their name because they are not involved in basic metabolic pathways such as respiration or photosynthesis (that is, primary metabolic reactions), not because they are of secondary importance. Indeed, many organisms probably could not survive in their natural envi-

This badger bares his sharp and powerful teeth to ward off a threatening presence. (Digital Stock)

ronment without the protection of their secondary metabolites.

Stink bugs get their names because of the smelly secondary metabolites they release from pores located on the sides of their thorax. These smelly compounds repel predators, and may even indicate toxicity to the predator. These insects are common garden pests that are usually controlled with chemical pesticides. However, it appears that the eggs of stink bugs are not defended against roly-poly pill bugs, which can control stink bug numbers (and hence, garden damage) by preying on eggs.

Bombardier beetles take chemical defenses a step further, erupting a boiling hot spray of chemicals in the direction of a predator. To accomplish this, the bombardier beetle has a pair of glands that open at the tip of its abdomen. Each gland has two compartments, one that contains a solution of hydroquinone and hydrogen peroxide, and the other that contains a mixture of enzymes. When threatened by a predator, the bombardier beetle squeezes the hydroquinone and hydrogen peroxide mixture into the enzyme compartment, where an exothermic reaction that produces quinone takes place. The large amount of heat generated brings the quinone mixture to its boiling point, and it is forcefully emitted as a vapor toward the threat. An average bombardier beetle can produce about twenty loud discharges of repulsive, hot chemicals in quick succession.

Chemical defenses are common among small, slow animals such as insects, sponges, cnidarians, and sea slugs, which might be limited in their ability to flee from predators. However, chemical defenses are rather rare among large, fast animals. One of the few mammals that uses chemical defenses is the black-and-white-striped skunk. Most people are familiar with the smelly chemical brew emitted from these animals, as it is distinctly detectable along roads when skunks get hit by cars, and can be detected up to a mile from the location where a skunk sprays. These mammals hold their smelly musk in glands located below their tail, and squirt the liquid through ducts that protrude from the anus. When threatened by a predator, the skunk raises its tail and directs its rear end toward the predator. A predator that has had prior experience with a skunk might retreat from this display, but if the predator is persistent at harassing the skunk, the striped mammal will deliver a spray of smelly chemicals that usually sends the predator running. The musk also causes intense pain and temporary blindness if it gets in the eyes of the predator.

Associational Defenses: The Guard Dog Approach

Associational defenses occur when a species gains protection from a natural enemy by associating with a protective species, such as when humans gain protection from enemies by keeping a guard dog on their property. Types of protection provided to the defended species through this coevolution can be structural, chemical, or aggressive.

Small animals can avoid predators by using a defended species as habitat. For example, small fishes defend themselves by associating with sea urchins, gaining protection by hiding among the sharp spines. Some species of shrimp inhabit the cavities and canals of sponges. Sponges are known to be chemically and structurally defended against most predators, with the exception of angel fishes and parrot fishes. Finally, much of the diverse coral reef fauna seeks protection among the cracks and the crevices in the reef. Reefs, slowly built by coral animals, are the largest structures ever made by living organisms, and serve a protective role for thousands of species that inhabit reefs.

Associational defenses can also be chemically mediated. For example, bacteria that grow symbiotically on shrimp eggs produce secondary metabolites that protect the egg from a parasitic fungus. The numerous examples of sequestration of chemical defenses can be categorized as associational defenses, as they involve associating with chemically defended prey.

An organism might even be defended by protective species that aggressively attack would-be predators, especially if the protected species is a resource for the aggressive defender. For example, humans are protected by guard dogs because dogs view people as a resource that provides them with food, water, and shelter. Stop feeding the dog, and it is likely to look elsewhere for somebody to protect. There are several nonhuman examples of aggressive defensive associations, especially among ants. Aphids are insects that feed on the sugary phloem stream of plants. In the process of feeding and processing phloem, the aphids secrete large amounts of honeydew, which the ants harvest and consume; that is, aphids provide ants with a resource. Ants tend to aphids in the same way that dairy farmers tend to their cows. The ants carry aphids to prime feeding locations, defend aphids from predators, and periodically "milk" the aphids of their honeydew by stroking them with their antennae.

Defensive Behaviors: Advertising and Trickery
Being chemically defended does not protect an animal from being accidentally eaten. Therefore, chemically defended animals often advertise the fact that they are nasty to avoid such accidents. This advertisement is often in the form of outlandish colors and patterns that flaunt the animal's distastefulness to predators. Using bright warning patterns is called aposematic coloration.

One problem with aposematic coloration is the training of predators: Bright coloration is only useful if the predator understands the warning. Otherwise, the coloration simply makes the animal a conspicuous prey item. An interesting way that different species with aposematic coloration share the cost of training naïve predators is through mimicry. A predator that eats an individual of species A (assume species A is bright red with blue stripes) and vomits shortly thereafter may learn to avoid things that are red with blue stripes, though at the cost of that first individual's life. This educated predator will now avoid other members of species A, and any other organism that looks like species A (the mimic), whether the mimic is toxic or not. If the mimic is toxic, the system is termed Müllerian mimicry. If the mimic is a palatable species that looks like a toxic model, the system is termed Batesian mimicry.

Mimicry is common within groups of closely related organisms (for example, snakes, butterflies, and bees) which are already similar in appearance. However, mimicry can also occur even when the model and mimic are distantly related. For example, there are caterpillars that mimic the head of a snake, moths that mimic the eyes of a cat, and beetles, moths, and flies that mimic stinging bees and wasps.

Autotomy: Throw the Predator a Bone
Sometimes, despite the best defenses, a predator will get hold of a prey. If this happens, some animals are able to sacrifice a portion of their body to the predator, with the hope that the remaining parts will survive, and perhaps even regrow the lost parts. This ability to lose a body part intentionally is called autotomy.

Many lower animals, such as sponges, cnidarians, and worms, have great regeneration abilities, and can regrow body parts well. In fact, these animals can even use regeneration as a form of asexual reproduction: Break the animal into four parts, and the parts will generate four complete individuals.

Sea cucumbers, in addition to being chemically defended, are able to eviscerate (autotomy of intestines) when harassed by a predator. These are not fast animals, so this action does not allow them to escape, but it might satisfy (or disgust) the predator enough to make it lose interest in the sea cucumber. Losing a large portion of its digestive tract interferes with feeding, but the sea cucumber can regenerate those parts of the gut that were eviscerated, restoring itself to original function. Sea cucumbers also play an important role in a defensive association with the pearlfish. When the pearlfish feels threatened, it locates the anus of a sea cucumber, then backs into its intestine, where it hides until the danger has passed.

The regenerative ability of higher animals is generally less than that of lower animals. However, autotomy does occur even in some vertebrates. Lizards are well known for their ability to release the tips of their tails when grabbed by a predator. The predator is distracted, and perhaps satisfied, by the wiggling piece of flesh, and in the meantime, the remainder of the lizard scampers off to safety. Geckos release skin instead of tails. The part of the skin that is grabbed by the predator is released, enabling the gecko to break free and escape.

Nutritional Defenses: Not Worth the Effort

Some animals, such as corals, jellyfish, anemones, and gorgonians (phylum Cnidaria), possess a type of combined structural and chemical defense in the form of specialized stinging cells called nematocysts. When nematocysts are stimulated, they rapidly discharge a barb that punctures the skin of a predator, often releasing toxic chemicals at the same time. The stinging sensation that people get when they swim into a jellyfish is caused by nematocysts. Some of these jellyfish stings are so potent that they can result in death.

Not only do many predators avoid jellyfish because they posses nematocysts, but predators may avoid jellyfish because they are jellylike, being composed of more than 95 percent water. It takes time and effort for predators to locate, handle, ingest, and digest prey. If the prey item is basically a bag of seawater (as jellyfish are), then predators might not bother eating these nutrient-deficient animals. Thus, these animals are "nutritionally" defended. Nutritional defenses are also used by plants, but they are generally not an avail-

Acacia-Ant Mutualism

Acacia ants are found throughout Central America and only inhabit the hollow thorns of acacia trees. The ants harvest and feed on nectar from extrafloral nectaries and special leaf tips, called Beltian bodies, produced by the acacia trees. In a sense, these ants are herbivores of acacia trees. However, in return for the shelter and food provided by the tree, the ants defend the tree from other herbivores and competitors. When an herbivore begins feeding on the acacia tree, the ants release an alarm order that signals the colony to attack the herbivore with painful bites and stings. The busy ants also remove competing vegetation that comes in contact with the tree or that grows near the trunk of the tree. The weeding activity of the ants results in a circle of cleared ground surrounding the acacia tree that also protects the tree from the damaging effects of fire. This mutualistic relation is obligate, meaning that each species is absolutely dependent on the other: The tree cannot survive without the ants and vice versa. Other species take advantage of the acacia-ant mutualism: Some birds preferentially nest in acacia trees, presumedly because the ants deter egg predators as well as herbivores. How the birds avoid attack by the ants is not well understood.

able strategy for animals other than jellyfish, as most animal tissue is relatively nutritious.

—*Greg Cronin*

See also: Adaptations and their mechanisms; Camouflage; Carnivores; Claws, nails, and hooves; Coevolution; Communication; Competition; Death and dying; Displays; Ethology; Exoskeletons; Food chains and food webs; Herbivores; Instincts; Learning; Mimicry; Nutrient requirements; Pheromones; Poisonous animals; Predation; Regeneration; Shells; Teeth, fangs, and tusks; Territoriality and aggression; Vocalizations.

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DEMOGRAPHICS

Type of animal science: Ecology
Fields of study: Environmental science, population biology, zoology

Demography is the study of the numbers of organisms born in a population within a certain time period, the rate at which they survive to various ages, and the number of offspring that they produce. Many different patterns of birth, survival, and reproduction are found among organisms in nature.

Principal Terms

COHORT: a group of organisms of the same species, and usually of the same population, that are born at about the same time

FECUNDITY: the number of offspring produced by an individual

LIFE TABLE: a chart that summarizes the survivorship and reproduction of a cohort throughout its life span

MORTALITY RATE: the number of organisms in a population that die during a given time interval

NATALITY RATE: the number of individuals that are born into a population during a given time interval

POPULATION: a group of individuals of the same species that live in the same location at the same time

SURVIVORSHIP: the pattern of survival exhibited by a cohort throughout its life span

No animal lives forever. Instead, each individual has a generalized life history that begins with fertilization and then goes through embryonic development, a juvenile stage, a period in which it produces offspring, and finally death. There are many variations on this general theme. Still, the life of each organism has two constants: a beginning and an end. Many biologists are fascinated by the births and deaths of individuals in a population and seek to understand the processes that govern the production of new individuals and the deaths of those already present. The branch of biology that deals with such phenomena is called demography.

The word "demography" is derived from Greek; *demos* means "population." For many centuries, demography was applied almost exclusively to humans as a way of keeping written records of new births, marriages, deaths, and other socially relevant information. During the first half of the twentieth century, biologists gradually began to census populations of naturally occurring organisms to understand their ecology more fully. Biologists initially focused on vertebrate animals, particularly game animals and fish. Beginning in the 1960's and 1970's, invertebrate animals, plants, and microbes also became subjects of demographic studies. Studies clearly show that different species of organisms vary greatly in their demographic properties. Often, there is a clear relationship between those demographic properties and the habitat in which these organisms live.

Demographic Parameters

When conducting demographic studies, a demographer must gather certain types of basic information about the population. The first is the number of new organisms that appear in a given amount of time. There are two ways that an organism can enter a population: by being born into it or by immigrating from elsewhere. Demographers generally ignore immigration and concentrate instead on newborns. The number of new individuals born into a population during a specific time interval is termed the natality rate. The natality rate is often based on the number of individuals already in the population. For example, if ten newborns enter a population of a thousand individuals during a given time period, the natality rate is 0.010. A specific time interval must be expressed (days, months, years) for the natality rate to have any meaning.

A second demographic parameter is the mortality rate, which is simply the rate at which individuals are lost from the population by death. Losses that result from emigration to a different population are ignored by most demographers. Like the natality rate, the mortality rate is based on the number of individuals in the population, and it reflects losses during a certain time period. If calculated properly, the natality and mortality rates are directly comparable, and one can subtract the latter from the former to provide an index of the change in population size over time. The population increases whenever natality exceeds mortality and decreases when the reverse is true. The absolute value of the difference denotes the rate of population growth or decline.

When studying mortality, demographers determine the age at which organisms die. Theoretically, each species has a natural life span that no individuals can surpass, even under the most ideal conditions. Normally, however, few organisms reach their natural life span, because conditions are far from ideal in nature. Juveniles, young adults, and old adults can all die. When trying to understand the dynamics of a population, it makes a large difference whether the individuals are dying mainly as adults or mainly as juveniles.

Patterns of Survival

Looking at it another way, demographers want to know the pattern of survival for a given population. This can best be determined by identifying a cohort, which is defined as a group of individuals that are born at about the same time. That cohort is then followed over time, and the number of survivors is counted at set time intervals. The census stops after the last member of the cohort dies. The pattern of survival exhibited by the whole cohort is called its survivorship. Ecologists have examined the survivorship patterns of a wide array of species, including vertebrate animals, invertebrates, plants, fungi, algae, and even microscopic organisms. They have also investigated organisms from a variety of habitats, including oceans, deserts, rain forests, mountain peaks, meadows, and ponds. Survivorship patterns vary tremendously.

Some species have a survivorship pattern in which the young and middle-aged individuals have a high rate of survival, but old individuals die in large numbers. Several species of organisms that live in nature, such as mountain sheep and rotifers (tiny aquatic invertebrates), exhibit this survivorship pattern. At the other extreme, many species exhibit a survivorship pattern in which mortality is heaviest among the young. Those few individuals that are fortunate enough to survive the period of heavy mortality then enjoy a high probability of surviving until the end of their natural life span. Examples of species that have this pattern include marine invertebrates such as sponges and clams, most species of fish, and parasitic worms. An intermediate pattern is also observed, in which the probability of dying stays relatively constant as the cohort gets older. American robins, gray squirrels, and hydras all display this pattern.

These survivorship patterns are usually depicted on a graph that has the age of individuals in the cohort on the x axis and the number of survivors on the y axis. Each of the three survivorship patterns gives a different curve when the number of survivors is plotted as a function of age. In the first pattern (high survival among juveniles), the curve is horizontal at first but then swings downward at the right of the graph. In the second pattern (low survival among juveniles), the curve drops at the left of the graph but then levels out to form a horizontal line. That curve resembles a backward letter J. The third survivorship pattern (constant mortality throughout the life of the cohort) gives a straight line that runs from the upper-left corner of the graph to the lower right (this is best seen when the y axis is expressed as the logarithm of the number of survivors).

In the first half of the twentieth century, demographers Raymond Pearl and Edward S. Deevey labeled each survivorship pattern: Type I is high survival among juveniles, type II is constant mortality through the life of the cohort, and type III is low survival among juveniles. That terminology became well entrenched in the biological literature by the 1950's. Few species exhibit a pure type I, II, or III pattern, however; instead, survivorship varies so that the pattern may be one type at one part of the cohort's existence and another type later on. Perhaps the most common survivorship pattern, especially among vertebrates, is composed of a type III pattern for juveniles and young adults followed by a type I pattern for older adults. This pattern can be explained biologically. Most species tend to suffer heavy juvenile mortality because of predation, starvation, cannibalism, or the inability to cope with a stressful environment. Juveniles that survive this hazardous period then become strong adults that enjoy relatively low mortality. As time passes, the adults reach old age and ultimately fall victim to disease, predation, and organ-system failure, thus causing a second downward plunge in the survivorship curve.

Patterns of Reproduction

Demographers are not interested only in measuring the survivorship of cohorts. They also want to understand the patterns of reproduction, especially among females. Different species show widely varying patterns of reproduction. For example, some species, such as octopuses and certain salmon, reproduce only once in their life and then die soon afterward. Others, such as humans and most birds, reproduce several or many times in their life. Species that reproduce only once accumulate energy throughout their life and essentially put all of it into producing young. Reproduction essentially exhausts them to death. Conversely, those that reproduce several times devote only a small amount of their energy into each reproductive event.

Species also vary in their fecundity, which is the number of offspring that an individual makes when it reproduces. Large mammals have low fecundity, because they produce only one or two progeny at a time. Birds, reptiles, and small mammals have higher fecundity because they typically produce a clutch or litter of several offspring. Fish, frogs, and parasitic worms have very high fecundity, producing hundreds or thousands of offspring.

A species' pattern of reproduction is often related to its survivorship. For example, a species with low fecundity or one that reproduces only once tends to have type I or type II survivorship. Conversely, a species that produces huge numbers of offspring generally shows type III survivorship. Many biologists are fascinated by this interrelationship between survivorship and reproduction. Beginning in the 1950's, some demographers proposed mathematically based explanations as to how the interrelationship might have evolved as well as the ecological conditions in which various life histories would be expected. For example, some demographers predicted that species with low fecundity and type I survival should be found in undisturbed, densely populated areas (such as a tropical rain forest). In contrast, species with high fecundity and type III survival should prevail in places that are either uncrowded or highly disturbed (such as an abandoned farm field). Ecologists have conducted field studies of both plants and animals to determine whether the patterns that actually occur in nature fit the theoretical predictions. In some cases the predictions were upheld, but in others they were found to be wrong and had to be modified.

Age Structures and Sex Ratios

Another feature of a population is its age structure, which is simply the number of individuals of each age. Some populations have an age structure characterized by many juveniles and only a few adults. Two situations could account for such a pattern. First, the population could be rapidly expanding, with the adults successfully reproducing many progeny that are enjoying high survival.

Second, the population could be producing many offspring that have type III survival. In this second case, the size of the population can remain constant or even decline. Other populations have a different age structure, in which the number of juveniles only slightly exceeds the number of adults. Those populations tend to remain relatively constant over time. Still other populations have an age structure in which there are relatively few juveniles and many adults. Those populations are probably declining or are about to decline because the adults are not successfully reproducing.

Since most animals are unisexual, an important demographic characteristic of a population is its sex ratio, defined as the ratio of males to females. While the ratio for birds and mammals tends to be 1:1 at conception (the fertilization of an egg), it tends to be weighted toward males at birth, because female embryos are slightly less viable. After birth, the sex ratio for mammals tends to favor females, because young males suffer higher mortality. The posthatching ratio in birds tends to remain skewed toward males, because females devote considerable energy to producing young and suffer higher mortality. As a result, male birds must compete with one another for the opportunity to mate with the scarcer females.

The Age-Specific Approach

To understand the demography of a particular species, one must collect information about its survivorship and reproduction. The best survivorship data are obtained when a demographer follows a group of newly born organisms (this being a cohort) over time, periodically counting the survivors until the last one dies. Although that sounds relatively straightforward, many factors complicate the collection of survivorship data; demographers must be willing to adjust their methods to fit the particular species and environmental conditions.

First, a demographer must decide how many newborns should be included in the cohort. Survivorship is usually based on one thousand newborns, but few studies follow that exact number. Instead, demographers follow a certain number of newborns and multiply or divide their data so that the cohort is expressed as one thousand newborns. For example, one may choose to follow five hundred newborns; the number of survivors is then multiplied by two. Demographers generally consider cohorts composed of fewer than one hundred newborns to be too small. Second, methods of determining survivorship are much more different for highly motile organisms, such as mammals and birds, than for more sedentary ones, such as bivalves (oysters and clams). To determine survivorship of a sedentary species, demographers often find some newborns during an initial visit to a site and then periodically revisit that site to count the number of survivors. Highly motile animals are much more difficult to census because they do not stay in one place waiting to be counted. Vertebrates and large invertebrates can be tagged, and individuals can be followed by subsequently recapturing them. Some biologists use small radio transmitters to follow highly active species. The demography of small invertebrates such as insects is best determined when there is only one generation per year and members of the population are all of the same age-class. For such species, demographers merely count the number present at periodic intervals.

Third, the frequency of the census periods varies from species to species. Short-lived species, such as insects, must be censused every week or two. Longer-lived species need be counted only once a year. Fourth, the definition of a "newborn" may be troublesome, especially for species with complex life cycles. Demographic studies usually begin with the birth of an infant. Some would argue, however, that the fetus should be included in the analysis because the starting point is really conception. Many sedentary marine invertebrates (sponges, starfish, and barnacles) have highly motile larval stages, and these should be included in the analysis for survivorship to be completely understood. Parasitic roundworms and flatworms that have numerous juvenile stages, each found inside a different host, are particularly challenging to the demographer.

The Time-Specific Approach

The survivorship of long-lived species, such as large mammals, is really impossible to determine by the methods given above. Because of their sheer longevity, one could not expect a scientist to be willing to wait decades or centuries until the last member of a cohort dies. Demographers attempt to overcome this problem by using the age distribution of organisms that are alive at one time to infer cohort survivorship. This is often termed a "horizontal" or "time-specific" approach, as opposed to the "vertical" or "age-specific" approach that requires repeated observations of a single cohort. For example, one might construct a time-specific survivorship curve for a population of fish by live-trapping a sufficiently large sample, counting the rings on the scales on each individual (which for many species is correlated with the age in years), and then determining the number of one-year-olds, two-year-olds, and so on. Typically, demographers who use age distributions to infer age-specific survivorship automatically assume that natality and mortality remain constant from year to year. That is often not the case, however, because environmental conditions often change over time. Thus, demographers must be cautious when using age distribution data to infer survivorship.

Methods for determining fecundity are relatively straightforward. Typically, fertile individuals are collected, their ages are determined, and the number of progeny (eggs or live young) are counted. Species that reproduce continually (parasitic worms) or those that reproduce several times a year (small mammals and many insects) must be observed over a period of time.

Demographers usually want to determine whether the production of new offspring (natality) balances the losses attributable to mortality. To accomplish this, they construct a life table, which is a chart with several columns and rows. Each row represents a different age of the cohort, from birth to death. The columns show the survival and fecundity of the cohort. By recalculating the survivorship and fecundity information, demographers can compute several interesting aspects of the cohort, including the life expectancy of individuals at different ages, the cohort's reproductive value (which is the number of progeny that an individual can expect to produce in the future), the length of a generation for that species, and the growth rate for the population.

Uses of Demography

Demographic techniques have been applied to nonhuman species, particularly by wildlife managers, foresters, and ecologists. Wildlife managers seek to understand how a population is surviving and reproducing within a certain area, and therefore to determine whether it is increasing or decreasing over time. With that information, a wildlife biologist can then estimate the effect of hunting or other management practice on the population. By extension, fisheries biologists can also make use of demographic techniques to determine the growth rate of the species of interest. If the population is determined to be increasing, it can be harvested without fear of depleting the population. Alternatively, one can conduct demographic analyses to see whether certain species are being overfished.

An often unappreciated benefit of survivorship analyses is that they can help ecologists pinpoint factors that limit population growth in an area. This may be especially important in efforts to prevent rare animals and plants from becoming extinct. Once the factor is identified, the population can be appropriately managed. Increasing amounts of public and private money are allocated each year to biologists who conduct demographic studies on rare species.

—*Kenneth M. Klemow*

See also: Birth; Communities; Competition; Death and dying; Ecological niches; Ecology; Ecosystems; Endangered species; Groups; Habitats and biomes; Herds; Insect societies; Life spans; Mammalian social systems; Mark, release, and recapture methods; Mating; Offspring care; Packs; Population analysis; Population fluctuations; Population genetics; Population growth; Reproductive strategies.

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DESERTS

Types of animal science: Ecology, evolution, geography, physiology
Fields of study: Ecology, environmental science, evolutionary science, wildlife ecology

Deserts are home to many living things, despite their treacherous climate. In fact, deserts are second only to tropical rain forests in the variety of plant and animal species that live there. Study of deserts and the organisms that live within them will help us understand and appreciate this unique biome.

Principal Terms

BIOME: a terrestrial ecosystem that occupies an extensive geographical area and is characterized by a specific type of plant community, such as deserts

PERENNIAL: plants that live for several years

RAIN SHADOW: a local dry (desertlike) area created by the modification of rainfall patterns by a mountain range

Deserts are usually defined by their annual rainfall, climate, and the plants and animals that live in them. Most deserts are found in bands along 30 degrees north and south latitude. Other deserts are caused by the rain shadow effect. Deserts are biomes in which less than twenty-five to fifty centimeters of precipitation drops each year. There may be no vegetation or widely spaced vegetation combined with large areas of bare ground. The plants tend to be spaced evenly, as if planted by hand. The desert is a land of extremes: extreme heat and extreme dryness. It is often very hot in the daytime, and somewhat chilly or even very cold at night. The desert is dry most of the year; even the wettest deserts get only ten inches or less of precipitation per year. The scarce precipitation comes from a few very large rains or snows. Due to such extreme conditions, deserts often have names like "Death Valley," "the empty quarter," and "the place from which there is no return." Overall, about one fifth of the land surface of the earth is desert.

Depending upon whether the precipitation comes from rain or snow, deserts can be divided into hot (rain) or cold (snow) deserts. The deserts of Arabia, Australia, Chihuahua, Kalahari, Monte, Sonora, and Thar are all considered hot deserts. Cold deserts include the Atacama, Gobi, Basin, Iranian, Namib, and Turkestan deserts. Regardless of whether the desert is hot or cold, organisms living within desert biomes have to adapt to cope with the scarcity of water and violent swing of temperatures.

Plant Life in Deserts

Desert plant life includes wildflowers, cacti and succulents, and grasses and trees. The desert is renowned for its explosions of spring wildflowers and the succulent cactus that adorn its landscapes. Desert wildflowers assume a variety of shapes and colors; some are beautiful, some are poisonous. Apache plume (*Fallugia paradoxa*) is an evergreen shrub that grows up to six feet high, with small grayish, downy leaves, and round white flowers with yellow centers. Jimson weed (genus *Datura*) has large, white, trumpet-shaped flowers that bloom from March through November. This foul-smelling flower opens after dusk and closes by midmorning of the following day. All parts of datura plants are poisonous and can be fatal if ingested. Desert dandelion (*Malacothrix glabrata*) grows six to fourteen inches high with three- to five-inch leaves. In spring, this bright wildflower will form broad, brilliant patches of gold across the sandy desert floor. Many other species, including desert lily, desert paintbrush, ghost flower, and prickly poppies, help contribute to the beauty of the desert's spring.

The pleated shape of the barrel cactus (genus *Ferocactus*) allows it to expand when it rains so that it can store water in its spongy tissue. It shrinks in size during dry times as it uses the stored water. The fishhook cactus (*Mammillaria microcarpa*) has fishhook-shaped spines that help divert heat and shade the growing tip of the plant. Prickly pear cactus (genus *Opuntia*) includes about a dozen species, all with modified stems and leaves for water storage, photosynthesis, and flower production. The saguaro cactus (*Carnegiea gigantea*) is equipped with a green stem to store water and perform photosynthesis, and large nets of roots that collect water after rain.

The Crucifixion thorn tree (*Chaparro amargosa*) exhibits no leaves but has intricately branched, thick, rigid, sharp spines, which perform photosynthesis and conserve water. The Joshua tree (*Yucca brevifolia*) grows only in the Mojave Desert. This picturesque, spike-leafed evergreen can grow to forty feet tall, with a diameter of one to three feet. Poison ivy (*Toxicodendron rydbergii*) is a small, woody shrub that lacks the climbing, vine-like structure of its better-known eastern relative, *T. radican*. At least ten species and subspecies bear the common name "poison ivy," a notoriously poisonous plant. Plants that live in the desert help animals by providing them with food, water, and shade.

Animal Life in Deserts

Animals living in the desert include mammals, birds and fish, reptiles and amphibians, and insects and spiders. A few examples of mammals

Deserts are arid but not entirely devoid of life: Scrub vegetation, cacti, and animals adapted to dry conditions can flourish there. (PhotoDisc) include bats, bighorn sheep, bobcats, and coyotes. Desert bats, members of the suborder Microchioptera, are often considered to be flying mice, but they are more closely related to primates. Bats are unique among mammals because they can fly. Most bat species also possess a system of acoustic orientation, technically known as echolocation. The bighorn sheep lives in dry, desert mountain ranges and foothills near rocky cliffs. Its body is compact and muscular; the muzzle is narrow and pointed; the ears, short and pointed; the tail, very short. The fur is deerlike and usually a shade of brown, with whitish rump patches. Bighorns are grazers, consuming grasses, sedges, and other low-lying plants. The bobcat (*Felis rufus*) has long legs, large paws, and a short tail (six to seven inches long), with average body weight of fifteen to twenty pounds. However, it is quite fierce and is equipped to kill animals as large as deer. The desert coyote (*Canis latrans*), a member of the dog family, weighs about twenty pounds, less than half the weight of its mountain kin, which can weigh up to fifty pounds. Its body color is light gray or tan, which helps it survive in the desert.

A variety of birds reside in the desert due to the abundance of insects and spiders. Golden eagles (*Aquila chrysaetos*) get their name from the golden feathers on the back of their neck. They are birds of the open country, building large stick nests in trees or cliff walls where they have plenty of room to maneuver. Adults weigh 9 to 12.5 pounds, with females usually larger than males. Ravens (*Corvus corax*) are the largest birds of the crow family, averaging twenty-four inches tall, with a wingspan of forty-six to fifty-six inches. Ravens are strong fliers that can soar like a hawk, and may form large flocks of over several hundred individuals during their autumn migration. The American turkey (*Meleagris gallopavo*), the largest upland game bird in North America, is thirty-six to forty-eight inches long, with four- to five-foot wingspans. Males average ten inches longer than females, which are paler and of a more buff color. Turkeys inhabit a variety of habitats from open grassland and fields to open woodlands and mature deciduous or coniferous forests.

Many species of reptiles and amphibians live in desert, including the black-collared lizard (genus *Crotaphytus*), bullfrog (*Rana catesbeiana*), desert dinosaur (orders Saurischia and Ornithischia), desert iguana (*Dispsosaurus dorsalis*), rattlesnake (genus *Crotalus*), and many others. Insects and spiders include dragonflies (suborder Anisoptera), scorpions (order Scorpionida), and black widow spiders (*Latrodectus hesperus*). It is nothing short of a miracle that such an abundance of lives, both plants and animals, can survive in the extreme conditions of the desert.

The Survival of Plants in the Desert

Desert plants have adapted to the extremes of heat and cold and of aridity by using both physical and behavioral mechanisms. Plants that have adapted by altering their physical structure are called xerophytes, having special means for storing and conserving water. They often have few or no leaves, which reduces transpiration. Phreatophytes are plants that have adapted to arid environments by growing extremely long roots, allowing them to acquire moisture at or near the water table. Other desert plants, using behavioral adaptations, have developed a lifestyle in conformance with the seasons of greatest moisture and/or coolest temperatures. Desert perennials often survive by remaining dormant during dry periods of the year, then springing to life when water becomes available. Most annual desert plants germinate only after heavy seasonal rain, then complete their reproductive cycle very quickly. They bloom prodigiously for a few weeks in the spring, accounting for most of the annual wildflower explosions of the deserts. Their seeds are drought- and heat-resistant and remain dormant until the next year's rains.

Animal Survival in the Desert

Among the thousands of desert animal species, there are many remarkable behavioral and structural adaptations developed for avoiding excess heat. Equally ingenious are the diverse mechanisms various animal species have developed to acquire, conserve, recycle, and actually manufacture water.

Certain species of birds, such as the *Phanopepla*, breed during the relatively cool spring, then leave the desert for cooler areas at higher elevations or along the Pacific coast. The Costa's hummingbird begins breeding in late winter and leaves in late spring when temperatures become extreme. Many birds, as well as other mammals and reptiles, are crepuscular, meaning they are active only at dusk and again at dawn. Many animals, including bats, many snakes, most rodents, and some larger animals such as foxes and skunks, are nocturnal, restricting all their activities to the cooler temperatures of the night, and sleeping in a cool den, cave, or burrow by day. A few desert animals, such as the round-tailed ground squirrel, sleep away the hottest part of summer and also hibernate in winter to avoid the cold season. Yet other animals, such as desert toads, remain dormant deep in the ground until the summer rains fill ponds. They then emerge, breed, lay eggs, and replenish their body reserves of food and water for another long period.

Various mechanisms are employed to dissipate heat absorbed by desert animals. Many mammals have long appendages to release body heat into their environment. The enormous ears of jackrabbits, with their many blood vessels, dissipate heat when the animal is resting in a cool, shady location. Their close relatives in cooler regions have much shorter ears. New World vultures, dark in color and thus absorbing considerable heat in the desert, excrete urine on their legs to cool them by evaporation, and circulate the cooled blood back through the body. Many desert animals are paler than their relatives elsewhere, ensuring that they not only suffer less heat absorption, but also are less conspicuous to predators in the bright, pallid surroundings.

The mechanisms by which water is retained by desert animals are even more elaborate. Reptiles and birds excrete metabolic wastes in the form of uric acid, an insoluble white compound, wasting very little water in the process. Other animals retain water by burrowing into moist soil during the dry daylight hours. Some predatory and scavenging animals can obtain their entire water needs from the food they eat. Most mammals, however, need access to a good supply of fresh water at least every few days, if not daily, due to the considerable water loss from excretion of urea, a soluble compound.

Many desert animals obtain water from plants, particularly succulent ones such as cactus and saguaro. Many species of insects thrive in the desert, as they tap plant fluids for water and nectar. The abundance of insect life permits insectivorous birds, bats, and lizards to thrive in the desert. Certain desert animals, such as kangaroo rats, have multiple adaptation mechanisms to acquire and conserve water. First, they live in underground dens that they seal off to block out heat and to recycle the moisture from their own breathing. Second, they have specialized kidneys with extra microscopic projections to extract most of the water from their urine and return it to the bloodstream. Third, and most fascinating of all, they actually manufacture their water metabolically from the digestion of dry seeds. These are just a few examples of the ingenious variety of adaptations animals use to survive in the desert, overcoming the extremes of heat and the paucity of water.

—Yujia Weng

See also: Bats; Birds; Chickens, turkeys, pheasant, and quail; Dogs, wolves, and coyotes; Eagles; Ecosystems; Fauna: Africa; Fauna: Asia; Fauna: Australia; Fauna: North America; Foxes; Frogs and toads; Habitats and biomes; Hibernation; Insects; Lizards; Mice and rats; Nocturnal animals; Rabbits, hares, and pikas; Reptiles; Rodents; Scorpions; Sheep; Skunks; Snakes; Spiders; Squirrels; Thermoregulation; Turtles and tortoises; Vultures; Water balance in vertebrates.

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DETERMINATION AND DIFFERENTIATION

Type of animal science: Reproduction
Fields of study: Anatomy, cell biology, physiology

Determination is the process whereby the fate of embryonic cells becomes fixed, and differentiation is the process whereby cells acquire their ultimate specialized structure and function. These processes lead to the wide diversity of cell types found in multicellular organisms.

Principal Terms

COMMITMENT: the "decision" by an embryonic cell to develop in a certain way, which may be reversed if the cell is removed from its normal surroundings

EMBRYONIC INDUCTION: the point at which one embryonic tissue signals another embryonic tissue to develop in a certain way

GENOME: all the genes of one organism or species

MORPHOGENESIS: the development of form, including the overall form of the organism and the form of each organ and tissue

MOSAIC DEVELOPMENT: the process whereby early embryonic cells are determined by the cytoplasm they receive from the egg; also called determinate development

REGULATIVE DEVELOPMENT: the process whereby early embryonic cells are determined by their interactions with other cells; also called indeterminate development

RESTRICTION: reduction of the developmental potency of a cell

TOTIPOTENT: the ability of a cell to develop into any kind of cell in the body

From the time a fertilized ovum begins to divide (cleavage) until it forms a complete organism, it passes through successive stages in which groups of cells become increasingly specialized. This process of cell specialization involves two key steps: determination, in which cells become committed to a certain developmental pathway, and differentiation, in which cells acquire their ultimate structure and function. The term "differentiation" may also be used in a broader sense to describe the entire process of cell specialization. A third process, called morphogenesis, is needed in order to mold the embryonic cells structurally into the various tissues and organ systems of the mature organism. For example, in eye development the specialized photoreceptor cells of the retina are a product of determination and differentiation, but their organization into the overall structure of the eye is a product of morphogenesis.

The Process of Specialization

In animal development, the fertilized ovum (zygote) has the potential to develop into any type of cell in the body; it is said to be totipotent. As it undergoes cell division beyond the first few cleavages, the resulting cells (blastomeres) lose their totipotency. This point is reached at different stages in different species. In the sea urchin, for example, isolated cells of the two- or four-cell embryo are capable of developing into complete new adults; in other species, such as the tooth shell clam (*Dentalium*), these early cleavage cells, when isolated, do not have the potential to develop into a complete organism. In all animals, the cells of later embryos lose their ability to form complete new organisms. This loss of developmental potency of cells is called restriction and is dictated to some extent both by the type of cytoplasm with which the cell is endowed and the influence of surrounding cells. As development progresses, restricted cells become "committed" to develop into a specific tissue. Under normal conditions, these cells will always develop into this designated tissue; if, however, the cells are moved experimentally to some other part of the embryo or to another embryo, they will develop in a different way. That is why commitment is said to be reversible but determination is not.

Determination occurs when a group of cells becomes irreversibly assigned to develop into a specific tissue. Determination is the final step in restriction; beyond this point, the cells have no other developmental options. Determined cells may or may not look different from other embryonic cells, but they have changed internally so that they are committed to a particular developmental pathway. Determined cells are said to be self-perpetuating, because they can pass on heritable information about their identity and do not require stimulation by surrounding cells to develop in a certain way.

Once the fate of a cell is determined, then differentiation (also called cell differentiation or cytodifferentiation) can take place. During differentiation, the cell undergoes structural and functional changes which result in a highly specialized, mature, differentiated cell. For example, the red blood cell becomes specialized by losing its nucleus and other organelles in order to fill itself completely with the oxygen-carrying molecule hemoglobin. It also maximizes its surface area by becoming flattened and doughnut shaped. Primitive muscle cells, called myoblasts, become specialized by fusing together to form elongated multinuclear cells called myotubes. These cells further specialize by forming contractile organelles called myofibrils, composed primarily of the proteins actin and myosin.

The Role of Genes

At one time it was believed that the genetic determinants (genes) were divided up and parceled out as determination and differentiation progressed, such that each cell type received certain genes. This hypothesis was disproved in several ways, one of them being nuclear transplantation experiments, in which adult cell nuclei were transplanted into fertilized eggs whose nuclei had been removed or inactivated. A small percentage of these eggs were able to develop into normal adults, thus proving that the adult nuclei implanted in them retained all the genes necessary to form a complete organism. These and other experiments have led to the conclusion that both determination and differentiation occur because certain genes are expressed at certain times during the life history of the cell. There remains, however, the question of how genes are turned on and off to control development.

All developmental processes are believed to be controlled by genes as part of an intricate developmental program. The genes of individual cells are activated or deactivated via various signaling mechanisms in order to provide the correct cellular responses at the appropriate times. This process begins very early in development and even occurs in the egg before fertilization. Messenger ribonucleic acid (RNA) and proteins are produced by the egg and distributed unequally in the cytoplasm of different parts of the egg. When cleavage occurs, blastomeres in one part of the embryo receive cytoplasm that differs from the cytoplasm received by blastomeres in another part of the embryo; thus, some cells are endowed with one kind of messenger RNA and protein and other cells with another kind. In some species, cleavage is even unequal, in order to ensure that certain cells receive the desired cytoplasm. For example, in the nematode *Caenorhabditis elegans*, unequal cleavage results in the establishment of five different tissue types by the sixteen-cell stage. As the messenger RNA is expressed in the form of new proteins, it gives unique qualities to the cells. Some of these new proteins and the proteins made earlier in the egg may be signal molecules, which stimulate new and unique gene expression in the nucleus.

Another mechanism for turning genes on and off is called embryonic induction, which occurs when one embryonic tissue influences the development of another by releasing chemical factors called inductors. The inductors are signal molecules that instruct cells of another tissue how to develop by directly or indirectly activating certain genes. Induction is especially noticeable after the formation of distinct tissues, such as the three germ layers, ectoderm, endoderm, and mesoderm. In vertebrates, the mesoderm induces the formation of the neural tube and various other parts of the nervous system.

Another set of mechanisms, similar to embryonic induction, that controls differentiation involves the microenvironment in which the embryonic cells exist. These mechanisms include such parameters as the position of a cell in relation to other cells in the embryo; the interactions of cells with the extracellular milieu, including ions, pH, oxygen, and extracellular matrix proteins such as collagen; direct cell-to-cell contact; and the presence of specific growth and differentiation factors. The cells in one part of the developing embryo will experience a completely different set of microenvironmental influences from that of cells in another part of the embryo and consequently will be prompted to express their genes in different ways. Once the genes have been expressed, there must be a means for the daughter cells to retain the unique gene expression of the parent cell. That is most likely accomplished by proteins passed on to the daughter cells that continue to activate or deactivate the appropriate genes.

Genetic Recombination and Transcription

Although the genome is not modified extensively during embryonic development, there is evidence that certain changes occur in order to enhance differentiation. One of these mechanisms is called genetic recombination and involves breaking and rejoining deoxyribonucleic acid (DNA) at defined sites. For example, in maize, segments of DNA called transposons move around the genome and presumably take control of specific genes at certain times during development. Another example of genome modification occurs in the nematode *Ascaris*, in which parts of the chromosomes are discarded (in a process called chromosome diminution) during cleavage. The discarded chromatin is believed to be composed of extra copies of DNA sequences that are not ordinarily transcribed. The genome is also modified through the making of extra copies of essential genes (gene amplification). For example, some genes in the follicle cells surrounding the maturing oocyte of *Drosophila* are amplified about thirty times in order to code for the large amount of protein needed to make the egg chorion. As cells differentiate, the types of messenger RNA and protein they produce become increasingly selective, so that eventually each cell type has a unique pattern of gene expression. There will always, however, be common genes expressed in every cell that are needed for basic housekeeping processes, such as respiration and transport.

Selective gene transcription is carefully controlled by various mechanisms involving the blocking and unblocking of DNA. Two classes of nuclear proteins are believed to be involved in switching genes on and off: histones and nonhistones. Histones associate with DNA molecules in such a way that they block the DNA from being transcribed. The nonhistones are believed to remove or rearrange histones so that the DNA can be replicated or transcribed. Some nonhistone proteins are gene-regulatory proteins, which recognize a particular DNA sequence. The binding of these proteins with DNA can either facilitate or inhibit transcription. An additional control found only in vertebrates is methylation, by which methyl groups are added to the DNA base cytosine. In general, the inactive genes of vertebrates are more highly methylated than active genes; thus, methylation may serve to strengthen decisions involving gene expression that are made during differentiation.

Once the appropriate messenger RNA has been produced, it still must be translated into protein and the protein must be assembled and made functional. For example, hemoglobin protein (globin) translation is controlled by the presence of heme, the iron-containing portion of the hemoglobin molecule. In the absence of heme, the factor that initiates globin translation is inactivated; thus, even though the appropriate messenger RNA and other necessary ingredients are present, without heme no hemoglobin protein will be produced. Even after proteins are translated, they are subject to further regulatory mechanisms, such as assembly into functional units, activation or inactivation by various enzymes and other factors, and transport to their cellular destination.

Studying Embryology

The study of embryology was transformed from a purely descriptive science into an experimental science by investigators who developed microsurgical techniques in the 1890's. They discovered that the separated blastomeres of some early embryos, such as the sea urchin, could develop into complete normal larva (regulative or indeterminate development) and that the blastomeres of others, such as the tunicate, could form only parts of embryos (mosaic or determinate development). This led to an appreciation of the importance of nuclear-cytoplasmic interactions and the fact that egg cytoplasm distribution plays an important role in determining how certain blastomeres develop. Further microsurgical separation studies on embryos in later stages (thirty-two-cell to sixty-four-cell stages) demonstrated that the microenvironment of some embryos approximates a double gradient consisting of animal pole factors in one half and vegetal pole factors in the other half. These two chemical gradients influence the cell nuclei in their respective zones and cause the cells to become progressively determined in certain ways. Thus, simply by manipulating embryonic cells, scientists were able to demonstrate the concepts of restriction and determination.

Another microsurgical technique developed in the first half of the twentieth century involves transplanting tissue from one embryo to another. When tissue that normally forms the brain is transplanted to an area of another embryo that normally forms skin, the transplanted tissue develops independently and begins to form into brain. Thus, the tissue has become irreversibly committed or determined to form a particular adult tissue. If the same transplant is done at an earlier stage, the transplanted tissue conforms to its surroundings and forms epidermis. These results indicate that tissues are capable of changing their normal fate if they are influenced by another tissue before determination. In some instances, the transplanted tissue induces the surrounding tissue to change its normal fate. Such is the case when tissue from the dorsal lip of the blastopore of an amphibian gastrula is transplanted to the lateral lip area of another gastrula. The transplanted tissue induces the formation of a second complete embryonic axis, resulting in laterally conjoined twins.

Another elementary method that has yielded a large amount of information about determination is cell marking and tracing. At first, investigators took advantage of different natural pigments that are present in certain animal embryos by following the fate of each blastomere. They discovered that each colored cytoplasm gives rise to a specific embryonic fate. For example, the yellow crescent cytoplasm of the tunicate (*Styela partita*) embryo gives rise to adult muscle cells. In other studies, cells were marked with vital dyes, carbon particles, enzymes, radioactive labels, and distinctive cells transplanted from another embryo. By tracing these labeled cells, investigators were able to ascertain their ultimate fate and when and where cell determination takes place.

One question that needed to be answered by experimental embryologists was whether the nuclei of determined and differentiated cells are irreversibly modified. That all the genetic material is present in differentiated cells could be shown by microscopic observations of the chromosomes, especially the large polytene chromosomes of larval flies, such as *Drosophila*. The only way to show whether these chromosomes were functional, however, was to transplant the nucleus of a differentiated cell into an enucleated egg and see if it could direct the development of a complete organism. The technique of nuclear transplantation (sometimes called cloning), developed in the 1950's, did indeed prove that nuclei from differentiated cells are totipotent. Success was not universal with all tissue types, however, and only a small percentage of the transplants actually succeeded, which indicates that restriction of potency does involve changes in the nucleus but not permanent modification of the genome itself.

Methodology

The study of differentiation can be approached by several methods. The simplest is to observe tissues microscopically as they differentiate. That is done most often by fixing embryos at various stages of development and observing thinly sliced sections of them with a light or electron microscope. Another method is to explant cells, tissue, or organs from embryos and observe them in culture (in vitro). By doing so, scientists can manipulate the environment of the cultured cells in order to find out precisely what conditions are necessary for differentiation to occur. In vitro culture also makes possible such techniques as synchronizing cell growth in order to study the relationship between cell division and cell differentiation, and cell fusion in order to see how the contents of one cell affect the behavior of another.

Various biochemical and molecular techniques are used to study the roles of many biological molecules in differentiation. Of particular interest are separation methods that allow scientists to isolate and identify proteins and other factors involved in the differentiation process. These molecules can be isolated by first homogenizing the cells and then separating the desired molecules by centrifugation (based on density), electrophoresis (based on electrical charge), or chromatography (based on molecular size). Once the molecules are isolated, their properties can be studied, including the biological activity. At times it is important to know if a particular sequence of DNA or RNA is present in an embryonic cell. That can be determined by a technique called hybridization, whereby single-stranded DNA is allowed to match up and adhere to a complementary strand of DNA or RNA. Usually one of the strands is radioactively labeled so that the sequence in question can be detected and measured. The usefulness of this technique has become greatly enhanced by the development of recombinant DNA technology, which allows for the construction of specific molecular probes (DNA sequences) that can be radiolabeled and used to detect cellular DNA and RNA by hybridization. One step beyond this is the technique of DNA transformation, whereby isolated genes are modified and then reintroduced into cells to determine the new properties of the altered gene when it is expressed.

Determination and differentiation are the foundations of cell diversification. There are approximately two hundred distinctly different cell types in mammals. Without cell specialization, organisms would not be able to move, breathe, think, or perform any of the many other functions necessary to sustain life.

—Rodney C. Mowbray

See also: Cell types; Cleavage, gastrulation, and neurulation; Development: Evolutionary perspective; Embryology; Gametogenesis; Genetics; Morphogenesis; Multicellularity; Mutation; Physiology; Regeneration.

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DEVELOPMENT: EVOLUTIONARY PERSPECTIVE

Type of animal science: Development
Fields of study: Evolutionary science, genetics, invertebrate biology, systematics (taxonomy), zoology

The relationship between ontogeny (individual development) and phylogeny (the evolution of species and lineages) is an enduring theme in the life sciences. Changes in developmental timing produce parallels between ontogeny and phylogeny. The subject illuminates the biology of regulation, the evolution of ecological strategies, and the mechanisms for evolutionary change in form.

Principal Terms

ACCELERATION: the appearance of an organ earlier in the development of a descendant than in the ancestor as a result of an acceleration of development

HETEROCHRONY: changes in developmental timing that produce parallels between ontogeny and phylogeny; changes in the relative time of appearance and rate of development for organs already present in ancestors

NEOTENY: either the retention of immature characteristics in the adult form or the sexual maturation of larval stages

ONTOGENY: the successive stages during the development of an animal, primarily embryonic but also postnatal

PAEDOMORPHOSIS: the appearance of youthful characters of ancestors in later ontogenetic stages of descendants

PHYLOGENY: a series of stages in the evolutionary history of species and lineages

RECAPITULATION: the repetition of phylogeny in ontogeny or of the ancestral adult stages in the embryonic stages of descendants

RETARDATION: the appearance of an organ later in the development of a descendant than in the ancestor as a result of a slowing of development

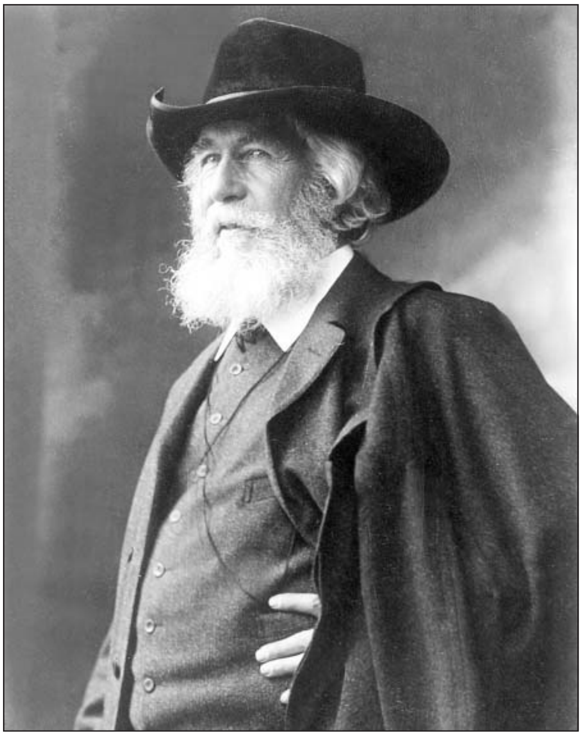
The idea of a relationship between individual development, or ontogeny, and the evolutionary history of a race, or phylogeny, is an old one. The concept received much attention in the nineteenth century and is often associated with the names of Karl Ernst von Baer and Ernst Haeckel, two prominent German biologists. It was Haeckel who coined the catchphrase and dominant paradigm: Ontogeny recapitulates (or repeats) phylogeny. Since Haeckel's time, however, the relations between ontogeny and phylogeny have been portrayed in a variety of ways, including the reverse notion that phylogeny is the succession of ontogenies. Research in the 1970's and 1980's on the parallels between ontogeny and phylogeny focused on the change of timing in developmental events as a mechanism for recapitulation and on the developmental-genetic basis of evolutionary change.

Concepts of Biogenetic Law in the Nineteenth Century

During the early nineteenth century, two different concepts of parallels between development and evolution arose. The German J. F. Meckel and the Frenchman E. R. Serres believed that a higher animal in its embryonic development recapitulates the adult structures of animals below it on a scale of being. Baer, on the other hand, argued that no higher animal repeats an earlier adult stage but rather the embryo proceeds from undifferentiated homogeneity to differentiated heterogeneity, from the general to the specific. Von Baer published his famous and influential four laws in 1828: The more general characters of a large group of animals appear earlier in their embryos than the more special characters; from the most general forms, the less general are developed; every embryo of a given animal, instead of passing through the other forms, becomes separated from them; the embryo of a higher form never resembles any other form, only its embryo.

By the late nineteenth century, the notion of recapitulation and Baer's laws of embryonic similarity were recast in evolutionary terms. Haeckel, and others, established the biogenetic law: That is, ontogeny recapitulates the adult stages of phylogeny. It was, in a sense, an updated version of the Serres-Meckel law but differed in that the notion was valid not only for a chain of being but also for many divergent lines of descent; ancestors had evolved into complex forms and were now considered to be modified by descent. More specifically, Haeckel thought of ontogeny as a short and quick recapitulation of phylogeny caused by the physiological functions of heredity and adaptation. During its individual development, he wrote, the organic individual repeats the most important changes in form through which its forefathers passed during the slow and long course of their paleontological development. The adult stages of ancestors are repeated during the development of descendants but crowded back into earlier stages of ontogeny. Ontogeny is the abbreviated version of phylogeny. These repeated stages reflect the history of the race. Haeckel considered phylogeny to be the mechanical cause of ontogeny.

The classic example of recapitulation is the stage of development in an unhatched bird or unborn mammal when gill slits are present. Haeckel argued that gill slits in this stage represented gill slits of the adult stage of ancestral fish, which in birds and mammals were pressed back into early stages of development. This theory differed from von Baer's notion that the gill slit in the human embryo and in the adult fish represented the same stage in development. The gill slits, explained the recapitulationists, got from a large adult ancestor to a small embryo in two ways: first, terminal addition (in which stages are added to the end of an ancestral ontogeny); and second, condensation (in which development is speeded up as ancestral features are pushed back to earlier stages of the embryo). Haeckel also coined another term widely used currently in another sense: "heterochrony." He used the term to denote a displacement in time of the appearance of one organ in ontogeny before another, thus disrupting the recapitulation of phylogeny in ontogeny. Haeckel was not, however, interested primarily in mechanisms or in embryology for its own sake, but rather for the information it could provide for developing evolutionary histories.



Ernst Haeckel coined the phrase, "Ontogeny recapitulates phylogeny," meaning that in their individual development, animals repeat the major evolutionary steps taken by the species as a whole. (Library of Congress)

Recapitulation in the Twentieth Century

With the rise of mechanistic experimental embryology and with the establishment of Mendelian genetics in the early twentieth century, the biogenetic law was largely repudiated by biologists. Descriptive embryology was out of fashion, and the existence of genes made the two correlate laws to recapitulation—terminal addition and condensation—untenable. One of the most influential modifications for later work on the subject was broached in a paper by Walter Garstang in 1922, in which he reformulated the theory of recapitulation and refurbished the concept of heterochrony. Garstang argued that phylogeny does not control ontogeny but rather makes a record of the former: That is, phylogeny is a result of ontogeny. He suggested that adaptive changes in a larval stage coupled with shifts in the timing of development (heterochrony) could result in radical shifts in adult morphology.

Stephen Jay Gould resurrected the long unpopular concept of recapitulation with his book *Ontogeny and Phylogeny* (1977). In addition to recounting the historical development of the idea of recapitulation, he made an original contribution to defining and explicating the mechanism (heterochrony) involved in producing parallels between ontogeny and phylogeny. He argued that heterochrony—"changes in the relative time of appearance and rate of development for characters already present in ancestors"—was of prime evolutionary importance. He reduced Gavin de Beer's complex eight-mode analysis of heterochrony to two simplified processes: acceleration and retardation. Acceleration occurs if a character appears earlier in the ontogeny of a descendant than it did in an ancestor because of a speeding up of development. Conversely, retardation occurs if a character appears later in the ontogeny of a descendant than it did in an ancestor because of a slowing down of development. To demonstrate these concepts, Gould introduced a "clock model" in order to bring some standardization and quantification to the heterochrony concept.

He considered the primary evolutionary value of ontogeny and phylogeny to be in the immediate ecological advantages for slow or rapid maturation rather than in the long-term changes of form. Neoteny (the opposite of recapitulation) is the most important determinant of human evolution. Humans have evolved by retaining the young characters of their ancestors and have therefore achieved behavioral flexibility and their characteristic form. For example, there is a striking resemblance between some types of juvenile apes and adult humans; this similarity for the ape soon fades in its ontogeny as the jaw begins to protrude and the brain shrinks. Gould also insightfully predicted that an understanding of ontogeny and phylogeny would lead to a rapprochement between molecular and evolutionary biology.

By the 1980's, Rudolf Raff and Thomas Kaufman found this rapprochement by synthesizing embryology with genetics and evolution. Their work focuses on the developmental-genetic mechanisms that generate evolutionary change in morphology. They believe that a genetic program governs ontogeny, that the great decisions in development are made by a small number of genes that function as switches between alternate states or pathways. When these genetic switch systems are modified, evolutionary changes in morphology occur mechanistically. They argue further that regulatory genes—genes that control development by turning structural genes on and off—control the timing of development, make decisions about the fates of cells, and integrate the expression of structural genes to produce differentiated tissue. All this plays a considerable role in evolution.

Description Versus Experimentation

Both embryology and evolution have traditionally been descriptive sciences using methods of observation and comparison. By the end of the nineteenth century, a dichotomy had arisen between the naturalistic (descriptive) and the experimentalist tradition. The naturalists' tradition viewed the organism as a whole, and morphological studies and observations of embryological development were central to their program. Experimentalists, on the other hand, focused on laboratory studies of isolated aspects of function. A mechanistic outlook was compatible with this experimental approach.

Modern embryology uses both descriptive and experimental methods. Descriptive embryology uses topographic, histological (tissue analysis), cytological (cell analysis), and electron microscope techniques supplemented by morphometric (the measurement of form) analysis. Embryos are visualized using either plastic models of developmental stages, schematic drawings, or computer simulations. Cell lineage drawings are also used with the comparative method for phylogenies.

Experimental embryology, on the other hand, uses more invasive methods of manipulating the organism. During this field of study's early period, scientists subjected amphibian embryos to various changes to their normal path of development; they were chopped into pieces, transplanted, exposed to chemicals, and spun in centrifuges. Later, fate maps came into usage in order to determine the future development of regions in the embryo. It was found that small patches of cells on the surface of the embryo could be stained, without damaging the cell, by applying small pieces of agar soaked in a vital dye. One could then follow the stained cells to their eventual position in the gastrula.

Interdisciplinary Studies

Evolutionary theory primarily uses paleontology (study of the fossil record) to study the evolutionary history of species, yet Gould has also used quantification (the clock model, for example), statistics, and ecology to understand the parallels between ontogeny and phylogeny. Most scientists interested in the relationships between ontogeny and phylogeny chiefly use comparative and theoretical methods. They, for example, compare structures in different animal groups or compare the adult structures of an animal with the young stage of another. If similarities exist, are the lineages similar? Are the stages in ontogenetic development similar to those of the development of the whole species?

Yet, the study of relationships between ontogeny and phylogeny is an interdisciplinary subject. Not only are methods from embryology and evolutionary theory of help, but also, increasingly, techniques are applied from molecular genetics. Haeckel's method was primarily a descriptive historical one, and he collected myriad descriptive studies of different animals. Although scientists in those days had relatively simple microscopes, they left meticulous and detailed accounts.

A fusion of embryology, evolution, and genetics involves combining different methods from each of the respective disciplines for the study of the relationship between ontogeny and phylogeny. The unifying approach has been causal-analytical, in the sense that biologists have been examining mechanisms that produce parallels between ontogeny and phylogeny as well as the developmental-genetic basis for evolutionary change. The methods are either technical or theoretical. The technical ones include the use of the electron microscope, histological, cytological, and experimental analyses; the theoretical methods include comparison, historical analysis, observations, statistics, and computer simulation.

Ramifications Beyond Science

The relationship between ontogeny and phylogeny is one of the most important ideas in biology and a central theme in evolutionary biology. It illuminates the evolution of ecological strategies, large-scale evolutionary change, and the biology of regulation. This scientific idea has also had far-reaching influences in areas such as anthropology, political theory, literature, child development, education, and psychology.

In the late nineteenth century, embryological development was a major part of evolutionary theory; however, that was not the case for much of the twentieth century. Although there was some interest in embryology and evolution from the 1920's to 1950's by Garstang, J. S. Huxley, de Beer, and Richard Goldschmidt, during the first three decades of the twentieth century genetics and development were among the most important and active areas in biological thought, yet there were few attempts to integrate the two areas. It is this new synthesis of evolution, embryology, and genetics that has emerged as one of the most exciting frontiers in the life sciences.

Although knowledge to be gained from a synthesis of development and evolution seems not to have any immediate practical application, it can offer greater insights into mechanisms of evolution, and a knowledge of evolution will give similar insights into mechanisms of development. A study of these relations and interactions also enlarges humankind's understanding of the nature of the development of individuals and their relation to the larger historical panorama of the history of life.

—Kristie Macrakis

See also: Aging; Apes to hominids; Determination and differentiation; Embryology; Evolution: Historical perspective; Genetics; Growth; Heterochrony; *Homo sapiens* and human diversification; Invertebrates; Morphogenesis; Paleontology; Pregnancy and prenatal development; Phylogeny; Regeneration; Sex differences: Evolutionary perspective; Systematics; Zoology.

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DIGESTION

Type of animal science: Physiology
Field of study: Biochemistry

The structure of different organisms' digestive systems and the presence of various digestive enzymes are correlated with the physical and chemical nature of the food they eat. Plant eaters (herbivores) and meat eaters (carnivores) have predominantly carbohydrate- and protein-digesting enzymes, respectively, while omnivores, which feed on both plants and meat, have all enzymes.

Principal Terms

ENZYME: a protein that acts as a catalyst under appropriate physiological conditions to break down bonds of a large protein, fat, or carbohydrate

ESOPHAGUS: the part of the oral cavity (pharynx) that transfers morsels to the stomach; it is usually a long, muscular tube with no digestive function other than transport

HORMONE: a chemical released into the blood for transport to a specific site, where it will perform a specific function; many hormones stimulate chemical and mechanical aspects of digestion

INTESTINE: the part of the digestive system involved in completing the process of digestion and absorption of nutrients; usually divided into the small intestine and the large intestine, which opens to the exterior by way of the anus

MOUTH: the anterior part of the digestive system, used for ingesting food; it leads into the oral cavity, which opens into the esophagus

MUCUS: a secretion of the salivary glands and other parts of the digestive system which lubricates passages

STOMACH: the part of the digestive system where mechanical breakdown of food is completed and chemical digestion begins

The bulk of animal food consists of proteins, carbohydrates, and fats. In addition, smaller molecules that make up these complex molecules—such as vitamins, nucleic acids, and minerals—are essential components of animal food. Animals obtain their food in the form of solutions, suspensions, dry particles, aggregates, and masses of particles, or whole animals and plants and their parts. It is the selection of food and the feeding behavior of animals that distinguish different animal populations and allow them to live together in the same habitat without competing for the same resources. The organs that break down the food mechanically into small particles and particles into molecules by the processes called digestion constitute what is called a digestive system. Usually the fore (anterior) part of the digestive system of animals is adapted for capturing and breaking down food (the bills and beaks of birds and the jaws of mammals are examples), and the remaining system can become specialized to store, chemically digest, and absorb the digested food and eliminate the unabsorbed food.

The Digestive Sequence

A typical functional sequence of digestion can be summarized as follows: First is the mouth, its appendages, and the oral cavity. These are involved in selecting (by taste, smell, touch), capturing, ingesting, and initial breaking down of food. Secretions here can include lubricants (mucus coming from salivary glands as well as other fluids), anticoagulants (in blood suckers), paralyzing toxins (in carnivorous coelenterates, spiders, reptiles), proteases (in cephalopod mollusks), and carbohydrases (in plant eaters). In microphages, locomotory appendages, oral tentacles with cilia, can drive currents of water containing food toward the mouth. In macrophages, locomotory appendages can be modified to capture food and ingest it. Most small aquatic animals and some large ones strain small particulate material with the help of their body surface projections (cilia, setae, bristles, legs, mucus, or nets); these microphages are called filter-feeders. In vertebrates, movable jaws, and in invertebrates, hard structures or surfaces, can be used for crushing food. The mouth leads into an oral cavity whose posterior chamber is a muscular pharynx that opens into the esophagus.

Second, the muscular, tubular esophagus transfers the food, in bits, to the stomach. Sometimes, a distension in this part of the digestive system (the crop, found in cockroaches and birds, for example) is used to store food.

Third, the stomach, a muscular vessel into which the esophagus leads, mechanically breaks down the food through contractions and wavelike motions, and begins the process of chemical digestion via enzymes. Sometimes the stomach is equipped with hard projections (such as the gizzards and gastric mills of birds, cockroaches, earthworms, or alligators). The lining of the stomach or of its diverticula (branches) secretes digestive enzymes and, in vertebrates, hormones and hydrochloric acid. The stomach opens into the next chamber, the intestine.

Fourth, the small intestine completes the digestive process. Its cells and the cells of its glands (the pancreas, liver, hepatic cecae) secrete digestive fluids containing enzymes and hormones that enable absorption of the resulting molecules and water into the cells of the intestine and from there into the blood. The inner lining of the intestine can be thrown into ridges and microridges, which greatly increase the surface area and thus the amount of absorption.

Fifth, the large intestine, or hindgut, reabsorbs water. The undigested food is evacuated in the form of feces through an opening to the exterior called the anus. This part of the digestive tract also stores colonies of microorganisms, especially in plant eaters, to digest cellulose, lignin, and other substances, and to provide some vitamins that the animal cannot synthesize.

Continuous and Noncontinuous Feeders

In animals that feed on soluble or suspended particles, called continuous feeders, digestion is a continuous process. In these animals, which include sponges, coelenterates, and flatworms, the digestive system is in the form of a tube open at one end only, and the chemical digestion of particles takes place inside each cell lining this tube. Annelids, arthropods, mollusks, and echinoderms have digestive systems that are open at both ends. These animals have developed various other systems, and the digestive system has become independent of the circulatory system. The opening of the digestive tube has allowed these animals to specialize their parts into various regions for capturing, grinding, masticating, mechanically breaking down, chemically digesting, absorbing, and eliminating their food. That, in turn, has allowed them to conduct extracellular digestion in the digestive cavity: to become discontinuous feeders.

Hence, with the evolution of a digestive tube dedicated to digestion only, animals started secreting their cellular enzymes into this cavity in response to food. This, then, constituted extracellular digestion. Extracellular digestion is present in small animals that feed on particles (microphages) or larger animals that feed on bulk food (macrophages). The animals with intracellular digestion and those microphages with extracellular digestion feed continuously and nonselectively. The evolution of a complete digestive tract, opening at both ends, and extracellular digestion have allowed evolution of larger, more active, and more advanced animals. These macrophages feed discontinuously and select their food. The time that they have saved from feeding had been spent to perform other activities and evolve complex behavior patterns. Also, ingestion of a large mass of food has enabled them to obtain the bulk of their energy from this food, which provides a tremendous amount of dependable power to move and even fly.

Digestive Specialization

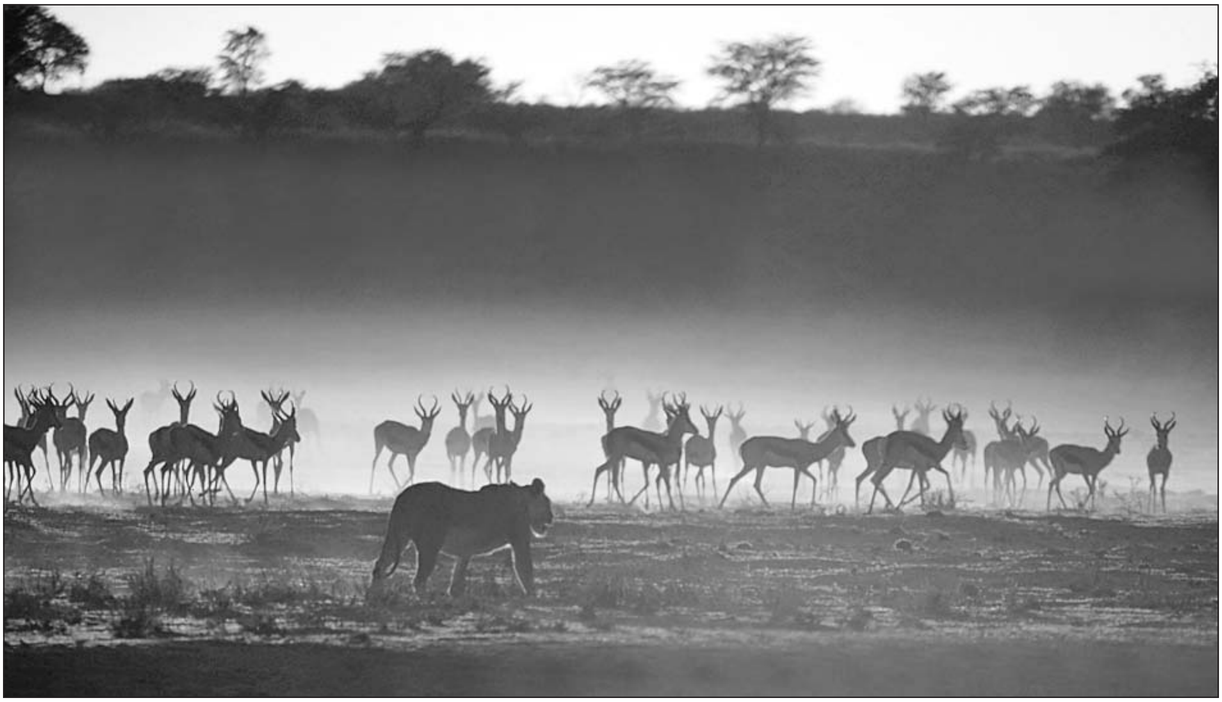
The evolution of a complete digestive tube has resulted in the specialization of its parts for various digestive processes. The general pattern of functional sequence that was outlined above is evident: The digestive system is usually divided into foregut (mouth and its appendages), midgut (for chemical digestion and absorption), and hindgut (for absorption of water and elimination of undigested food). Within this general structure, however, are innumerable and complex variations in adaptation to the type of food and feeding mechanisms of different animals. Those animals that feed on solid food, for example, have appendages (such as jaws and teeth) to enable them to grind, crush, or masticate it. In addition, these may have parts of the stomach modified for storage (such as rumen in ruminants, the crops of birds) or for further grinding (the gizzards of various insects, birds, and alligators). Cows and goats, for example, have four-chambered stomachs, one of which stores colonies of bacteria. These ruminants swallow the food as a whole while grazing. Then, later, while resting, they bring the food and bacteria back to the mouth as cud to mix them together, subsequently swallowing the food. The bacteria then digest cellulose by fermentation. The microorganisms are then digested by the animal in the intestine. These animals also secrete copious amounts of saliva, which prevents abrasive damage by the solid food to the cells lining the foregut.

In fluid feeders, by contrast, the oral end is equipped with sucking apparatus containing piercing devices (as in moths, bees, flies, mosquitoes, and leeches). Some feeders on plant juices ingest large amounts of water with sugars. The last part of their foregut becomes connnected with the anterior part of the hindgut, forming a filtering apparatus (as in insect leaf hoppers). Only water passes from the foregut to the hindgut, while food enters the midgut, which now does not have to process large amounts of water.

The Role of Enzymes

The chemical breakdown of food particles takes place by means of enzyme catalysts, which are proteins that are released into the stomach and intestine (midgut) from their cells or from cells of appendages (hepatic cecae in insects, hepatopancreas in crustaceans and mollusks, and pancreas and liver in vertebrates) opening into the intestine. These enzymes are secreted in response to the entry of food in the gut. Moreover, the presence and release of specific enzymes depend on the chemical nature of the food. In plant-eating herbivores, which eat an abundance of carbohydrates (sugars), these secretions are rich in carbohydrates (carbohydrate-hydrolyzing enzymes), while in animal eaters (carnivores) protein-digesting enzymes, proteases, and fat-hydrolyzing enzymes, lipases, are predominant. In omnivores (which feed on both plants and animals), all three groups of enzymes are present. In food specialists, such as sheep blow flies (which feed on wool keratin), head lice (which feed on hair keratin), cloth moths (which feed on textile fibers), wax moths (which feed on wax), or carpet and leather beetles (which feed on keratin), the digestive fluid is rich in specific enzymes for handling one kind of food. In wood-eating termites, snails (*Helix*), and ruminant mammals, the cellulose is digested by colonies of microorganisms that are carried in parts of these animals' guts.

In addition, different enzymes are present in different stages of an animal's life cycle. For example, maggots feeding on flesh have proteinases, while adult flies feeding on sugars have sucrases. The intestinal enzyme lactase, which breaks down the milk sugar lactose, is always present in land mammals at or before birth. It usually decreases after weaning. Among insects, certain leaf hoppers and moths which feed on soluble sugars (which do not require further breakdown) have no enzymes, while hoppers feeding on mesophyll cells and caterpillars actively chewing plant parts have carbohydrases and lipases. Among bees, nurses have more proteases than foragers; wax bees have no proteases; the carbohydrases are predominant in foragers, especially during midsum-



Herbivores, such as antelope, must have more complex digestive systems in order to obtain sufficient nutrition from plants. Carnivores, such as lions, need much simpler digestive systems in order to process their meat diets. (Digital Stock)

mer, and lipase is found only in wax bees. The carnivorous turbellarians, coelenterates, cephalopod mollusks, crustaceans, scavenger insects, and starfish have more proteases and fewer carbohydrases.

In mammals, most of the enzymes (pepsinogen, trypsinogen, chymotrypsinogen, lipase) are secreted as zymogens (proenzymes) and are activated by other secretions. For example, hydrochloric acid converts pepsinogen into active pepsin in the stomach; enterokinase converts chymotrypsinogen into active chymotrypsin, which in turn activates trypsinogen to trypsin. Secretion of zymogens and their activation are precisely controlled and occur when food is present in the gut. For example, when chyme leaves the stomach, the duodenal hormone enterogastrone inhibits the release of hydrochloric acid from parietal cells so that no activation of pepsinogen occurs; otherwise, pepsin could destroy the proteins in the membranes of cells lining the gastric cavity. The digestive epithelia of animals are thereby protected from damage by physical (solid food) and chemical (enzymes, acids) sources. This digestive strategy became necessary as discontinuous feeding evolved, since the presence of food for digestion was intermittent.

Studying Digestion

A variety of observations and experiments have been performed to study the different types of digestive systems. Simple examination of the anterior (mouth) end of different animals, for example, reveals the broad range of strategies used to collect and initially break down food.

Soluble food feeders, for example, can be examined under the microscope. Observation of a microscopic slide of the head of a human tapeworm shows that it is equipped with hooks and suckers by means of which it attaches itself to the digestive tract of a person. The soluble, predigested food in the intestine needs no further breakdown and is absorbed through the flat body surface of the worm, which lacks any digestive organs. Observed under the microscope, the anterior end of a liver fluke has hooks and suckers to suck fluid; a lamprey has a round mouth and rasping tongue with which to suck the blood of its host fish; a mosquito has a piercing device to break skin and suck blood; and the mouth parts of an adult moth include a long, coiled proboscis designed to suck nectar from flowers.

Intracellular digestion of food by a variety of microorganisms can be observed in progress under the microscope. Amoebas can be starved for one or two days and then transferred to drops of a culture on a shallow depression slide. The amoebas will exhibit phagocytosis (cell eating) with the help of their "feet" (pseudopodia), surrounding the food and ingesting it. A change in the color of the Blepherisma pigment (in the food vacuole of the amoeba) can be seen—from red (indicating acidic) to neutral or colorless (indicating alkaline pH). This indicates that earlier stages of digestion are acidic; later stages, alkaline.

Paramecium can also be observed feeding on starch solution with and without a drop of iodine (which turns starch blue and inhibits feeding). If this procedure is repeated using compressed yeast in a 3 percent solution of Congo red, one can observe the direction of movement of the yeast (which has taken on the red color) as it travels in the direction of the beating of the paramecium's cilia and into the food vacuole, then as it circulates through the cytoplasm. The change in color from red to blue indicates digestion. Paramecia will also reject algae particles and ingest only yeast, indicating the presence of chemical sensory mechanisms.

Solid food eaters, which can be observed with the naked eye, reveal a variety of specially adapted parts: hard, strong mandibles for crushing leaves in the caterpillar; similar mandibles for handling solid food in the cockroach; the "Aristotle's lantern" of the sea urchin, used for grinding; the tentacles of the *Hydra*, which feeds on fine, suspended food particles; and the human jaw and teeth, with incisors, canines, and molars designed to break down a variety of food in a variety of ways.

The activity of various digestive enzymes can be determined by using appropriate substrates (the food molecules) and physiological conditions in a test tube. The source of the enzyme is the part of the digestive tract where it is produced and used. Tissue from this area is ground in a small blender or homogenizer using an appropriate buffer at about 4 degrees Celsius. The homogenate of the tissue is either used as is or fractionated using a high-speed, refrigerated centrifuge, which can fractionate cell membranes, various organelles, and cytoplasm. Then the subcell fraction, where the enzyme is located, can be used as the source of the enzyme. The enzyme is further purified by means of biochemical devices. The substrate is either natural or synthetic. The pH, temperature, and other conditions are controlled in the incubation mixture containing enzyme and substrate. Time-course aliquots (samples) are withdrawn, and the activity of the enzyme is measured by analyzing the hydrolysis product of the substrate using various spectrophotometric devices. The enzymes, from the same tissue or its subcell fraction, of animals feeding on plants, meat, or both are compared to determine how active various enzymes are in these animals. The presence of certain enzymes can be related to the chemical nature of the food.

Digestion and Survival

Food selection, feeding behavior, and the structure and function of the digestive apparatus of animals form an important mechanism of survival, by which animals in a population isolate themselves from other populations to avoid competition for the same source of food. The feeding behavior depends on the type of food available (soluble, suspended, aggregates, or large organisms), and the form of the feeding apparatus (shapes and sizes of bills of birds and jaws and teeth of mammals, for example) depends on the physical nature of the food. The anatomy of the digestive system is closely adapted to the physical nature of the food, while the chemical functioning (enzymes) of the digestive systems depends on its chemical nature.

The adaptations of the digestive systems have enabled the evolution of larger and more active animals, which feed less frequently on greater bulks of food as compared with less active small animals, which may have to feed more often and even continuously.

The broad variety of different digestive systems and their enzymes has enabled animals to make the best use of the food resources available in their environment. Those animals able to exploit their environment more fully than others (such as omnivores, including humans) have a wide array of digestive enzymes that can chemically break down a wide variety of foods. They are more successful at survival than those confined to a particular type of food (food specialists with a limited ability to digest only one type of food) and, hence, are likely to survive longer as a group.

—M. A. Q. Khan

See also: Anatomy; Cannibalism; Carnivores; Digestive tract; Food chains and food webs; Herbivores; Ingestion; Kidneys and other excretory structures; Nutrient requirements; Omnivores; Physiology; Ruminants; Teeth, fangs, and tusks.

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DIGESTIVE TRACT

Type of animal science: Anatomy
Fields of study: Cell biology, histology, physiology

The digestive tract is the group of organs where nutrients brought into the animal from the environment are broken down to molecules that can be absorbed into the animal's body. Knowledge of the digestive tract and its functions allows an appreciation of the importance of correct diet and the causes of gastrointestinal diseases.

Principal Terms

ABSORPTION: the movement of nutrients out of the lumen of the gut into the body

BILE SALTS: organic compounds derived from cholesterol that are secreted by the liver into the gut lumen and that emulsify fats

DIGESTION: the process by which larger organic nutrients are broken down to smaller molecules in the lumen of the gut

DUODENUM: the first part of the small intestine, where it joins the stomach

ENTEROCYTES: the cells that line the lumen of the small intestine

LUMEN: the central opening through the digestive tract, which is continuous from the mouth to the anus

LYMPHATIC VESSELS: very thin tubes that carry water, proteins, and fats from the gut to the bloodstream

MUCOSA: the lining of the inner wall of the gut facing the lumen

PANCREAS: an organ derived from the gut that secretes digestive enzymes; it is connected to the gut by a duct through which its secretions enter the gut

PLEXUS: a group of nerve cells and their connections to one another

SPHINCTER: a ring of muscle that can close off a portion of the gut

Digestion is the process by which food is broken down into molecules that are small enough to be absorbed into the body. Digestion takes place in the digestive tract of animals. The digestive tract is a continuous tube that acts on ingested food in a sequential manner. Each part of the digestive tract is adapted to reduce the size of food particles, either mechanically or enzymatically, until they are small enough to be absorbed into the body. Consideration of the mechanisms of food intake in lower animals will illustrate the evolution of complexity as an adaptation to the changing environments of these animals.

Digestive Tracts of Simple Animals

Sponges are primitive water-dwelling animals that are attached to a fixed point in the water. They bring food into their bodies from currents of water containing particulate food passing through openings in their outer wall. These currents are created by movements of flagella on cells called choanocytes. Food enters the choanocytes by phagocytosis. Phagocytosis is the process in which a cell surrounds a particle with extensions of its cell membrane until the particle is completely surrounded and thus becomes enclosed within a small sac, or vesicle, within the cell. Intracellular enzymes then digest the food particles dissolved in the fluid into their component molecules, which then become available to the metabolic systems in the cytoplasm of the cell. Some cells, called amoebocytes, carry the food particles to other cells in the sponge by crawling through the spaces between the cells. Their travel is by amoeboid motion, in which the cell sends out an extension, called a pseudopod, and then follows it.

This method of feeding and digestion is adequate for a sponge because most of the sponge cells are in close contact with the water currents in which it lives. Thus, these cells can have direct access to food carried in the water currents. The cells that are not in close contact with water currents can be adequately supplied by the amoebocytes. The digestion, or breakdown, must be carried on inside the cells by cytoplasmic enzymes because if these enzymes were released to the extracellular surface, they would be washed away.

The coelenterates, such as jellyfishes or hydras, are more advanced than sponges and require a more elaborate digestive mechanism. These water-dwelling animals are either attached to a surface or float in the water currents. Thus, like sponges, they are dependent on food carried in the water. These animals, however, can eat live prey as well as particulate food. They are equipped with tentacles that can reach out and trap smaller animals and paralyze them with poisoned darts called nematocysts. The tentacles then bring the food into a distinct body cavity, the gastrovascular cavity, through its one opening. The digestive cavity is, at least partially, not in direct contact with the water currents around the animal. Digestion can take place through extracellular enzymes secreted by the cells lining this cavity. The resulting molecules are then absorbed through the cell membranes. Amoebocytes also function in these animals. These animals have limited motion through musclelike cells and this motion moves fluid within the gastrovascular cavity, thus carrying fluid to all parts of the animal.

Flatworms are more advanced than sponges and coelenterates and live in a moist, but not watery, environment. They have a distinct nervous and muscular system and can move to search for food. Their digestiv e tract, as that of sponges, has only a single opening. Food is pushed into this opening by the muscle action of the first part of the digestive tract, which can be protruded to the outside of the animal. Digestion is extracellular and carried to the rest of the animal through muscle contractions of the digestive tract. The digestive tract is highly branched and extends to all parts of the animal.

Digestive Tracts of More Complex Animals

Animals more highly evolved than flatworms, including roundworms, insects, fish, mammals, and birds, have a functionally similar digestive tract. These animals all have similar requirements, which have necessitated further, more efficient digestion. These animals are more active and thus must ingest more food. Their digestive tracts have two openings, allowing a continuous digestion: Food enters at one end and is excreted at the other. In contrast, an animal with only one digestive opening cannot excrete and ingest at the same time. The greater size of these more-evolved animals also requires that digested food be absorbed into the circulatory system so that distribution to the rest of the body cells is quick. The absorbing portion of the gut is therefore surrounded by blood vessels.

Further adaptations have required sophisticated specializations of the digestive tract. These include initial chewing devices that can mechanically reduce the size of food so that it can be swallowed. Parts of the digestive system have evolved to store food until it can be efficiently digested. This adaptation allows animals to eat sporadically, when food is available, and allows time for other activities, such as hunting or hiding. Other portions of the digestive tract have become specialized to secrete powerful enzymes that sequentially break down the molecules in food to smaller and smaller molecules. Last, the terminal portions of the digestive tract retain food and extract any remaining nutritional value and eliminate the rest at a convenient time. Many of these adaptations required the formation of a space, called a coelom, between the digestive tract and the rest of the body. This space allows the gut to coil and thus become much longer than the animal, with a resulting increase in the surface area available for digestion and absorption.

The mouth, or buccal cavity, is designed for the entry of food into the digestive tract. The lips and tongue are highly sensitive to the texture and taste of food. They are capable of very precise movements because their musculature is supplied with an extensive nerve supply. The tongue can move laterally, up and down, and in and out, because it has both longitudinal and circular muscles. Movements of the jaws during chewing (mastication) cause the teeth to crush and tear food in the mouth. The teeth have an outer covering of very tough enamel, which protects them against abrasion. Some animals have teeth that grow throughout their life and replace the worn-out ends. Salivary glands in the sides or base of the jaw secrete saliva through ducts that empty into the mouth at the sides of or under the tongue. Saliva has the primary function of lubricating and wetting chewed food. Saliva contains an enzyme, called salivary amylase, which begins the digestion of starch, although the digestion is greatly slowed after the food enters the acidic stomach lumen.

After the food has been reduced to small particles and mixed with saliva, it is swallowed (deglutition). Swallowing is partly a reflex action, controlled by a center in the base of the brain. The tongue rises to the roof of the mouth, pushing the rounded mass of chewed food, called a bolus, into the opening of the esophagus. Further propulsion is created by contraction of the area between the mouth and the esophagus, called the pharynx. The esophagus is a muscular tube leading to the stomach. Contractions of muscles which encircle the esophagus cause a moving ring of contraction, called peristalsis, which propels the bolus into the stomach.

Mucous Layers

The wall of the gastrointestinal tract is similar throughout its length. The layers, from lumen outward, are the mucosa, submucosa, submucosal nerve plexus, circular muscle, myenteric nerve plexus, longitudinal muscle, and the thin connective tissue covering called the serosa. The stomach and intestines are suspended from the back wall of the abdominal cavity by a sheet of connective tissue called the mesentery. Nerves, blood vessels, and lymphatic vessels reach the gut in the mesentery.

The cavity of the gut, or lumen, is lined by a single sheet of cells called the mucosa. The mucosa contains a wide variety of cell types. Most of the mucosa is composed of a cell type which is called columnar epithelium because the cells are longer than their diameter. Mucous, or goblet, cells secrete mucus, which is the viscous slippery material that protects the cells of the gut against mechanical abrasion and chemical attack. Other cells secrete enzymes into the lumen. Hydrochloric acid is secreted by parietal cells in the stomach. Other cells in the small intestine secrete basic bicarbonate ion. These cells provide the degree of acidity or basicity appropriate to the different regions of the gut. Other cells are adapted to absorb nutrients from or to secrete fluid into the lumen of the gut.

There are also many endocrine cells in the mucosa. These cells secrete hormones into the blood when they are stimulated by nerves or by the contents of the gut. These hormones control the degree of motility or secretion of the gut and the metabolic and physiological responses of the body following feeding. Indeed, the digestive system is the largest endocrine gland in the body. These same hormones are found in the brain, where they act as neurotransmitters, and in other endocrine glands. They have numerous functions revolving around the digestive tract. Some of these hormones can increase or decrease hunger. Others prepare the body for the nutrients that will be absorbed from the digestive tract so that the nutrients can be efficiently utilized. Certain hormones can be released by different types of nutrients in the lumen of the digestive tract. Other hormones can be released through the action of nerves when food is eaten.

The layer next to the mucosa, called the submucosa, is composed of fibrous connective tissue. It provides a mechanical support for the mucosa and also contains the nerve and blood supply leading to and from the mucosa. The lymphatic vessels draining the mucosa also travel through the submucosa.

Nerve and Muscle Layers

The next, more external layer, is a sheet of nerves, called the submucous (Meissner) plexus. These nerves send fibers inward to the mucosa and also outward to the other layers. They respond to the luminal contents and to other nerves and hormones. There are as many nerves in the gut as there are in the spinal cord. They are an intrinsic nervous system of the gut—that is, they begin and end in the gut. They are considered a separate category along with the autonomic (involuntary) and somatic (voluntary) nervous systems.

The next layer of the gut wall is a layer of visceral smooth muscle oriented circularly around the circumference of the gut. Contraction of these muscles causes a ring of contraction that may or may not move down the intestine. Next, there is another layer of nerves called the myenteric (Auerbach) plexus. Both nerve plexuses are responsible for controlling and integrating the functions of the intestine. Motility of the muscles of the gut, absorption of salt, water, and nutrients, and blood flow are all regulated by these nerves. The outermost layer of the gut is composed of visceral smooth muscle oriented longitudinally along the gut. Contractions of these muscles shorten the length of the gut.

There are also rings of smooth muscle, called sphincters, which control the movement from one part of the gut to the adjacent part. These sphincters are found between the esophagus and the stomach, the stomach and small intestine, the small and large intestine, and the large intestine and the outside.

Food that enters the stomach is partially digested by the enzyme pepsin, which is secreted by the chief cells of the gastric mucosa. Pepsin begins the digestion of protein. The hydrochloric acid secreted by the parietal cells has the functions of activating the pepsin and killing bacteria. The most necessary function of the stomach is storage of food (now reduced to a semiliquid state called acid chyme, or chyme) and slowly propelling it into the small intestine. Additionally, the stomach secretes a substance called intrinsic factor, required for absorption of vitamin B12, which promotes red blood cell formation.

Ruminants, such as cattle and sheep, have the end of the esophagus and the beginning of the stomach modified into large chambers, called the rumen and reticulum, in which food is stored. These portions of the stomach are alkaline because of the enormous volume of basic saliva secreted by the animal. Bacterial digestion of the chyme occurs in these chambers. In addition, the contents can be regurgitated into the mouth and this cud then chewed further. After the cud is chewed and reswallowed, it bypasses the previous chambers and enters a third chamber, called the omasum, where it is churned by muscular contractions. Finally, it enters the abomasum, which is similar to the stomach of other animals.

Birds have specialized adaptations of the stomach, called the crop and gizzard. The crop is a large structure at the beginning of the stomach that stores food until it enters the stomach. The gizzard is a muscular portion of the stomach that grinds the food. This grinding by the gizzard is necessary because birds have no teeth. Frequently, birds will ingest small stones, which are stored in the gizzard and help grind the food.

The Small Intestine

The stomach empties into the small intestine. The first portion of the small intestine is called the duodenum, the middle portion the jejunum, and the terminal portion the ileum. There are two large organs that are connected to the duodenum through ducts that empty into its lumen. These organs are the liver and the pancreas. The liver secretes bile salts, which are necessary to emulsify fats into small particles for absorption. Bile salts are stored in the gallbladder between meals. The gallbladder is connected, by a branch, to the duct leading from the liver to the duodenum. The pancreas secretes basic bicarbonate, which helps neutralize stomach acids that enter the duodenum. The pancreas also secretes many different digestive enzymes, which break down proteins, fats, carbohydrates, nucleic acids, and other large molecules. Thus, as soon as chyme enters the duodenum, it is immediately mixed with digestive enzymes and bile salts that entered the lumen from the pancreatic and bile ducts.

The chyme is mixed and propelled along the small intestine by longitudinal and circular muscle contractions. These contractions continually mix the chyme with the pancreatic enzymes and bile salts and present the digested molecules to the mucosal surface, where further digestion takes place. Most of the mucosal cells, called enterocytes, produce enzymes and absorb nutrients. Enterocytes are continuously formed in mucosal pits, called crypts. They migrate up tiny fingerlike projections, called villi, which protrude into the lumen of the gut. It takes about three days for the enterocyte to travel from the base of the crypt to the tip of the villi, and then it is sloughed into the lumen. The villi are thought to increase the surface area of the gut on which digestion and absorption take place. The enterocytes produce enzymes that are attached to the mucosal surface of the cells. These enzymes are responsible for the final stages of digestion, producing the smallest molecules, which are now in a form that can be absorbed by the intestine. Because the digestion takes place on the cells' surface, it is called contact digestion.

After molecules are in their completely digested form, they are absorbed by enterocytes, which transport them from the lumen of the gut to the circulatory or the lymphatic system. Most organic nutrients, such as amino acids, fats, and glucose, are absorbed in the first half of the small intestine, the duodenum and jejunum. Salt, water, and bile salts are absorbed primarily in the ileum. Absorption is virtually complete as long as the digestive system is functioning normally. Usually, the main problems that arise during gastrointestinal disorders are associated with malabsorption of fats. Fats require bile salts to be emulsified. Emulsification is necessary for enzymes to break down fats and also to reduce the final size of the fat microdroplet that results. If any step in this process is not functioning well, then the fats come out of suspension in the intestine and are excreted.

The final contents of the small intestine consist mostly of salts, water, indigestible fiber, and the debris from sloughed enterocytes. The small intestine empties into the large intestine, where some bacterial digestion occurs, which produces mostly small fatty acid molecules. The debris from these bacteria add to the bulk of the undigested material. Muscle contraction propels these feces through the large intestine until it is eliminated by defecation. Sphincters control the final evacuation.

Studying the Digestive Tract

The structural features of the digestive tract can be determined by classical techniques of anatomical dissection and histological examination of the cellular characteristics of the different sections of the digestive tract. The secretions and the digestive steps can be determined by sampling the luminal contents. The sampling can be done by passing a tube through the digestive tract until the end reaches the desired portion and then withdrawing a sample for biochemical analyses.

Motility can be measured by attaching a balloon to a tube passed into the digestive tract and measuring the changes in pressure from muscle contractions. Absorption can be measured by perfusing a solution of known composition from one opening in a double tube and collecting the solution remaining after it has passed through the gut lumen from a second opening.

Motility of the intestine or the presence of obstructions that prevent the passage of food along the gastrointestinal tract can be observed by X-ray techniques. A liquid substance, such as a barium suspension, which is opaque to X rays, is swallowed. A series of X rays is taken, or continuous monitoring by an X-ray camera is used. Obstructions can be visualized from the buildup of barium above the blockade. The speed of movement can be estimated to determine if the overall motility of the gastrointestinal tract is abnormal. X rays can also be used to determine directly the presence of abnormal structures such as gallstones, which form in the bile ducts, or tumors. The bile duct and gallbladder system can be visualized with X rays by administering a radioopaque dye that is secreted by the liver into the duct system.

The overall integrity of the gastrointestinal tract can be determined by ingesting inert substances of different molecular sizes and determining if they appear in the blood. Normally, only relatively small molecules can penetrate the very tight mucosal lining of the gut, unless they are nutrients of the body. The penetration of larger molecules across the mucosa indicates leaks resulting from damage to the gastrointestinal lining.

—*David Mailman*

See also: Anatomy; Cannibalism; Carnivores; Digestion; Food chains and food webs; Herbivores; Ingestion; Kidneys and other excretory structures; Nutrient requirements; Omnivores; Physiology; Ruminants; Teeth, fangs, and tusks.

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DINOSAURS

Types of animal science: Classification, evolution
Fields of study: Anatomy, archaeology, evolutionary science, paleontology, physiology, zoology

Dinosaurs were one of the most successful early life-forms, thriving for more than 150 million years before becoming extinct by the end of the Cretaceous period. The reasons behind their longevity and their sudden extinction hold important implications for humankind's own survival.

Principal Terms

ANKYLOSAURS: a group of later ornithischians characterized by heavy armor
CEROTOPSIANS: a group of later ornithischians characterized by a beaked snout and a bony frill on the back of the head
ORNITHISCHIANS: one of the two orders of dinosaurs; it comprises the "bird-hipped" dinosaurs
ORNITHOPODS: the early, bipedal ornithischians
SAURISCHIANS: one of the two orders of dinosaurs; it comprises the "reptile-hipped" dinosaurs
SAUROPODS: the herbivorous, quadrupedal saurischians
STEGOSAURS: a group of later ornithischians characterized by a row of plates down the back
THECODONTS: an order of Triassic reptiles that were the ancestors of dinosaurs, birds, and crocodiles
THEROPODS: the carnivorous, primarily bipedal saurischians

The word "dinosaur," which is derived from the Greek term for "terrible lizard," is the popular name for a group of extinct land-dwelling reptiles. They were the dominant vertebrate animals during most of the Mesozoic era, which began 225 million years ago and ended 65 million years ago. Among the dinosaurs were the largest animals that ever walked the earth, although some of the earliest dinosaurs were very small.

The Mesozoic era is divided into three periods, Triassic, Jurassic, and Cretaceous, of approximately equal length. Dinosaurs first appeared in the later third of the Triassic period. Experts believe that dinosaurs developed from a group of archosauromorph reptiles such as *Marasuchus*, which was a lightly built flesh eater about 1.3 meters long. It was clearly a biped, running on its hind legs, and the long tail was presumably used as a balancing organ.

Dinosaurs are divided into two separate orders, depending on the arrangement and shape of the hip bones, which determine the way an animal walks and holds its body. The saurischians, or "reptile hips," as they are commonly called, arose in the early part of the Late Triassic; the ornithischians, or "bird hips," arose toward the end of the Triassic period.

Saurischians

The earliest dinosaurs were saurischians, which are best known from the Ischigualasto Formation of Argentina. The order Saurischia may be divided into two major suborders: the theropods, or "beast-footed dinosaurs," and the sauropods, or "reptile-footed dinosaurs." The theropods, which were more primitive than the sauropods, were primarily bipedal, although many of them probably used all four feet when walking or resting. The hind legs were strong and bore birdlike feet, while the forelimbs bore sharp, curved claws for seizing and holding prey. All theropods had long tails that functioned as stabilizers. The head was large, and the jaws of most of the theropods contained sharp teeth.

The theropods are divided into two major groups. A basal group, the ceratosaurs, includes such dinosaurs as *Coelophysis*, a small, agile carnivore with a long, narrow skull represented by many hundreds of specimens from the Ghost Ranch Quarry in New Mexico. However, larger dinosaurs, such as *Ceratosaurus*, are included within this group. The remaining theropods, termed tetanurans, include the Maniraptoriformes, which share many advanced characteristics with birds. The largest of these is *Tyrannosaurus rex*, from the Late Cretaceous period of North America, which grew to a weight of 4,500 kilograms, a height of 6 meters, and a length of 15 meters.

The sauropods, which appeared slightly later in the Triassic than the theropods, have come to stand as a symbol of gigantism in land animals. They were all quadrupeds and vegetarians. They had small skulls, long necks and tails, large barrel-shaped bodies, padded feet, and large claws on the innermost toe of the forefoot and the innermost toe of the hind foot. The ancestral stock of the sauropods were the prosauropods, which were much smaller than the sauropods. Like most prosauropods, *Plateosaurus* had blunt, spatulate teeth, was an herbivore, and was quadrupedal, although it was capable of bipedal posture and gait.

The later sauropods had longer necks, and their skulls were relatively small. The limb bones became solid and pillarlike to support their great weight. This category contained the largest of the dinosaurs, *Brachiosaurus*, which is estimated to have weighed 73,000 kilograms. The best known sauropods are *Brontosaurus* and *Diplodocus*, from the Late Jurassic period of North America. Although it was once assumed that these huge beasts had to live in swamps where the water could support their great weight, it is now clear that they were terrestrial animals that used their long necks to eat from trees.

Ornithischians

The sauropods reached their zenith in the Late Jurassic; the ornithischians replaced them as the dominant herbivores in the Cretaceous period. The expansion of this group was associated with the advent of the flowering plants during the Cretaceous period. Characteristically, a horny beak was developed at the front of the mouth, and the toes ended in rounded or blunt hooves instead of claws.

The earliest ornithischians were the ornithopods. A typical example is *Hypsilophodon*, a small, swift dinosaur with a long, slender tail and long, flexible toes. The most specialized of the ornithopods were the "duck-billed dinosaurs," also known as hadrosaurs. Although they had flat beaks and no anterior teeth, the cheek region had rows of grinding teeth. The various types of duck-billed dinosaur can be distinguished by modifications of the bones associated with the nostrils. Some were molded into hollow, domelike crests, bizarre swellings of the nasal region, or long, projecting tubular structures that were used to warm the air or to produce sounds. The remaining three groups of ornithischians presumably evolved from the primitive ornithopods.

The earliest of these three groups of highly specialized quadrupeds was the "plated dinosaurs," or stegosaurs, which first appeared early in the Jurassic period. This large dinosaur was more than 6 meters long. In comparison to its body size, its head was extremely small. *Stegosaurus* had an average of twenty plates arranged alternately in two parallel rows down the back. The plates were originally thought to have been used for protection, but scientists now believe that the plates could have been used for thermoregulation. *Stegosaurus* died out in the Early Cretaceous period.

The "armored dinosaurs," or ankylosaurs, are not very well known, even though their remains have been found over much of the world. Their armor consisted of a mosaic of studs over the body, spikes that protected the legs, and, in some cases, spikes on the tail. They protected themselves by crouching and drawing in their head and legs.

The last dinosaurs to develop were the "horned dinosaurs," or ceratopsians. The skull was characterized by a beaked snout and a bony frill that extended from the back of the head. The ceratopsians were also distinguished from others by various patterns of horns. The skull of *Triceratops*, for example, had three sharp horns, one on the snout and one above each eye. The best known of the small ceratopsians was *Protoceratops*, which was a small, hornless dinosaur from the Gobi Desert in Mongolia.

Studies of dinosaur eggs, nests, trackways, and bone structures have shown that smaller dinosaurs probably had a warm-blooded, or endothermic, metabolism similar to mammals. This is supported by the discovery of small theropods in China that show a covering of feathers, presumably for insulation. Large dinosaurs, such as sauropods, would have been more efficient as ectotherms, similar to most modern reptiles.

Extinction Theories

Several theories regarding the dinosaurs' extinction were first proposed in the late nineteenth and the early twentieth centuries. According to one popular theory, dinosaurs were wiped out because early mammals of the Cretaceous period ate their eggs. Yet the eggs of many modern reptiles have faced the same threat and have survived, primarily because reptiles lay so many eggs. Another theory suggested that the same animals ate the plants on which the dinosaurs depended. Although that is possible, virtual plagues of mammals would have been required to eradicate the dinosaurs. Some early scientists also believed that the dinosaurs became too big for their environment; that is unlikely, however, because gigantic dinosaurs had been successful for millions of years. Changes in the physical environment also occurred in the Late Mesozoic. Evidence indicates that the sea levels fell. Geologic evidence shows, though, that drastic environmental changes had occurred many times during the dinosaurs' reign without any detrimental effect.

A theory proposed in early 1979 by Luis Alvarez and Walter Alvarez suggests that the iridium that has been found in several samples of sedimentary layers between the rock of the Cretaceous and Tertiary periods came from an asteroid that struck the earth at that time. Such a catastrophic event could have caused an enormous cloud of dust to circle the earth and cut off the sunlight, destroying the plants and the dinosaurs that depended on them. This theory, however, fails to explain why so many other animals, such as the mammals, managed to survive.

Another modern theory places the blame on the greenhouse effect. It has been argued that the reduction of the seas that occurred during the Cretaceous period caused a reduction of marine plants. As a result, the amount of carbon dioxide in the air increased, trapping heat from the earth's surface. A similar theory suggests that the eruption of a tremendous volcano produced a fatal amount of carbon dioxide. Neither theory, however, explains why other animals, especially heat-sensitive reptiles, survived.

The main alternative to the extraterrestrial catastrophist explanation is a gradual ecosystem change model. Declines in many groups of organisms that started well before the Cretaceous-Tertiary boundary are seen as being caused by long-term climatic change, as lush tropical environments were replaced by strongly seasonal, temperate climates. The best explanation may be a combination of the two main theories.

Study of Dinosaurs

Scientists study dinosaurs by examining fossils, which are animal remains that have turned to stone. If a dinosaur died near a river or in a swamp, it stood an excellent chance of being preserved. Its body might sink into the mud, or floodwaters might float it downstream, where it would end up on a sandbar, on the bottom of a lake, or even in the sea. After the flesh decayed, the bones would be covered by sediments, such as mud or sand. The weight of accumulated layers of sediment would compress the remains and turn them into rock: mud into shale, sand into sandstone, limey oozes into limestone or chalk.

The way a fossil is studied is determined by the category to which it belongs. The first category is petrified fossils. They may be preserved in two ways. In replacement, minerals replace the original substance of the animal after water has dissolved the soft body parts. In permineralization, minerals fill in the small air spaces in bones or shells, thereby preserving the original bone or shell. The second group of fossils is composed of natural molds that form when the bodies dissolve. Scientists make artificial casts of these molds by filling them with wax, plastic, or plaster. The third type is prints, which are molds of thin objects, such as feathers or tracks. Sometimes, even skin is preserved. Prints are formed when the soft mud in which they are made turns to stone. Scientists can determine the length and weight of the dinosaur that made a set of footprints by studying the depth, size, and distance between them.

Most fossils are found in sedimentary rocks, which lie beneath three-fourths of the earth. The best collecting areas are places where the soil has worn away from the rocks. Areas in Colorado, Montana, Wyoming, and Alberta, Canada, have been especially rich in fossils. Most of the finds consist of no more than scraps of limb bones, odd vertebrae, loose teeth, or weathered lumps of rock with broken bone showing on the surface. Once a

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scientist has discovered a few fossilized fragments, he or she combs the area to find the rest of the animal. If the skeleton is embedded, it is extracted with the help of a wide variety of tools, ranging from picks and shovels to pneumatic drills. Loose fragments are glued back into place, and parts that are too soft or breakable are hardened by means of a special resin solution that is sprayed or painted on.

As the fossil is uncovered, it is encased in a block of plaster of paris. (A more modern method uses polyurethane foam instead of plaster.) After the entire surface is covered, the fossil is rolled over, and another layer of plaster is added. After the fossil has been transported to the museum, the plaster is removed. The "development" stage involves the removal of the rock around the bones. The oldest way is by hand, using tools such as hammers and chisels; a more modern technique uses electrically powered drills similar to dentists' drills. Sandblasting and chemicals may also be employed. After the fossil is cleaned, it is ready for mounting. The bones are fastened to a steel framework that makes the skeleton appear to stand by itself.

Life-Earth Interaction

From the dinosaurs, scientists are learning new lessons about the physiology of such beasts, their relationship to the world in which they lived, their distribution and the bearing of that distribution on the past arrangements of the continents, various aspects of evolution, and the reasons that they became extinct. The dinosaurs played a major part in the shaping of the natural world. Birds, for example, are probably their descendants, as evidenced by the intermediary species *Archaeopteryx*, a primitive bird that lived during the Late Jurassic period; although its beak contained teeth, *Archaeopteryx* also had feathers and could fly.

The disappearance of a species that seemed to rule the world for more than 100 million years brings into question the notion of a "dominant" species. Most people believe that mammals are now the dominant form of life; however, dinosaurs did not "rule," and neither do mammals. If one were to list the biological organisms whose influence on the planet is such that their removal would produce chaos, then that list would be headed by microorganisms so small that they can be seen only through powerful microscopes. The list would also include the green plants and the fungi.

The extinction of the dinosaurs also brings into question the ability of humans to destroy the world. All species, from the simplest microorganism to the largest plant or animal, modify their immediate surroundings. They cannot avoid doing so. The success of one group, however, does not imply the failure of the groups it exploits. The complexity of individual organisms may increase, but the simpler forms do not necessarily disappear. Life continued after the demise of the dinosaurs and would probably continue to do so if humankind were destroyed.

—Alan Brown

See also: *Allosaurus*; *Apatosaurus*; *Archaeopteryx*; *Brachiosaurus*; Evolution: Animal life; Extinction; Fossils; Hadrosaurs; Ichthyosaurs; Paleoecology; Paleontology; Prehistoric animyals; Pterosaurs; Sauropods; Stegosaurs; *Triceratops*; *Tyrannosaurus*; Velociraptors.

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DISEASES

Type of animal science: Pathology
Fields of study: Anatomy, histology, immunology, physiology

Diseases may be caused by infectious agents, such as bacteria or viruses, by parasites, by inheritance, by developmental mistakes, or as a result of aging. The major way in which animals are able to overcome disease is through the activity of the immune system.

Principal Terms

BACTERIA: single-celled microorganisms that are often the cause of infectious diseases in animals

DEVELOPMENTAL DISORDERS: diseases caused by embryonic or fetal mistakes in normal development

DISEASES OF AGING: loss of functions required for health due to age-related degeneration of tissues

GENETIC DISEASES: disorders caused by lack of enzymes or structural proteins caused by mutations

IMMUNE SYSTEM: system that produces antibodies and cells that attack foreign substances and pathogens that invade the body

PARASITES: protozoans, fungi, or animals that survive by obtaining nourishment from a living host, from inside the host or on its surface

PRIONS: infectious proteins that cause neurological diseases such as "mad cow disease"

VIRUSES: noncellular infectious agents that must enter a host cell to infect it

A disease is essentially any disturbance in the structure or function of the body, and may be accompanied by characteristic and well-defined areas of damage, or lesions, of specific tissues. The study of diseases is called pathology, and the causes of a disease are referred to as its etiology. An agent that can cause a disease is a pathogen. A particular disease has characteristic objective physical signs that may be seen by the examining physician or other outside observer, such as redness or swelling. Subjective feelings associated with disease, which can be described by an affected human but not by an animal or outside observer, are symptoms that might include pain or weakness. A set of signs and symptoms associated with a particular disease is called a syndrome. Diseases are often diagnosed by recognizing the signs and symptoms that characterize a particular disease and are not seen together in other diseases.

Inflammation and Immunity

Diseases related to tissue damage may be caused by pathogens such as bacteria and viruses, or by trauma, toxins, heat or cold, or exposure to chemical pollutants. When the body first responds to damage, certain cells release chemicals that produce a localized, nonspecific reaction called inflammation. Histamine causes blood vessels to dilate and become leaky, so inflamed areas show redness, swelling, pain, and heat, and may have a loss of function. Inflamed tissues also send out chemical messages that call in wandering cells (neutrophils and macrophages) from the blood and connective tissues to engulf pathogens and cellular debris by phagocytosis. This response is usually restricted to a localized area where tissue damage has occurred, and the area may be walled off from the rest of the body to restrict movement of pathogens or toxins.

The immune system involves other cells from the blood, lymph, and connective tissues called lymphocytes, which respond to specific antigens, usually small fragments of proteins that are not part of the "self" antigens the lymphocytes recognize. A bacterium may have thousands of different antigens associated with it, fragments produced by a macrophage during processing of the bacterium after phagocytosis. Each lymphocyte can respond against only one kind of antigen, but millions of different kinds of lymphocytes in each individual produce a widespread immune response specific to each foreign antigen associated with the invading pathogens, their toxins, or other materials.

The first time the immune system encounters a foreign antigen, its primary response is slow, and a disease may result from a pathogen's metabolic effects. Eventually, the immune response generates activated lymphocytes and antibodies that kill the bacteria or the virally infected cells to end the disease process. Memory lymphocytes are also produced that will respond against the same antigen if needed later. When the animal recovers, it will usually be immune to a second infection by the same disease-producing agent. The ability to resist a second infection is called immunological memory, and it may last for the life of the individual, as long as the memory lymphocytes live. Modern disease prevention techniques use immunizations to prevent the first experience of disease caused by a pathogen. In immunization, a derivative of the pathogen is injected into the individual to produce the slow primary response, so that memory is generated and the individual will be immune when the same agent is encountered naturally in the environment. In some cases, a booster shot must be given regularly to maintain memory and immunity to that agent, as in repeated immunizations of pets against rabies.

In some cases, however, diseases are caused by an overreaction by the immune system and the inflammation that it helps to generate. Allergies, for example, are not directly caused by pollen or dust particles, but by the body's responses to these allergy-producing antigens, or allergens. An allergic reaction is an immediate hypersensitivity response that may just cause an irritating, itchy swelling of the mucous membranes or skin, or may be extreme and even life threatening. In highly allergic individuals responding to allergens, the respiratory passages close, blood vessels leak fluid into the tissues, and death can result in a hyperallergenic process called anaphylactic shock. Much more often, though, both the inflammatory and immune responses are protective, causing the destruction of invading pathogens or other foreign materials that get into the body past the barriers of the skin and mucous membranes. The extent to which the immune system protects against disease can be seen when it is not functioning, as in humans who have acquired immunodeficiency syndrome (AIDS) and die of infections or cancer

Bacterial Infections and Antibiotic Resistance

Bacteria are prokaryotes (cells without nuclei) that have three basic shapes, called cocci (spheres), bacilli (rods), and spirilla (corkscrews). Most have a cell wall surrounding the plasma membrane and may also have a protective capsule. The cell wall may stain gram-positive (purple) or gram-negative (pink), distinctions that help identify the bacteria, determine what disease they cause, and indicate antibiotics that may be effective in treating infections they produce. Antibiotics are antimicrobial drugs that usually work by interfering with the structure or function of bacterial cell membranes, cell walls, or proteins. Since bacterial cells are so different from those of the infected host animal, antibiotics usually do not affect the host cells. Antibiotics are often given to domestic agricultural animals to increase their rates of growth and productivity. Unfortunately, mutations in normal bacteria can make them resistant to antibiotics, and this resistance can be passed from one bacterium to others, so that many drug-resistant strains of bacteria have resulted, some of which cause diseases that may become untreatable.

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that would be prevented by a fully functioning immune system. Viruses similar to the human immunodeficiency virus (HIV) cause related immunodeficiency diseases and leukemias or anemias in animals as well, including simian immunodeficiency virus (SIV) in monkeys and feline leukemia virus (FeLV) in cats or murine leukemia viruses (MuLVs) in mice. Studying these related viruses has been very important in scientists' understanding of HIV.

Bacterial Diseases

Most inflammatory diseases are caused by pathogenic or infectious microorganisms. Infections occur when pathogens enter the body, replicate, and cause metabolic changes or toxic damage. Pathogens are often easily spread directly from an infected host to uninfected individuals, or may be spread indirectly through air, food, water, soil, or other materials. Infectious and other disease-causing agents include bacteria, fungi, viruses, prions, protozoans, and parasitic animals.

Bacteria are unicellular, prokaryotic organisms that have much simpler cells than those of multicellular organisms such as animals, which are eukaryotic (having a nucleus). Some bacteria are pathogenic in humans and other animals. Bacteria can reside normally on the skin or in the digestive tracts of animals without harmful effects, comprising the "normal flora" of those animals. A common bacterium, *Escherichia coli*, is found in the colons of humans and many other animals, but different strains may cause diseases in some hosts while being harmless in others. *E. coli* strain O157:H7 causes no disease in cattle, but has caused deadly infections in children who ate undercooked hamburger contaminated with fecal material from the infected cattle. *Salmonella* are bacilli common in and on animals such as chickens (and their eggs) and turtles, but can cause food poisoning in humans. In some cases, bacteria that are normal on the skin or in internal organs of an animal may cause diseases when their number increases abnormally or when they are transferred to other body regions. Certain bacteria can cause disease in both animals and humans, such as the anthrax bacterium *Bacillus anthracis*, which may be used in weapons for germ warfare. Infectious anthrax spores can persist in soil or on contaminated wool, leather, or other animal products for many years, then can enter through skin or lungs to cause a lethal disease of animals or humans. Wild animal populations may serve as reservoirs of bacteria that can cause epidemics in both humans and animals, such as plague bacteria in modern-day prairie dogs of the American Southwest. The same bacteria, *Yersinia pestis*, were also a major problem in medieval Europe, when the Black Plague was carried to humans by dying rats and their fleeing fleas.

Viral Diseases

Viruses are not cells, and so are not actually microorganisms, but are still infectious agents. All viruses can infect only certain cells of particular host organisms, and they must be inside host cells to replicate. Viral infections can be latent (the cell is infected but uninjured); in some latent infections the virus is totally silent and inactive, while in others new virus particles may be released into the tissue fluid surrounding the cell. In cytopathogenic infections, host cells may increase in size and number, causing tissue enlargement (hyperplasia), or the cells may die. Some latent viral infections can become activated to produce disease, cell death, and viruses that infect other cells or organisms. Activation of latent viruses occurs when the host's immune defenses are diminished by stress or illness. Antibiotics are ineffective against viruses, whether they are free in tissue fluids or inside host cells, because the actions of antibiotics are directed against bacteria. Drugs that counteract viral infections often kill the infected cells, and may cause toxic reactions in the host as a result. Most viral infections can be handled at some level by the immune system, but in some cases the viruses may be present in the host organism for the rest of the host's life span.

Prion and Fungal Diseases

A very unusual kind of infectious pathogen is an abnormal protein called a prion, not associated with either DNA or RNA. Neurodegenerative diseases such as scrapie in sheep and bovine spongiform encephalopathy (BSE, or mad cow disease), as well as kuru and Creutzfeld-Jacob disease in humans, are prion diseases. The abnormal protein is a refolded form of a normal brain protein, and prions cause the normal proteins to fold into the prion form in brains of infected individuals. Prions are very stable and are not destroyed by heat, light, or acid, so prions eaten in animal proteins can cause rapid or very delayed disease in the individual that ingested the prions. Animal tissues have been banned in animal feed in Europe and elsewhere, and many Europeans have stopped eating beef because of outbreaks of mad cow disease in England.

Fungi are plantlike parasites without chlorophyll, subdivided into yeasts and molds. They may cause skin infections or localized or systemic internal infections. Yeasts are single cells that are much more complex than bacteria, while molds have branching filaments (hyphae) extending into host cells to obtain nutrients. Fungi that colonize the skin (dermatophytes) may cause diseases such as mange or ringworm, while yeasts infect mucous membranes or other moist surfaces. The immune response can often control or eliminate fungal infections, but such infections can be lethal in immunocompromised hosts.

Parasites may enter the body or remain on the body surface as they obtain nutrients from a living animal host. The condition of having parasites is called infestation rather than infection, but disease generally results from the parasites' effects on the host. Diseases caused by protozoan parasites include amebic dysentery, giardiasis, toxoplasmosis, malaria, and pneumocystis pneumonia. Important parasitic worms are roundworms, tapeworms, and flukes, which infest nearly all animals, and often have multiple host species during their complex life cycles. Worms may reside in the digestive tract, heart, liver, lungs, eyes, lymphatic system, skeletal muscle, or other organs and systems, where they can cause malnutrition, tissue damage, and death of the host. Blood-sucking insects such as lice and mosquitoes, or other arthropods such as ticks and mites, may act as vectors that transmit protozoan parasites, bacteria, or viruses to a host animal during blood removal. Arthropod-vectored diseases with animal reservoir hosts have caused many major diseases in humans as well, such as malaria, yellow fever, hantavirus diseases, sleeping sickness, and several forms of encephalitis. All animals are subject to infestation by many parasites against which the immune system responds; reduction of parasite load in humans and domestic animals in industrialized societies is thought to be related to the increased incidence of allergy in both humans and pets.

Genetic and Congenital Diseases

Diseases that result from genetic abnormalities may be present at birth, or may not become apparent until later in life when metabolic processes fail to function because of inherited errors. Both single gene mutations and chromosomal abnormalities may occur, or diseases can be caused by interaction of genetic predisposition and environmental factors. Congenital diseases are present at birth, and can be genetic or developmental in cause. Developmental problems may be associated with nutrient deficiency, intrauterine injury, inadequate placental support for the fetus, or environmental agents such as radiation, toxins, or pathogens. Genetic problems tend to occur particularly in inbred lines of animals, such as purebred dogs, where breeding selection for desirable characteristics also inadvertently produces recessive inherited diseases such as hip dysplasia and deafness. Some congenital defects are considered desirably exotic in companion animals, such as curled ears or stubby tails in cats, droopy ears in rabbits, or short legs, flattened faces, or lack of hair in dogs.

Metabolic, Neoplastic, and Degenerative Diseases

Metabolic disorders include those that are strictly genetic, and those that have a combined etiology involving inheritance and environment. Disturbances of metabolism can include changes in endocrine functions or metabolic imbalances when an enzyme is missing due to a genetic mutation. The enzyme's substrate would then build up and cause damage, while the enzyme's product would not be formed, also causing problems.

Neoplastic diseases are characterized by abnormal cell division and tumors, enlarged growths that may be benign or malignant. Benign tumors do not spread throughout the body, but are usually enclosed in a dense connective tissue capsule. While their cells remain relatively normal aside from their unrestrained growth, benign tumors may grow to enormous size and cause death by compressing organs or blocking passageways.

Finding New Viruses

Viruses are smaller and less complex than cells, and generally contain only a protein coat surrounding either deoxyribonucleic acid (DNA) or ribonucleic acid (RNA) as the genetic material. Some viruses may also have a covering membrane derived from the plasma membrane of the host cell from which they budded out during replication. DNA viruses include adenoviruses (respiratory infections); herpesviruses (cold sores, genital herpes, "pox" diseases, mononucleosis); papillomaviruses (certain warts); and hepatitis B virus. Viruses with genetic information in RNA include hepatitis A and C viruses; myxoviruses (measles, mumps, influenzas); picornaviruses (polio, respiratory infections); rabies virus; and retroviruses (AIDS, some leukemias). Viruses that infect animals without causing disease may jump species to infect humans or mutate to produce major disease epidemics, such as influenzas from recombinant bird or pig viruses, or the AIDS and Ebola viruses. In some cases, the animal source or reservoir is known, while often it is unknown. Many emerging diseases in human populations have originated in animals native to rain forest jungles or other habitats that humans have invaded and taken over, encountering previously unknown viruses.

Malignant tumors contain many more abnormal cells, which can leave the primary tumor site and form secondary tumors, especially in the liver, bone marrow, lungs, or brain, that usually cause death in cancer conditions. Malignant cells lose their original characteristics and become much less specialized and less efficient in using nutrients and energy, causing the body to waste away.

Degenerative diseases are associated with the aging process, when body tissues lose the ability to repair themselves effectively. The immune system also becomes less functional in combating foreign antigens or even recognizing the difference between self and foreign antigens, thus attacking self antigens by mistake. In some cases, degenerative diseases are not directly linked to aging, but to damage caused by pathogens, toxins, nutrient deficiency, or even nutrient excess. As normal tissues are damaged by the standard wear and tear of life, repairs become less effective and scar tissue replaces normal tissues such as muscle or liver. Nervous system damage is particularly problematic, since neurons are unable to replicate in mature animals, and lost cells are not replaced, producing sensory reception, muscle control, and memory loss. Problems caused by diseases and trauma lead to continued loss of function over time in aging animals, eventually reaching a point that repairs can no longer be made or infections resisted, and the animal dies.

—Jean S. Helgeson

See also: Aging; Biology; Cell types; Death and dying; Ecosystems; Food chains and food webs; Genetics; Immune system; Life spans; Mutations; Nutrient requirements; Pollution effects; Protozoa; Symbiosis; Veterinary medicine.

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DISPLAYS

Type of animal science: Behavior
Fields of study: Ethology, evolutionary science

Displays are specialized behaviors that act as communication signals within, and occasionally between, species.

Principal Terms

APOSEMATIC DISPLAY: use of bright, non-camouflaged colors to indicate toxicity or dangerousness

PAIR-BONDING: prolonged and repeated mutual courtship display by a monogamous pair, serving to cement the pair bond and to synchronize reproductive hormones

PHEROMONE: a modified hormone that, through sense of smell, communicates information to, and has effects on, individuals other than the individual producing it

PRINCIPLE OF ANTITHESIS: the observation that signals communicating opposite meaning tend to be expressed using displays having opposite characteristics

RITUALIZATION: an evolutionary process that formalizes the context and performance of a display so that its meaning is clear and straightforward

SPECIES-SPECIFIC: a behavior or trait that characterizes members of a species, is innate, and is exclusive to that species

STATUS BADGE: a visual feature that, based on its size or color or some other variation, indicates the social status of the bearer

Why do birds sing? Not because they are happy. They sing to communicate. By singing, a bird communicates its location, its species, its sex, its approximate age and size, and perhaps its current reproductive status, territory ownership, health, dominance status, and motivational state. Birdsong and other nonlinguistic forms of communication are called displays.

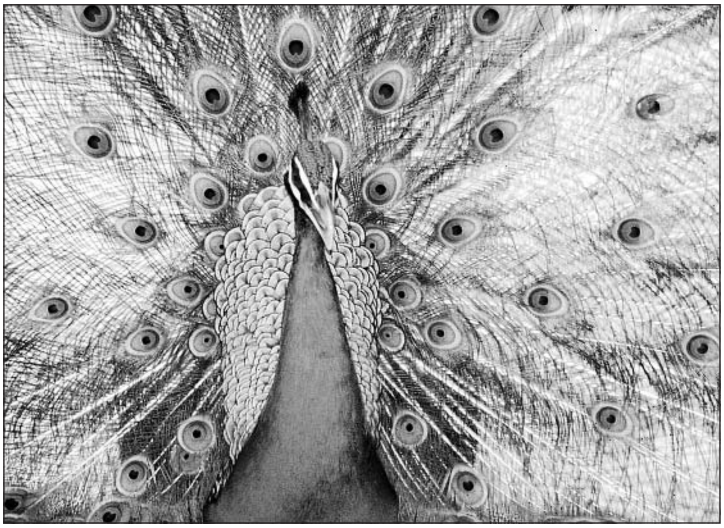
Types of Displays

Some displays involve, literally and simply, the visual display of a physical feature. Among insects, for example, green or brown coloring is often used for camouflage. Insects that are poisonous do not need camouflage and often advertise themselves with warning colors, such as black and red, or black and orange. This is referred to as aposematic coloration or an aposematic display.

Physical features can also indicate an individual's sex, age, and reproductive status—as do peacock tails, turkey wattles, deer antlers, the canine teeth of male baboons, and the swollen genitals of estrous female chimpanzees. Many such features vary in size, shape, or color in relation to an animal's health, hormones, or social status, and are therefore referred to as status badges or signs.

Often, meaningful physical features are further highlighted by behavioral displays. A courting peacock or turkey will fan open his tail and shake it back and forth for emphasis; a challenged buck will load plant material onto his antlers so as to exaggerate their size; an angry baboon will curl back his lip to further expose his canine teeth; and an estrous chimpanzee will approach a friendly male and assume a posture displaying her fertile state.

A particularly energetic or dramatic behavioral display not only calls attention to a physical feature, but indicates the health and vitality of the performer. The principle of honest signaling refers to the fact that large and healthy individuals tend to have brighter or more contrasting colors,



Male peacocks fan their tails and shake them in a courting display to attract female attention. (Digital Stock)

make deeper-pitched and louder sounds, and produce longer, more intense performances than small or weak ones. Such differences in display quality are readily noticed by predators, potential competitors, and potential mates.

Most displays are performed by individuals and are one way: sender to receiver. Threat displays, however, may involve reciprocal signaling between two challengers or between two groups of challengers. Courtship displays also may occur in groups: In some species, males gather together to perform in what is called a lek or a lekking display. Courtship of monogamous species may include long sequences of frequently repeated, ritualized interactions in which both partners participate. Such pair-bonding displays may continue well into the breeding season and the mateship; initially serving to familiarize the pair with one another and to synchronize their hormones and breeding behavior, they may later serve as greeting displays after separation.

Interpreting Displays

Darwin noted that displays having opposite characteristics often signal opposite meaning. In humans, for example, a face with upturned corners of the mouth (a smile) signals friendliness, whereas a face with downturned corners of the mouth (a frown) signals displeasure. In most animals, loud, deep-pitched sounds (for example, roars and growls) indicate aggression, whereas quiet, high-pitched sounds (for example, mews and peeps) indicate anxiety or fear. Similarly, body postures exaggerating size tend to signal dominance, whereas postures minimizing size tend to signal submission. Darwin called his observation the Principle of Antithesis.

Although some rules of display can be applied across species, most displays are specialized for intraspecific (within-species) communication—male to female, parent to offspring, or dominant to subordinate—and are therefore species-specific. That is, the ability to perform and interpret a particular display (such as a particular birdsong) is generally characteristic only of individuals of a particular species and is either innate (inborn) or learned from conspecifics (individuals of the same species) during an early critical period of development.

In order that their meaning is easily and quickly conveyed, most displays also tend to be highly ritualized; that is, they are performed only in certain contexts and always in the same way. This consistency in communication prevents errors of interpretation that could be disastrous. It would be a grave mistake, for example, to interpret an aggressive signal as a sexual overture, or an alarm call (predator alert signal) as an offspring's begging call. Mistakes of interpretation are also minimized by signal redundancy; that is, messages are often conveyed simultaneously in more than one sensory modality.

Display Modality

Displays utilize every sensory modality. Visual displays involve the use of bright, contrasting, and sometimes changing colors; changes in body size, shape, and posture; and what ethologists call "intention movements"—brief, suggestive movements which reveal motivational state and likely future actions. Auditory displays include vocal songs and calls, as well as a variety of sounds produced by tapping, rubbing, scraping, or inflating and deflating various parts of the body. Tactile displays include aspects of social grooming, comfort contacts (such as between littermates or parents and offspring), and the seismic signaling of water-striders, elephants, frogs, and spiders which, respectively, vibrate the water, ground, plants, or web beneath them. Olfactory displays include signals from chemicals that have been wafted into the air or water, rubbed onto objects, or deposited in saliva, urine, or feces.

Olfaction (sense of smell) is the most primitive, and therefore the most common and most important, sense in the animal kingdom. Species of almost every taxonomic group use smell to signal their whereabouts and, generally, their sex and reproductive state. (Birds seem to be an exception.) Animals may also use smell to identify particular individuals, to recognize who is related to them and who is not, and to determine the relative dominance status of a conspecific.

Chemicals used in displays are called pheromones. They may be derived from waste products or hormones, acquired by ingesting certain food items, or obtained directly from plants or other animals. Some pheromones not only communicate information, but also have physical effects on their receivers.

—*Linda Mealey*

See also: Adaptations and their mechanisms; Bioluminescence; Birds; Camouflage; Communication; Courtship; Defense mechanisms; Ethology; Hearing; Hierarchies; Language; Learning; Mating; Mimicry; Pair-bonding; Pheromones; Smell; Territoriality and aggression; Vision; Vocalizations.

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Chemical Aphrodisiacs

For thousands of years, people have used perfumes, lotions, and oils in an effort to enhance their sexual appeal. Several companies have even started to market chemicals thought to be human pheromones. Despite the huge appeal of such supposed aphrodisiacs, there is no evidence that any truly work. In other species, however, there exist naturally occurring chemicals that not only signal reproductive readiness, but also affect other individuals' reproductive capacity.

In many species, a female that is ready to mate will emit a pheromone to attract males. As many pet owners know, when a sexually mature female dog or cat is "in heat," her location and reproductive state can be detected by neighboring males simply through sense of smell.

In some species, males use pheromones as antiaphrodisiacs. When male sweat bees mate, they leave behind a scent which makes the female less appealing to other males who might pass by.

In other species, males use pheromones to intimidate or deter their competitors. Scent from a large bull elephant in musth (a prolonged state of heightened aggression and sexuality) can prevent a smaller male from going into musth, or bring him out of it prematurely.

Male pheromones have also been documented to cause miscarriage or fetal resorption in pregnant females, to hasten ovulation in adult females who are not already pregnant, and to hasten the onset of sexual maturity in young, prereproductive females.

Object Display

Courtship generally entails physical and behavioral displays that advertise the performer's age, sex, health, and vigor. However, males of some species have been discovered to use objects for sexual signaling. The best known of these are the bowerbirds of Australia and New Guinea, which collect colored fruits, feathers, leaves, and shells which they display in a cleared area called a court. Females inspect the decorations that local males have accumulated and mate with the male whose site they like best—generally the one with the most or the best objects. Males of a species of cichlid fish also build bowers: Males with tall, symmetrical sand towers—the most difficult type of bower to build—generally attract the most females.

While bowers have no utility other than display, males of some species display with objects that are of potential value for a female. In an act called courtship feeding, many male insects and spiders court females with food (called a nuptial gift), which the female consumes during mating. Males of vertebrate species, too, may court a female with gifts of food: Fish-eating birds offer fish; insect-eating birds offer insects. In some species, males offer nest material as part of a display, or perform a display which calls attention to a completed nest or nest site: Male weaver finches in Africa advertise nests they have built, as do house wrens in North America, and a variety of freshwater and marine fishes worldwide.

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DOGS, WOLVES, AND COYOTES

Type of animal science: Classification
Fields of study: Anatomy, genetics, zoology

Dogs, wolves, and coyotes are carnivorous mammals which belong to the Canidae family and share similar anatomical and behavioral traits.

Principal Terms

BULLA: hollow bony area
DIGITIGRADE: walks on the toes
LUCID: filled with light
OLFACTORY: related to sense of smell
OS: bone
TAPETUM: membrane layers
TYMPANIC: middle ear

Dogs, wolves, and coyotes represent four species of the thirty-eight dog species of the Canidae family. These carnivorous mammals are descendants of the prehistoric *Tomarctus* that lived fifteen million years ago. According to fossil evidence, dogs were probably the first animals to be domesticated, at least ten thousand years ago. Domestic dogs developed from wolves that humans tamed and selectively bred for hunting, retrieving, and guard duties. Specific wolf traits appear in various dog breeds.

Anatomy

Domesticated dogs vary from small to large animals according to which breed or mix of breeds they represent, such as the tall wolfhounds, standing an average of ninety-nine centimeters (thirty-nine inches) at the shoulder, the heavy St. Bernard weighing about 90 kilograms (200 pounds), and diminutive chihuahuas standing approximately thirteen centimeters (five inches) and weighing 2.7 kilograms (6 pounds). Each dog's skeleton has approximately 320 bones and varies according to tail length. Male dogs also have an additional bone, the os penis. Other exterior physical characteristics such as shape, color, and coat texture and length vary according to genetics.

Puppies have twenty-eight temporary teeth, which they begin to shed around twelve weeks old, and adult dogs have an average of forty-two permanent teeth which emerge when they are six months old. Dogs have twelve small incisors, which they use to groom themselves and to carry objects. Four large, sharp cuspids, often called canines, are used to tear meat, the foundation of dogs' diets. A total of twenty-six premolars and molars chew food. Wild dogs hunt a variety of prey, mostly small mammals such as rabbits, squirrels, and rodents. Dogs have nonretractable claws and walk on their toes. They have five toes on their front paws and four toes on their hind feet, where occasionally there is a dewlap or extra toe. Because they cannot perspire, dogs pant with their tongues to cool their systems.

Senses

Dogs with long, slim faces, such as collies, have eyes on the sides of their heads and can see wide areas, while dogs with short, broad faces, such as bulldogs, have eyes nearer the center of their faces and can view objects in the distance. Although dogs are unable to see objects as clearly as humans can, they are more sensitive to detecting motion. Dogs cannot see colors except for shades of gray. In dogs' retinas, the tapetum lucidum reflects light to enable dogs to see in the dark. These membranes cause dogs' eyes to appear glowing at night.

Dogs' ears are located on the sides of their skulls for optimum hearing. Some dogs, such as

German shepherds, have erect ears that resemble those of wolves and coyotes, while other dogs, such as basset hounds, have floppy ears that hang close to their faces. Dogs can hear high-pitched and distant sounds.

Dogs' olfactory systems are acutely sensitive. Like their wild cousins, dogs mark territories with urine and feces. Dogs use their noses to find food and track smells, often several days old. Scents are a significant way that all canines, both wild and domestic, communicate. Sounds also are important to convey messages. Canines emit noise variations to bark, growl, howl, yip, whine, and woof and engage in playful social behavior. Dogs express themselves with their bodies, eyes, and tail movements.

Life Cycle

Dogs reach sexual maturity before they attain full physical growth. Such maturation varies according to size, with smaller dogs reaching adult size within five to sixth months of birth and larger dogs sometimes not becoming fully grown until they are more than one year old.

Female dogs gestate for about nine weeks before whelping. Litter sizes depend on the mother's size and can average from one to more than ten puppies. Puppies' eyelids and ear canals are closed for almost two weeks. At about three weeks old, they begin walking, barking, wagging their tails, and eating solid food. Puppies are usually weaned at age six weeks. Dogs' life spans depend on their breed and environment, and range from eight to more than fifteen years.

Wolves

Wolves are wild relatives of dogs and are represented by two species, the gray and red wolf, with variations within each species for a total of thirty-two described subspecies. At one time, wolves lived throughout Europe, Asia, and North America. The gray wolf, also called the timber wolf, is the most common wolf species living in North America and can be found mostly in Canada and Alaska. Considered extinct in western Europe, with a few exceptions, gray wolves live in Russia, southeastern Europe, and Asia. Wolves' ranges have decreased due to urbanization. Most wolves live in sparsely populated forest, tundra, wilderness, and mountain regions and tend to avoid people, approaching settled areas only when they are starving or when natural crises, such as floods, fires, and blizzards, cause their migration to populated places to seek emergency food sources.

Gray wolves can attain a body length (from nose to base of the tail) of 1.2 meters (4 feet) and height of 90 centimeters (3 feet) at the shoulder. They average forty-five kilograms (one hundred pounds) in weight, with some wolves weighing twice that amount, and have sharp teeth, thick coats, tall legs, and bushy tails. Gray wolves have primarily gray coats with some black, yellow, and brown fur, although some gray wolves are solid black or white, particularly in the Arctic. An endangered species, red wolves live in the forests and brush of the south central United States and

Dog, Wolf, and Coyote Facts

Classification:
Kingdom: Animalia
Subkingdom: Metazoa
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Subclass: Eutheria
Order: Carnivora
Suborder: Canoidea
Family: Canidae
Genus and species: Ten genera and thirty-five species, including *Canis familiaris* (domestic dog), *C. lupus* (gray wolf), *C. rufus* (red wolf), *C. latrans* (coyote)

Geographical location: Dogs live on every continent except Antarctica; wolves are not found in Africa, South America, and Australia; coyotes live only in North and Central America

Habitat: Mostly prairies, forests, and mountains

Gestational period: Approximately two months

Life span: Ranges from an average of eight to twelve years, longer in captivity or domestication can be colored a hue ranging from reddish gray to black. Hunting of gray wolves escalated as farmers and ranchers penetrated wolf territory, their livestock offering easy targets for the wolves. Humans' retribution threatened decimation of the gray wolf population. Efforts to replenish the number of wolves include the reintroduction of gray wolves to Yellowstone National Park in 1995.

Pack Behavior

Hunting alone and in packs, wolves usually roam over large territories with a family group consisting of parent wolves and their offspring. Zoologists believe that wolves mate with the same partner for life, producing from three to nine cubs annually in late winter. Digging an underground den or appropriating a cave or hollow tree, wolves give birth and raise their cubs in this space, where the parents bring food until the cubs attain sufficient maturity to hunt. During winter and other stressful conditions, wolf families occasionally establish a larger pack of as many as thirty animals. The leader of a wolf pack, known as the alpha male, disciplines pack members.

Wolves prey on both large and small animals, including deer, moose, rabbits, birds, and mice and also eat vegetables, fruit, and carrion. They tend to hunt at night and can leap over obstacles 4.9 meters (16 feet) high, and travel up to fifty-six kilometers per hour (thirty-five miles per hour) to capture prey, sustaining thirty-two kilometers per hour (twenty miles per hour) for several hours when endurance is necessary to wear down elusive prey. Wolves migrate to follow prey to other areas. Scientists hypothesize that wolves howl in order to communicate with other wolf packs.

Coyotes

The scientific name for coyotes, *Canis latrans*, means "barking dog," which describes coyotes' staccato yips. Colored brown with gray and black flecks, coyotes grow to have a body length of approximately ninety centimeters (three feet) and can attain speeds of sixty-five kilometers per hour (forty miles per hour). Coyotes can adapt to many environmental situations and eat a variety of foods, including vegetables and insects. Although they tend to hunt alone, mostly at night, coyotes

Wolves are endangered by the loss of their natural wilderness habitat. (Corbis)

Working Dogs

Because of their keen senses, strength, and mobility, dogs have proven useful for a variety of jobs. Their endurance, alertness, and heightened hearing and smelling abilities supplement traits of intelligence, loyalty, and obedience. Dogs have served as scouts, messengers, sentries, and bomb detectors during wars. They are also used in peacetime to rescue earthquake victims, herd livestock, assist disabled people, pull dogsleds, and guard homes, stores, and museums. Secret Service dogs protect the United States President and other significant government officials and sites. Dog breeds especially suited for this work include German shepherds, dobermans, Belgian malinois, bloodhounds, and Labrador retrievers.

Dogs' sense of smell ranges from one thousand to ten thousand times greater than humans, depending on circumstances. Using their adept olfactory capacities, dogs can detect narcotics, explosives, termites, and humans, both alive and dead. Cadaver dogs can even find bodies underwater. Police and military dogs track criminals and sniff out illegal drugs and hidden explosives. Dogs' detection of illegal substances can be used as legal evidence in courts. Scientists and trainers at Auburn University's Institute for Biological Detection Systems and Canine Detection Training Center are preparing dogs for use in American schools as bomb and weapon detectors to deter violence.

Working dogs, such as the sled dogs who delivered diphtheria medicine to an ice-bound Alaskan town and Chips, a World War II military dog who located enemy snipers, have often become heroes celebrated in books and movies. In November, 2000, federal legislation was approved to discontinue the practice of automatically euthanizing retired American military working dogs. Memorials around the world have commemorated working dogs.

sometimes cooperate to kill a large animal such as an elk. Unafraid of people, coyotes often can be found in suburbs. The western coyote lives in western North America, from Panama to Alaska. The eastern coyote, considered a subspecies of the western coyote who probably mated with wolves, is larger than the western coyote and has darker fur.

Coyotes use abandoned dens to raise their pups, ranging from six to ten per litter. Born blind, the pups rely on their mother for milk at first, then eat food regurgitated by their parents before they are able to chew and hunt on their own. Most pups leave their parents by age one and start their own families, while other pups remain in the den to assist their parents to raise their siblings and learn parenting skills. The average coyote is fully mature by age two. Scientists believe that coyotes mate for life.

The *Canis* species can breed with each other and produce fertile offspring known as hybrids. Some people raise coydogs, a combination of coyotes and domestic dogs, while others, especially Eskimos, prefer wolf-dog genetic crosses, which result in strong animals capable of withstanding extreme climatic conditions and pulling heavy loads.

—Elizabeth D. Schafer

See also: Carnivores; Domestication; Endangered species; Groups; Packs; Predation; Scavengers; Smell; Tails; Teeth, fangs, and tusks; Urban and suburban wildlife; Wildlife management.

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DOLPHINS, PORPOISES, AND OTHER TOOTHED WHALES

Type of animal science: Classification
Fields of study: Anatomy, marine biology, physiology, zoology

Toothed whales are cetaceans, suborder Odontoceti. They use teeth to capture cuttlefish, squid, and other prey. Some are endangered species perceived to be quite intelligent.

Principal Terms

AMBERGRIS: waxy material from the intestines of sick sperm whales, used in perfume

CUTTLEFISH: a squidlike marine mollusk, eaten by Odontoceti

DIGIT: a finger, toe, or related bony animal structure

ECHOLOCATION: batlike location, from sound echoes, of unseen objects, used by toothed whales

SPERMACETI: a waxy substance in heads of sperm whales; usable for candles, ointments, lubricants, and cosmetics

Dolphins and porpoises are toothed whales of the order Cetacea, suborder Odontoceti. Like their distant relatives, baleen whales, toothed whales are mammals that spend their entire lives in earth's waters. Most toothed whales are found in oceans, but some inhabit harbors and rivers. Odontoceti make up sixty-seven of seventy-seven cetacean species, in six families: river dolphins (five species), porpoises (six species), dolphins (thirty-two species), sperm whales (three species), white whales (two species), and beaked whales (eighteen species).

All male toothed whales are larger than females. Male sperm whales, the largest toothed whales, are the largest toothed animals in the world. They grow to seventy-foot lengths and seventy-five-ton weights. Sperm whales dwarf all other Odontoceti—Herman Melville's "Moby Dick" was a male sperm whale. Like all whales, toothed whales are thought to be descended from a land animal, believed to have been an ungulate (hoofed mammal). However, their earliest ancestor was not the same as that of baleen whales. Why ancestors of toothed whales entered the oceans, seventy million years ago, is unknown. It may be that their return to the oceans was due to the need for a new food supply or to escape from predators.

Physical Characteristics of Odontoceti

The most characteristic physical feature of toothed whales is teeth that seize prey. Prey range from small crustaceans for small river dolphins, to squid and cuttlefish for larger dolphins and sperm whales, to walruses and seals or other whales for killer whales. As in all whales, evolution produced streamlined, fishlike mammals, whose front legs became flippers. Flipper bones resemble jointed limbs and some flippers show evidence of digit bones. External hind limbs are long gone, although their vestiges are still seen, internalized. Horizontal tail flukes that propel toothed whales are not anatomically related to hind limbs. As in baleen whales, flukes are made of boneless fibrous-elastic tissue, oriented horizontally, unlike fish tail fins, which are oriented vertically and differ in composition.

The bodies of whales are surrounded by thick blubber (fat) layers. This enhances buoyancy, insulates by preserving body heat, and is a fine energy store. Toothed whales are very fast, some swimming twenty-five miles per hour for prolonged periods and forty miles per hour in short bursts. Specially adapted Odontoceti lungs enable dolphins to dive to depths of almost one-quarter mile. Larger species dive deeper; for example, sperm whales dive to over 1.25 miles. This is because of the presence of waxy spermaceti around sperm whale nostrils. Cooling the spermaceti—by filling nasal passages with cold seawater—raises the whale's density and helps account for tremendously deep sperm whale dives.

Toothed whales have lungs and breathe air through a nostril. Nostrils, in blowholes atop the head, are closed tightly just before dives. Submerged indefinitely, out-of-breath Odontoceti would drown, though some can submerge for over an hour. Part of the ability to remain submerged is that 30 to 40 percent of oxygen in Odontoceti bodies is stored in muscle in a usable form (compared to 10 to 13 percent in humans). Also helpful to Odontoceti—especially dolphins—is the ability to move blood bidirectionally in blood vessels. This minimizes the effects of diving on the blood pressure and allows blood shunting to or from different organs as needed.

Toothed Whale Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Cetacea (whales)
Suborder: Odontoceti (toothed whales)
Families: Delphinidae (dolphins, seventeen genera); Monodontidae (white whales, two genera); Platanistidae (river dolphins, four genera); Phocoenidae (porpoises, three genera); Physeteridae (sperm whales, two genera); Ziphiidae (beaked whales, five genera)

Geographical location: Found in all earth's oceans, harbors, and some rivers

Habitat: Salt water in oceans, brackish water, or freshwater, depending on family

Gestational period: Between nine and sixteen months, depending on species; one large, well-developed calf (occasionally two) born, tail first; calves often half as long as mothers

Life span: Estimated twenty-five to forty years, depending on species

Special anatomy: Toothed mouth; lungs like land mammals; blow hole; flippers evolved from front legs; horizontal tail, nasal cavity that produces echolocation and vocalization

Dolphins, family Delphinidae, travel in groups that vary in number from thousands to a few members. Most dolphins are found in oceans and seas and have, as special characteristics, beaks of varied length. Best known are common dolphins (*Delphinus delphis*) and bottle-nosed dolphins (*Turisops truncatis*). Common dolphins, in legend and in reality, are great friends of humans. Bottle-nosed dolphins are frequent performers in marine aquariums. Both species cavort in the open oceans, leaping with backs arched from waters near ships. Smaller river dolphins live in Asia and South America. Examples are near-sighted buffeo dolphins (*Sotalia fluviatilis*) and blind Ganges dolphins (*Platanista gangetica*), which navigate solely by echolocation. Other beakless Delphinidae are large, dangerous killer whales (*Orcinus orca*) and intelligent pilot whales (*Globocephala malaena*).

The seven porpoise species are smaller than dolphins. They have beakless, rounded heads and triangular dorsal fins. Porpoises are rarely seen in open seas. The most plentiful, harbor porpoises (*Phocoena phocoena*), inhabit estuaries and inlets of large rivers. They do not follow ships or leap like dolphins. There are also three sperm whale species, the huge sperm whales (*Physeter catadon*) and two eight- to ten-foot dwarf or pygmy Kogia species. All have spermaceti in their heads. Arctic white whales lack dorsal fins and spermaceti. Male narwhals (*Monodon monoceros*) have spiral horns up to nine feet long, prized by the people who hunt narwhals for food. The white whale (*Delphinapterus leucas*, or beluga) is also sought for food. Beaked whales, family Ziphidae, are poorly studied and known

Dolphins, such as these Atlantic spotted dolphins, navigate by means of echolocation to identify other objects in the water. (Digital Stock)

most for toothed beaks and their ability to dive deeper and stay submerged longer than any other marine organism.

Special Senses and Odontoceti Intelligence

Odontoceti, especially dolphins, were thought very intelligent by the ancient Greeks. Current belief in dolphin intelligence has intensified due to the ability of captive dolphins, in sea aquariums, to learn complex tricks and invent games for themselves and their human keepers. Limited study of sperm whales suggests intelligence, supported by the twenty-pound brains of adult males. Intelligence is extrapolated to other Odontoceti, most of which have not been studied well. Almost all species have brains bigger than the three-pound brains of humans.

Many believe that dolphins and sperm whales have spoken languages. These are reported as vocalizations, including calls that keep groups together and signal danger. Dolphins appear chatty, almost constantly making variegated whistling sounds for alarm, sexual arousal, and other emotions. Moreover, they are very social. They show great affection and caring for each other and their calves. In addition, isolated from other dolphins and human keepers, captive dolphins pine away and die. Most linguistic authorities see dolphin and sperm whale intelligence as close to that of primates, but do not rate their communication as language.

Odontoceti and baleen whales have small eyes, lack external ears and noses but have well developed inner ears, and some river dolphin species are blind. These characteristics led to proof that Odontoceti use sound and hearing the way vision and smell are used by land mammals. In addition to vocalization (pseudolanguage) they make echolocation clicks as air moves between nostrils and nasal passages to the lungs. Clicks are bio-

Some Odontoceti Species

Bottle-nosed dolphin (*Turisops truncatis*): The dolphins usually found in sea aquariums; up to thirteen feet long; dark gray body and lighter gray belly and face; short, wide beak; inhabits temperate and tropical parts of all oceans.

Common dolphin (*Delphinus delphis*): This dolphin cavorts around ships; up to nine feet long; black, with white belly and face and yellow, white, or gray side stripes; black markings around eyes and across the long, narrow beak; inhabits temperate parts of all oceans.

Ganges dolphin (*Platanista gangetica*): The blind river dolphin; up to eight feet long; small dorsal fin, eighteen-inch beak; inhabits India's rivers.

Harbor porpoise (*Phocoena phocoena*): The common porpoise; up to six feet long; black, with white belly; has dorsal fin but no beak; inhabits shallow waters and estuaries of North Atlantic and North Pacific, as well as the Black Sea and Mediterranean Ocean.

Killer whale (*Orcinus orca*): A dolphin that grows up to thirty feet long; glossy black back, white marks on sides and belly, dorsal fin six feet tall, no beak; preys on other whales; inhabits coastal regions of all oceans.

Narwhal (*Monodon monoceros*): A member of the white whale family; up to twenty feet long; eight- to nine-foot-long spiral horn (actually the left top incisor); inhabits the Arctic Ocean.

Pilot whale (*Globocephala malaena*): Black dolphin; up to thirty feet long; square head with very short beak; tall, narrow dorsal fin and long flippers; inhabits temperate and tropical regions of all oceans.

Sperm whale (*Physeteridae catodon*): Up to seventy feet long; dark gray, shading to white belly; head 30 percent of body length; no dorsal fin, small flippers; inhabits all oceans; migrates to poles in spring and equator in autumn.

White whale (*Delphinapterus leucas*): Beluga whale; up to twenty-three feet long; white as adult, has no dorsal fin; lives mostly in the Arctic Ocean.

sonar, as in bats. That is, echolocation is the way Odontoceti explore the world. Directing clicks outward toward objects in the environment causes sound waves to hit the objects. Waves that bounce off are picked up by the whales and identify object size, distance, and so on. The great ability of water to carry and amplify sound is deemed to be why cetaceans discarded external ears. Operation of this sensory system has uses in navigation and predation in murky oceans.

The Life Cycle of Odontoceti

Toothed whales reproduce like other mammals, but in the water. Adults participate in complex courtship: swimming close together, caressing, nuzzling, and rubbing bodies. After copulation, females carry young for nine to sixteen months, depending on species. Then, a large, well-developed calf (occasionally two) emerges underwater, tail first. Only the reproduction of bottle-nosed dolphins and sperm whales is well studied. In both cases, when a calf is born, other females (aunts) ensure it gets to the surface quickly for a first breath. They reportedly continue to help the mother to protect her offspring.

Calves nurse from teats on the mother's belly. The milk is rich in minerals, protein, and fat, so calves grow quickly. High maternal affection and protection of calves is found in bottle-nosed dolphins, sperm whales, and the other Odontoceti studied. Calves are weaned in one to two years. They are adults, capable of reproduction, in five years. Life spans vary from twenty-five to forty years. As with other wild animals, not all whales—actually, only a few—get to grow old.

Odontoceti as an Endangered Species

In the past, uncontrolled whaling for spermaceti, blubber, and ambergris made sperm whales and narwhals endangered species. At the beginning of the twenty-first century, there is little sanctioned whaling for large Odontoceti, initially due to quotas set by the International Whaling Commission (IWC). By the early 1990's, most whaling by IWC nations stopped. These actions and the absence of clandestine whaling may allow whales to make a natural comeback. Dolphins, never hunted as much as baleen and sperm whales, are endangered because they are trapped and drown in nets used to catch tuna, a species with which many dolphin species swim. This has been reduced by the refusal of tuna canneries to buy tuna from fleets that do not protect dolphins, an attitude driven by activist consumer public opinion. A 1972 U.S. Marine Mammal Protection Act—amended in 1988 and 1992—diminishes exploitation of dolphins and related mammals.

—Sanford S. Singer

See also: Deep-sea animals; Endangered species; Evolution: Animal life; Evolution: Historical perspective; Fins and flippers; Intelligence; Language; Learning; Mammals; Marine animals; Marine biology; Respiration and low oxygen; Whales, baleen.

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DOMESTICATION

Type of animal science: Evolution
Fields of study: Anatomy, anthropology, archaeology, genetics, ethology, physiology, reproduction science

Animal domestication is the process of bringing an animal species under the control of humans and gradually changing it, through careful selection, mating, and handling, so that it becomes more useful to humans. Some animals are more amenable to being domesticated than others. Domestication is a symbiotic relationship between humans and the animals involved, and has been integral to the development of human societies.

Principal Term

DOMINANCE SOCIAL BEHAVIOR: organization around a dominant leader, whom the rest of the group follows

Although taming a wild animal, that is, acclimating it to the presence of people, is invariably a first step in domestication, the critical aspect is directing its breeding toward a functional goal. Genetic selection for desirable traits and against undesirable ones is a crucial feature of domestication. Captive wild animals in zoos or circuses cannot be considered domesticated, although they may be quite tame and their breeding is controlled by humans. However, this breeding is not directed toward some functional goal. Mere propagation of a species or maintaining genetic diversity is insufficient to constitute domestication. Domestication is a synergistic relationship between humans and the animals involved. Humans benefit from the resources and services that the animals provide, such as food, fiber, shelter, clothing, work, sentinel duty, and companionship. Animals benefit by having humans protect them from harm, provide for their needs, and increase their numbers and range.

Characteristics of Animals Favoring Domestication

In 1865, the English naturalist Francis Galton suggested the following six physiological and behavioral characteristics that make some animals good candidates for domestication: hardiness, dominance social behavior, herd behavior, utility to humans, facile (easy) reproduction, and facile husbandry. First, by hardiness, he refers to the ability of the young to be removed from its mother and to be around humans. The guinea pig is perhaps an extreme example of tolerating removal from its mother, as it is born ready to eat solid food. Most mammals, on the other hand, initially depend on their mother's milk. Primates are poor subjects for domestication because of their helplessness at birth and their relatively long dependence on their mothers for food and nurturing.

Second, dominance social behavior is in contrast to territorial behavior and refers to one animal assuming leadership, with the rest of the group acquiescing to him or her in the hierarchy. In domestication, humans co-opt the function of the leader, and animals remain submissive even as adults. Third, herd animals are contrasted to solitary animals, or ones that disperse in response to danger. Domesticated animals are penned or otherwise restricted at various times. If they remain together in herds, they are easier to manage. Fourth, utility to humans includes their use for food, fiber, work, companionship, and even worship. Humans would not make the effort to domesticate an animal unless it had some perceived value. The purpose for domestication may change with time, however. It is likely that the initial motivation for domesticating cattle was for worship—to capture the strength and aura of these animals, which were revered and used in religious ceremonies. Work, such as pulling carts, packing, and riding, became a subsequent goal, while contemporary utility in Western societies involves meat and milk production.

The fifth characteristic is facile reproduction under confined conditions; animals with finicky reproductive behaviors and/or elaborate courtship rituals make poor candidates for domestication. Sixth, facile husbandry refers to placid disposition and versatility in terms of nutrition. Animals that are high-strung or dependent on unique foodstuffs would be weak prospects for domestication. Koalas, which eat leaves from only certain eucalyptus trees, are poor candidates. On the other hand, pigs and goats are excellent choices because they are not very fastidious in their eating habits. These six characteristics, enunciated more than a century ago, apply strongly to livestock species, but less well to dogs and cats; with regard to the latter, it has been argued that cats are not so much domesticated as merely tolerant of humans.

Cats are the only species to have been domesticated since prehistory. (Corbis)

History of Animal Domestication

Archaeological evidence suggests that agriculture developed about ten thousand years ago, after the last ice age, at a time when the climate became warmer and more stable. Predictability of the weather is particularly crucial for plant domestication, which apparently developed synergistically with animal domestication, leading to agriculture. Domesticated animals simplified the acquisition of food and provided food storage, in the form of "walking larders"; larger animals, such as cattle, buffalo, and horses, permitted heavier work to be done and larger distances to be covered. Farming the land made it possible for humans to abandon the nomadic lifestyle of hunter-gatherers and to adopt a more sedentary lifestyle. This allowed for development of new technologies, professional specializations, and new forms of social organization.

Domestication of any animal did not occur at once, but rather over a substantial period of time, perhaps hundreds of years. Furthermore, estimating the dates for domestication is subject to considerable uncertainty and may need to be modified as new information becomes available. For some species, domestication occurred independently at more than one location. The process may have begun almost accidentally, as by raising a captured young animal after its mother had been killed and observing its behavior and response to various treatments. The domestication of an animal subsequently spread from the site of origin through trade or war.

Animal domestication occurred in various parts of the world. In the Middle East, the Fertile Crescent, stretching from Palestine to southern Turkey and down the valley of the Tigris and Euphrates Rivers, was an important site. Sheep, goats, cattle, and pigs were domesticated there by around 6000 B.C.E. The Indian subcontinent and east Asia were independent sites for domesticating cattle and pigs, respectively. Llamas, alpacas, and guinea pigs were domesticated in the Andes Mountains of South America. Domestication of cats occurred in Egypt and of rabbits in Europe. No native animals were domesticated in Australia, likely because none of them were suitable for domestication. It is worthy of note that few domestications have occurred in the past thousand years. It is also of interest that domesticatable species were not evenly distributed over the globe, which probably has had a lasting effect on the differential development of various cultures.

Archaeology, coupled with the natural history of domesticated animals and their wild relatives, has been essential in reconstructing the history of domestication. Examining skeletal remains at archaeological sites for changes in morphology and distribution by age and sex has helped scientists to deduce the extent of domestication. Lately, traditional archaeology has been supplemented by the methods of molecular biology. Examining extant breeds for their genetic relatedness has been particularly useful in distinguishing single versus dual sites of domestication.

Early Domesticates: Dogs and Reindeer

Dogs (*Canis familiaris*) are generally recognized as the earliest known domesticated animals. They were widespread across the Northern Hemisphere before other animals were domesticated. They were derived from wolves (*Canis lupus*), with whom they are fully interfertile. The earliest known dog is in a burial site in Northern Iraq that dates from 12,000 to 10,000 B.C.E. Other sites, dating from 10,000 to 7000 B.C.E., have been documented in England, Palestine, Japan, and Idaho. While it may have first occurred in China (a Chinese wolf has some of the detailed physical features of dogs), domestication probably occurred at a number of separate sites. Dogs accompanied the American Indians when they occupied the Americas in several waves prior to the end of the last ice age. Dingoes were brought to Australia by trade from Asia long after the Aborigines settled that continent 40,000 years ago. While dogs were considered a food animal, they have long been used for guarding, hunting, and companionship. Subsequently, they were developed for herding.

Reindeer (*Rangifer tarandus*) were another early domesticate, dating from around 12,000 B.C.E. in northern Scandinavia and Russia. The reindeer has been little changed by domestication and its range has not been extended by the process. They are well-suited to their environment, but attempts to establish reindeer industries in Canada and Alaska have not been successful. Herding reindeer continues as a principal occupation of the Laplanders of Finland, Sweden, and Norway. Reindeer are used for draft (pulling loads), clothing and shelter (skins), tools (antlers), and food (meat and milk). Farming several other deer species (such as *Cervus dama* and *Cervus elaphus*) has recently gained in importance in New Zealand and western Europe, where they are raised for meat (venison) and "velvet," the new growth of antlers, the basis for traditional medicines in Asia. However, because these latter species have had little opportunity to be changed, they cannot be considered domesticated.

Sheep, Pigs, and Cattle

Sheep (*Ovis aries*) were the first of the common food animals to be domesticated. They were derived from wild sheep (*Ovis orientalis*) and were first domesticated in the western Fertile Crescent around 7000 B.C.E. Goats (*Capra hircus*), derived from Persian wild goats (*Capra aegarus*), were first domesticated in the central Fertile Crescent slightly later, between 6000 and 7000 B.C.E. Sheep and goats were used for food, skins, and fiber (wool or hair). Both were later selected for milk production.

Pigs (*Sus domesticus*) probably originated at two separate sites, the central Fertile Crescent around 6000 B.C.E. and in eastern Asia around 5000 B.C.E. Derived from wild pigs, they were primarily raised for meat. Despite restrictions against eating pork by Muslims and Jews, it has long been the principal meat consumed in the world. The most populous country, China, has nearly 50 percent of the world's pigs.

Cattle (*Bos taurus* and *Bos indicus*) are derived from now-extinct wild cattle (aurochs, *Bos primigenius*) that ranged over much of Europe and Asia. They were probably domesticated independently at two locations, the western Fertile Crescent around 6000 B.C.E. for *Bos taurus* and the Indian subcontinent around 5000 B.C.E. for *Bos indicus*. Initially, the animals were worshiped and used in religious ceremonies. Reverence for cattle is still practiced by Hindus in India. Subsequently, they were developed for work, meat, and milk. Their hides are made into leather. Traditional cattle in Africa are derived from initial importations of *Bos taurus* and subsequent importations of male *Bos indicus*.

Other Domesticated Animals

Asiatic buffaloes (*Bubalus bubalis*) were domesticated as the water buffalo in India (3000 B.C.E.) and as the swamp buffalo in east or southeast Asia (2000 B.C.E.). While both were developed as draft animals, the water buffalo has also been selected as a dairy animal. Fully half of the milk production in India comes from buffaloes. In spite of its tropical origin, the Asiatic buffalo is not very heat tolerant and compensates by immersing in water or mud. Neither the African buffalo (*Syncerus caffer*) nor the American buffalo (more properly, bison, *Bison bison*) have been domesticated. Yaks (*Poephagus[Bos] grunniens*) were domesticated around 3000 B.C.E. in Tibet or surrounding areas, where they are used as pack animals and as a source of milk, hair, hides, and, usually after an otherwise productive life, meat.

Horses (*Equus caballus*) originated from wild horses in the Caucasus Mountains around 4000 B.C.E. Originally used for food and skins, they were also developed for draft and, much later, for riding. Because they came to the Middle East after the development of written language, their arrival is documented, so scholars do not need to depend solely on the archaeological record. Donkeys (*Equus asinus*) were domesticated in the Middle East or Northern Africa (3000 B.C.E.). They are used for carrying material or people, as is the mule, an infertile cross between a horse and a donkey.

Llamas (*Lama glama*) and alpacas (*Lama pacos*) were domesticated in Peru by Incas around 4000 B.C.E. Llamas are from wild guanacos and alpacas from wild vicuñas, found at higher elevations. Llamas are used as pack animals, alpacas are valued for their fine wool, and both serve as sources of meat. Camels, the one-humped dromedary (*Camelus dromedarius*) and the two-humped Bactrian (*Camelus bactrianus*) were domesticated in Arabia (2000 B.C.E.) and Central Asia (1500 B.C.E.), respectively. Both are pack animals, with the dromedary also used for meat.

Guinea pigs (*Cavia porcellus*) were domesticated in Peru around 3000 B.C.E. They continue to be used as a meat animal in parts of South America. Rabbits (*Oryctlagus cuniculus*) were domesticated between 600 and 1000 C.E. in France. They are primarily raised for meat and fur, with angora rabbits producing a fine wool.

Cats (*Felis catus*) are the animals least changed, morphologically, by domestication. In addition, they are quite capable of surviving without human intervention. Their domestication occurred relatively late, around 2000 B.C.E., in Egypt, the home of the African wild cat (*Felis catus libyca*), which resembles domestic tabby cats. The early Egyptians adopted cats enthusiastically, deifying them and prohibiting their export. After conversion to Christianity, Egyptians ceased worshiping cats, which were carried to all parts of the Roman Empire and thence to the rest of the world. Cats have been used for companionship and for rodent control.

Chickens (*Gallus gallus*), along with ducks and geese (from China, the Middle East and Europe), turkeys (from North America), Muscovy ducks (from South America), and guinea fowl (from Africa) are avian species that have been domesticated. Chickens were probably derived from wild red junglefowl in southeast Asia before 2000 B.C.E. Cockfighting was an initial purpose for their domestication. They acquired religious significance and were also used for meat and feathers. Their selection for egg production has been a recent development. Because of improvements in breeding, feeding, and management, poultry meat production is increasing rapidly and is second to pork worldwide. In the past few centuries, two other avian species, ostriches (from Africa) and emus (from Australia), have been farmed, but it is probably incorrect to call them domesticated, as they have so far been little changed from their wild relatives.

Two insects have also been domesticated: honeybees and silkworms. Honeybees were domesticated shortly after the last ice age and were the primary source of dietary sweetener until two hundred years ago. They were also valuable for wax and venom, the latter for medicinal purposes. Silkworms, one of the ten varieties of silk-producing insects, were domesticated around 3000 B.C.E. in China, producing fiber used in apparel.

—James L. Robinson

See also: Adaptations and their mechanisms; Breeding programs; Cats; Cattle, buffalo, and bison; Chickens, turkeys, pheasant, and quail; Dogs, wolves, and coyotes; Donkeys and mules; Ducks; Geese; Goats; Groups; Herds; Hierarchies; Horses and zebras; Pigs and hogs; Population genetics; Sheep; Urban and suburban wildlife; Veterinary medicine; Zoos.

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DONKEYS AND MULES

Type of animal science: Classification
Fields of study: Anatomy, evolutionary science, zoology

The donkey was domesticated from the African wild ass at least six thousand years ago. The mule is the result of crossing a male donkey (jackass) with a female horse (mare).

Principal Terms

BROWSERS: eaters of bushes, scrub vegetation, and bark

EQUIDS: members of the horse family (Equidae) including horses, asses (including the donkey), zebras, and their crosses (including the mule and the hinny)

GRAZERS: eaters of grasses

HYBRID: an organism resulting from the crossing of two species

HYBRID VIGOR OR HETEROSIS: the tendency of hybrids to be larger and more durable than their parent species

UNGULIGRADE: walking on the tips of the toes

The donkey and mule are members of the horse family (Equidae). Like other equids, they are fast runners adapted for life on open grasslands and deserts. Their posture is unguligrade, meaning that they run on the tips of their toes. Their legs are long and adapted for speed. Each foot has only one toe—the hoof—another adaptation for speed. Equids are grazers and sometimes browsers. Asses especially will browse.

The Donkey

The donkey or domestic ass is descended from the African wild ass. Donkeys first appeared on wall paintings and in burials six thousand years ago in Egypt and western Asia. They have been used widely by farmers and traders as pack animals and to pull wheeled vehicles.

Donkeys have been bred to be smaller than their ancestor, the African wild ass. The goal was to produce a thrifty animal that gave the greatest amount of work for the least amount of feed. Being descended from a desert animal, donkeys are better suited to the Mediterranean climate than to

Donkeys, descended from the African wild ass, have been domesticated for over six thousand years. They are used as pack animals and to pull wagons, but they are very uncomfortable to ride. (Corbis)

Donkey and Mule Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Subclass: Eutheria
Order: Perissodactyla
Family: Equidae (horses)
Genus and species: Equus asinus (donkeys or domestic asses); *E. asinus* bred with *Equus caballus* (mules)
Geographical location: The domestic donkey is descended from the wild ass of the hot deserts of Africa and Arabia; both the donkey and the mule were introduced to wide areas of Europe, Asia, Africa, and later to both North and South America
Habitat: Donkeys and mules are well-adapted to hot, dry deserts, yet selective breeding has produced donkeys that thrive in the damp climate of Ireland
Gestational period: 11.5 months
Life span: Twenty to twenty-five years on average
Special anatomy: Long ears dissipate heat; broad single toe (hoof) on each foot is an adaptation for running; capable of digesting large quantities of low-protein fodder

northern Europe. Donkeys were introduced to China in the third century B.C.E. Donkeys were brought to the Americas by the Spanish, who call them "burros," beginning in the seventeenth century.

It is possible, but awkward, to ride a donkey. Because of the animal's low withers, a human rider must sit far back in the donkey seat to avoid sliding forward. This produces a bumpy ride and has precluded the donkey's use as a mount in hunting or battle.

The Mule

The mule is the offspring of a male donkey (jackass) and a female horse (mare). The opposite cross—a female donkey (jenny) bred to a male horse (stallion)—produces a hinny. A mule has a donkey's large head and long ears, the body of a horse, and an asslike tail. Its voice is a bray that is somewhat different than that of the ass. Some mules are quite large: as much as sixteen hands (sixty-four inches) at the withers.

Mules are strong and durable. They are more surefooted and can bear heavier loads than either the horse or the donkey. This is a good example of hybrid vigor or heterosis: the tendency of hybrids to be larger and more durable than their parent species. It is often said that a mule is smarter than a horse because a horse may overeat and "lounder" (become ill from overeating) if given unlimited access to grain, but a mule will not. Mules are almost always infertile, apparently due to differing numbers of chromosomes in the gametes of the horse and the donkey.

Donkeys and Mules in History

Donkeys have been used in agriculture and transport for at least six thousand years. Mules were essential in transport for at least three thousand years, from ancient times until the invention of the steam engine and the building of railroads. Mules can be ridden but were used mostly in mule teams or mule trains to pull wheeled vehicles in both peace and war. For example, the twenty-mule teams of Death Valley, California, hauled two wagons loaded with borax plus a water wagon with a combined weight of over twenty-seven tons.

Wild populations of equids have been greatly reduced by humans through hunting and habitat destruction, some to the point of extinction. Domestic horses, donkeys, and mules, however, have thrived for thousands of years in association with humankind. Despite being largely replaced by mechanical power, domestic equids are still common.

—Thomas Coffield

See also: Claws, nails, and hooves; Domestication; Horses and zebras; Ungulates.

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DUCKS

Type of animal science: Classification
Fields of study: Anatomy, ornithology

Ducks are among the most common and widespread of aquatic birds. Like other members of the Anatidae family, they have webbed feet, a boat-shaped body, a dense covering of feathers, and a broad and somewhat flattened bill.

Principal Terms

ANATIDAE: the bird family that includes the ducks, swans, and geese

ECLIPSE PLUMAGE: the drab plumage of male ducks following the postbreeding molt in which their bright courtship feathers are replaced by dull earthy feathers that provide inconspicuous coloring

EIDERDOWN: rich, downy feathers of eider ducks noted for its insulation value; eiderdown has been gathered for centuries for use as stuffing for mattresses or parkas

HYBRID: the offspring of parents of different stock; hybrid ducks may result from the mating of mallards and barnyard geese

POLYGAMY: mating behavior in which a male mates with more than one female at the same time

POSTNUPTIAL MOLT: replacement of feathers following the mating season

RETICULATE: netlike covering of scales on legs

SCUTELLATE: overlapping of platelike or shieldlike scales

Some of the most common and widespread of all aquatic birds are the ducks. They breed on all continents except Antarctica, and are noted for their long-distance seasonal migrations along well-established flyways. Many species such as the mallard (*Anas platyrhynchos*) and northern pintail (*Anas acuta*) are indicator species of wetlands, waterways, and water courses, but others, such as the Baikal teal (*Anas formosa*) and Laysan duck (*Anas laysanensis*) are very limited in numbers and distribution. Most waterfowl are important food resources for native peoples, and revenues from duck hunters promote local economies and fund wildlife refuges. Wildlife enthusiasts value the rich variety of ducks and the brilliant colors of the males, called drakes, of many species.

Physical Characteristics

Ducks are placed in the avian order Anseriformes along with the screamers, swans, and geese. The long-legged screamers lack webbed feet and are placed in their own family, the Anhimidae. The ducks, geese, and swans are gathered in the family Anatidae and are collectively called waterfowl. The anatids are united in having webbed feet, a boat-shaped body, a dense covering of feathers, and a broad and somewhat flattened bill that is variously modified for straining minute surface organisms, gathering shellfish, grazing on aquatic plants, or catching fish.

Ducks differ from swans and geese in several ways. They are generally smaller and have shorter necks and legs, which are set well back on the body. They are good swimmers but walk with a peculiar waddling gait on land. Ducks are also distinguished in having scutellate (overlapping) scales on the front of their legs, while geese and swans have netlike or reticulate scaling.

Unlike their larger kin, ducks have two molts each year. The first molt occurs after breeding in males and shortly later in females. During this molt, ducks shed their flight feathers and males trade their bright breeding plumage for the plain plumage colors similar to those of females, called an eclipse plumage or hiding plumage. The plain colors of the eclipse plumage camouflages the flightless birds until their new flight feathers grow. The second molt occurs in late summer or early fall and produces the bright breeding plumage of males in preparation for courtship on their wintering grounds.

Ecologically, all ducks are birds of aquatic habitats that reach their greatest abundance in the innumerable ponds, shallow lakes, and marshes of the world. Several species are sea ducks that frequent shore habitats, estuaries, and coastal marshes during the nonbreeding season.

Courtship and Nesting

Courtship and pair formation occurs on wintering grounds as males and females engage in species-specific displays. Males of many species perform intricate head and tail jerks that "point" to the bright metallic colors of their wing speculum. Many sea ducks add a courtship finale by flicking water spurts with their head or feet, all the while bowing and cooing. The stiff-tailed ducks of the tribe Oxurinae twist their heads far over their backs, then violently thump their bills against the inflated necks, uttering a stream of bubbles and a series of burps.

Following courtship the female builds a nest of reeds, sedges, and grasses in marshes or along the shallow, weed-choked margins of lakes and ponds. The mergansers and wood ducks nest in cavities in trees, while shelducks are unique in selecting burrows in which to lay their eggs.

In most species, the female alone builds the nest of nearby materials and lines it with downy feathers plucked from her breast. The down feathers provide wonderful insulation for the eggs and are arranged in layers over the eggs for protection from predators when the female leaves the nest to find food.

Most ducks lay relatively large clutches of eight to twelve smooth, white eggs. A few species, such as the black-headed duck (*Heteronetta atricapilla*) of South America, are brood parasites that lay their eggs in nests of other ducks, coots, and ibis.

Incubation begins when the clutch is complete, ensuring that all of the young hatch at the same time. Incubation takes about a month (twenty-two to forty-one days). The precocial young are densely covered in a fluffy coat of down feathers. In most species, the young abandon the nest shortly after hatching to accompany the female, who leads them to nearby feeding grounds. The young instinctively feed themselves under the watchful eye of the female, who marshals them to safety in the weeds if danger threatens. Predation often decimates the young of a nest, as snapping turtles, fish, foxes, coyotes, hawks, and owls are quick to snap up the defenseless young. Those that survive fledge in about a month and may remain in the company for several more weeks.

In some species, the young accompany the female on the southward migration, but most young migrate on their own, relying on inbuilt genetic programming to fly hundreds and sometimes thousands of miles using the sun or stars or both as navigation aids. Many species memorize landmarks such as lakes and river courses, which supplement celestial navigation aids on future migrations. Studies have also suggested that at least some ducks are able to tap into the earth's magnetic field for directional aid on overcast days, when other cues are unavailable.

Duck Tribes: Anatini

The ducks are subdivided into several tribes on the basis of anatomical and behavior differences. Several tribes contain forms intermediate between ducks and their near relatives, the geese.

The familiar puddle ducks of ponds and marshes belong to the tribe Anatini. They are called tippers or dabblers because of their habit of tipping up to feed in shallow waters of ponds, marshes, and rivers. The dabblers have feet set farther forward on their bodies than other ducks and bound into the air when taking flight. Males of this group usually have a brightly colored, iri-

The mallard duck is a common sight on the ponds and lakes of North America. (Digital Stock)

bottom. Smaller species such as teals feed in shallower waters or on mudflats. The broad, spatulate bill of the northern shoveler (*Anas clypeata*) strains minute organisms from the water surface.

Dabblers are found on all continents, but they are especially plentiful along interior ponds, marshes, and creeks. In most dabblers, the male is jealously attentive to the female during courtship but deserts her shortly after the eggs are laid, leaving her to defend the nest and raise the young entirely on her own. She builds a crude nest of grasses and weeds lined with down from her breast. After abandoning the female, the male may seek another female to repeat the performance. If none is available, they spend the rest of the breeding season loafing and hiding while in the eclipse plumage. After their second molt, the males sport bright new feathers to enter the winter months, during which courtship and pair formation for the following breeding season takes place.

descent wing patch or speculum and are often brightly colored about the head and neck, while females are drab colored.

There are about forty-one species of dabbling ducks worldwide, of which ten breed in North America. Some typical dabblers include the teal, widgeons, pintails, gadwalls, and shovelers. The best-known dabbler is the mallard, which occurs in both wild and domesticated forms. Most of the domestic species, such as the barnyard duck and Indian duck, are probable descendants of the mallard. Dabbling ducks are surface or shallow water feeders of creeks, ponds, and marshes. Some strain food from soft mud, others feed on the water surface, and still other species tip up and then stretch their necks down into the water, taking food from submerged vegetation or feeding on the vegetation itself. Food consists of the leaves, roots, tubers, and seeds of floating or submerged vegetation and a wide variety of small animals, mostly shrimp, scuds, shellfish, and insects. Long-necked dabblers like the northern pintail (*Anas acuter*) tip up to feed directly on the

Aythyinae, Mergini, Cairini, and Oxyurinii

The pochards (redheads), canvasback (*Aythya valisineria*), and scaups belong to the tribe Aythyinae, which are called sea ducks or bay ducks. They frequent coastal locations in winter but build a floating nest among the reeds and grasses of interior lakes, rivers and marshes. Most diving ducks have short tails and wings, but large paddle feet with a distinctive, paddlelike flap on the hind toe for diving. They feed mostly on underwater plants and animals. If danger threatens, diving ducks submerge and can swim underwater for long distances. They take flight by skittering along the top of the water. Because they have short wings on large bodies, most bay ducks fly with rapid wing beats and always appear in a hurry in flight.

The tribe Mergini includes a varied mix of mergansers, scoters, eiders, goldeneyes, and the spectacularly colored harlequin (*Histrionicus histrionicus*) and oldsquaw (*Clangula hyemalis*). Mergansers are powerful divers that pursue fish underwater, catching and holding them with their narrow, serrated bill. They nest in cavities in trees or in rock crevices along rivers and streams, as do the goldeneyes of this tribe. The tribe also includes eiders, which nest in the circumpolar Arctic tundra. Eiders are the source of eiderdown, which the female plucks from her breast to line the nest and insulate the eggs and young. The most striking of the Mergini is the harlequin duck, with its patchwork quilt of chestnut, blue, and white plumage. Harlequins feed in cold, fast-flowing Arctic streams.

Members of the tribe Cairini have long legs and sharp claws which enable them to clamber about branches and limbs. Called wood ducks or tree ducks, they include the gorgeously colored wood duck (*Aix sponsa*) of North America and mandarin duck (*Aix galericulata*) of southeast Asia. This tribe also includes the drab muscovy (*Cairina moschata*), which occurs widely in both wild and domesticated forms. Unlike other tribes, the wood ducks frequent the gallery forests of rivers and lakes, forested swamps, and woodland pools. They typically nest in tree cavities just adjacent to water. When old enough, the downy young half tumble and half jump into the water below the nest cavity.

The ruddy duck (*Oxyura jamaicensis*) exemplifies the tribe of stifftails called Oxyurinii. These dumpy little ducks are predominantly reddish or brownish in color and have upright tails for which they are named. Except for teals, the stifftails are small ducks that are noted for laying exceptionally large eggs for their body size. For example, the female ruddy duck, although scarcely weighing a pound herself, lays a clutch of fourteen eggs, weighing a total of nearly three pounds, with each egg averaging over 2.5 by 1.75 inches in length and width.

Dendrocygnini, Merganettini, and Tadorini

The long-legged members of the tribe Dendrocygnini are whistling ducks. Considered by some to be more closely related to geese than to ducks,

Duck Facts

Classification:
Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Class: Aves
Order: Anseriformes (screamers, swans, geese, and ducks)
Suborder: Anseres (swans, geese, and ducks)
Family: Anatidae (swans, geese, and ducks)
Subfamily: Anatinae (ducks)
Tribes: Tadornini (steamer ducks and shelducks, eight genera, twenty-one species); Cairinini (wood ducks and allies, eight genera, fourteen species); Dendrocygnini (whistling ducks, one genus, eight species); Anatini (dabbling ducks, six genera, fifty-six species); Aythyini (pochards and allies, two genera, fifteen species); Mergini (mergansers, scoters, and allies, six genera, sixteen species); Oxyurini (stiff-tails, four genera, nine species); Somateriini (eiders, two genera, four species); Merganettini (torrent duck); Anseranatini (pied goose)

Geographical location: Worldwide, except Antarctica

Habitat: Freshwater ponds, shallow lakes, and marshes; some also live in coastal marshes and estuaries

Gestational period: Clutches of eight to twelve eggs are incubated approximately one month

Life span: Eight to twenty-three years for dabbling ducks, twelve to twenty-one years for diving ducks, eleven to eighteen years for sea ducks

Special anatomy: Webbed feet, broad bills, overlapping (scutellate) scales on legs they are named for the sound of their wings during flight and for their characteristic whistle when taking off. Like the wood ducks to which they are sometimes allied, whistling ducks frequent forested swamps and rivers where they feed by straining organisms from the water surface.

The smallest and perhaps the most unusual tribe of ducks is the Merganettini, which consists of a single species, the torrent duck. This long-legged duck seems to be the Latin American equivalent of the harlequin, as it makes its home in swift-flowing streams of the high Andes.

Several intermediate forms of waterfowl also take the name duck. The shelduck and sheldgeese of the tribe Tadorini are coastal forms that resemble geese but are probably related to the dabbling ducks. Mostly Old World in distribution, the males have the bright wing patch characteristic of the dabblers. They are larger ducks with heavy bills for pulling up rotting roots and tubers or extracting molluscs from bottom mud. The tribe also includes the steamer ducks of South America and the Falkland Islands. Although powerful swimmers and divers, two of the three steamer species are flightless. They typically wade in shallows or walk on water lilies and other aquatic plants as they feed on a variety of organisms. The magpie goose (*Anseranas semipalmata*) of Australia (tribe Anseranatini) is a gooselike duck with a long hind toe and slightly webbed feet. It differs from ducks in having a gradual molt so that a flightless period does not occur. Like geese, the magpie goose spends much time on land foraging for grains and other vegetation matter.

Food, Hunting, and Recreational Opportunities Offered by Waterfowl

All ducks are of interest to wildlife enthusiasts and birders because of their spectacular massed migrations, colorful males, and often intricate behaviors. For centuries, native peoples on all continents have found many species to be an important seasonal food source, eating the meat of adults and young and harvesting eggs. Eiderdown is famous for its heat-retaining qualities and has been used by generations of northern peoples for stuffing pillows, mattresses, quilts, and outerwear.

The ever-increasing impact of hunting resulted in a decline of many of the more desirable species which led, in turn, to the establishment of hunting regulations which strictly regulate bag limits. Since these regulations were established early in the twentieth century, the populations of most ducks have recovered and are now the basis of the single most popular and economically important sport hunting in North America.

—Dwight G. Smith

See also: Birds; Domestication; Feathers; Flight; Geese; Groups; Hierarchies; Imprinting; Lakes and rivers; Migration; Molting and shedding; Nesting; Respiration in birds; Swamps and marshes; Swans; Tidepools and beaches; Wings.

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EAGLES

Type of animal science: Classification
Fields of study: Anatomy, ornithology

The eagles of the world are swift, powerful birds of prey long admired for their power, ferocity, and regal bearing. All are characterized by a large, hooked bill, keen vision (called "eagle-eyed sight"), and long, broad wings for lifting prey.

Principal Terms

ACCIPITRIDAE: family of Falconiformes that includes the eagles, along with harriers, kites, accipiters, and hawks

EAGLE: name given to large to very large, diurnal birds of prey; although not a strictly taxonomic term, most eagles have large, hooked bills and long, broad wings, and are entirely carnivorous

FALCONIFORMES: avian order of diurnal birds of prey that includes the hawks, eagles, kites, falcons, and harriers

TALONS: the long, curved, and sharply pointed claws of a bird of prey; used for slashing and killing, for holding and carrying of prey, and for defense

TERRITORIALITY: all behaviors involved with the establishment, proclamation, and defense of a specific area; territory is the defended part of a home range

The eagles of the world are swift, powerful birds of prey long admired for their power, ferocity, and regal bearing. They range in size from the great Philippine eagle (*Pithecanthropos jefferyi*) of the Philippines and New Guinea to the Nicobar serpent-eagle (*Spilornis klossi*), which occurs only on the Great Nicobar Island off the coast of Malaysia, and is smaller than many hawks.

In the strict taxonomic sense, the term "eagle" is a generic term applied to any large, swift, and powerful bird or group of birds of prey. All are characterized by a large, hooked bill, keen vision (called "eagle-eyed sight"), and long, broad wings for lifting prey. The name "eagle" was originally applied to the largest birds of prey found in the northern hemispheres. The discovery of many species of tropical eagles that are smaller than some hawk species removed the eagle as the king of birds, at least in size. Furthermore, the four groups of birds of prey that bear the name eagle are apparently not very closely related; some are more similar to harriers, others to kites, and still others to buteo hawks.

Taxonomically, all eagles are placed in the avian order Falconiformes, which is split into two families, the slimmer and swifter falcons in the family Falconidae and the others—the harriers, kites, accipiters, and eagles—in the family Accipitrinae. The four groups of eagles include the sea eagles, snake or serpent eagles, crested eagles, and booted eagles.

The Fish Eagles

The eleven species of sea and fish eagles seem mostly closely related to the kites. They occur along all the world's oceans and inland along large lakes and waterways, being absent only from Latin America. All have bare legs and show white in their heads or backs. Two of the most familiar and most widespread of the sea eagles include the bald eagle (*Haliaetus leucocephalus*) of North America and the European sea eagle (*Haliaetus albicilla*) of Eurasia. The largest is the Steller's sea eagle (*Haliaetus pelagicus*), which has an eight-foot wingspan and can weigh fifteen pounds. These powerful eagles feed mainly on live or dead fish but are capable of taking sea calves. The smallest fish eagle is the fish and crab-eating Madagascar fish eagle (*Haliaetus vociferoides*), which is now confined to the northwest coast of Madagascar.

Ecologically, sea eagles often build large stick nests in trees, in sea stacks, or on ledges. Fish and offal are dietary mainstays, along with an occasional gull or other water bird. They scavenge carrion along beaches, waterways, and offshore islands. Some are kleptoparasites that pirate food from other birds such as the osprey. Sizable numbers of bald eagles winter along the coasts of the Pacific Northwest. Notable wintering concentrations also occur in the Wasatch front range of the Rockies, where their food is mostly jackrabbits and other medium-sized mammals. Because of the dietary mainstay of fish, the sea and fish eagles have proven most susceptible to chlorinated hydrocarbon pollution, which accumulates in their tissues and reduces nesting success and productivity. Several are considered threatened or endangered, although captive breeding programs have successfully led to the recovery of the bald eagle. Included in this group is the vulturine fish eagle (*Gypohierax angolensis*) of southern Africa, which feeds on the pericarp of oil palm nuts along with some crabs and fish. Some authorities prefer to regard this species separately from the bald eagle and rename it the palm-nut vulture.

The Snake and Serpent Eagles

The fifteen species of snake and serpent eagles are a primitive group that have long wings and bare legs as an adaptation for killing venomous snakes. They belong to the subfamily Circaetinae and may be allied to kites. All are Old World species; most live in Africa and southeast Asia, but one, the short-toed snake eagle (*Circaetus gallicus*) occurs as a breeding species across much of Europe. Serpent eagles are generally large, brown or grayish eagles with yellow eyes, and short toes adapted for killing reptiles. They feed almost entirely on snakes, lizards, and amphibians, mainly frogs. Serpent eagles hunt entirely by the perch-and-wait method and most have little difficulty in killing even the larger venomous snakes of Africa and southeast Asia. They are not immune to venom, but rather depend on quickness to avoid being fatally bitten. The European serpent or short-toed eagle (*Circaetus gallicus*) is also included in this group, although it seems more closely related to harriers. Another aberrant form is the dark, long-winged bateleur (*Terathopius ecudatus*) of central and southern Africa. Unlike the other snake eagles, the bateleur hunts for small mammals and reptiles across the African plains and savanna in low, searching flights, attacking in tight downward spirals. Groups of immature bateleurs gather to feed on abundant insects, especially at termite mounds when alates emerge.

The Crested Eagles

A third eagle group consists of four species of buzzardlike eagles, which are closely related to the buteo hawks and sometimes grouped with them in the subfamily Buteoninae. These include

Eagle Facts

Classification:
Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Class: Aves
Order: Falconiformes
Families: Accipitridae
Subfamilies: Buteoninae, Circaëtinae
Genus and species: Twenty-one genera and fifty-three species, including *Haliaetus leucocephalus* (bald eagle), *Aquila chysaetos* (golden eagle), *Harpia harpyja* (harpy eagle), *Haliaetus pelagicus* (Steller's sea eagle)
Geographical location: All continents except Antarctica
Habitat: Woods and woodland edges, grasslands, near water for fish-eating species
Gestational period: Thirty to forty-five days, depending on species
Life span: Twenty to thirty years in the wild; up to fifty years in captivity
Special anatomy: Talons; exceptionally keen eyesight; strong legs; sharp, hooked bills

The bald eagle became endangered through the use of DDT, which builds up toxicity as it makes its way up the food chain. Runoff into streams and lakes caused the pesticide to accumulate in the flesh of the fish caught and eaten by the eagles. (Corbis)

the largest and most powerful birds of prey in the world, the huge harpy and crested eagles and their relatives such as the harpy eagle (*Harpya harpyja*) of South America and the great Philippine eagle of the Philippines and New Guinea. These large to very large raptors can take monkeys and other medium-sized and larger mammals of the tropical rain forests.

Booted or True Eagles

The largest eagle group is the "booted" or aquiline eagles, which consists of thirty-three species found worldwide. Sometimes placed in the subfamily Aquilinae, all are large and some are very large, powerful birds of prey. They differ from all other eagles in having a fully feathered tarsus down to their toes. Booted eagles are more common in the Old World, but several species, such as the golden eagle (*Aquila chrysaetos*), are very widely distributed. The booted eagles also include many small forest species, such as the *spizaetus* species of Asia and South America. Many of these forest eagles have shorter wings and long tails for hunting birds and mammals within the triple-tiered forest canopy.

Most booted eagles are entirely carnivorous, taking a wide variety of vertebrates, especially medium-sized mammals and birds. The largest species, such as the Siberian golden eagle (a subspecies of the golden eagle) take wolves, foxes, and other large mammals. More specialized booted eagles include the black eagle (*Ictinateus malayensis*) of southeast Asia, which regularly robs nests of eggs and young, and the tawny eagle (*Aquila rapax*) of Africa and India, which seems to consume everything from termites to carrion up to dead elephants.

Conservation and Economic Importance of Eagles

Even after decades of environmental education, humans still remain the greatest threat to the eagles of the world. Many eagles are shot each year by hunters and sportsman who prefer live target practice. As with other birds of prey, some eagles are hunted for the taxidermy market, a few are taken for falconry, and some are captured as part of the lucrative international trade in zoo specimens, despite the fact that eagles are protected in most countries of the world.

Because of their position at the top the food chain, eagles accumulate pesticides and industrial wastes in their tissues, which can reduce nesting success and endangers the life of the eagle. Many toxic chemicals have been found in the eagles of the world, but the fish-eating eagles are most at risk.

Eagles need comparatively large home ranges and are constantly at risk from habitat destruction and fragmentation. The rapid demise of tropical rain forests places tropical eagles in the greatest risk. Several eagles are listed as endangered or threatened species in many areas of their range. Conservation efforts have included protective legislation, along with recovery programs that included captive breeding, nesting platforms, and reintroduction programs. Both the bald eagles and the white-tailed sea eagle (*Haliaetus albicilla*) in Scotland have benefitted from extensive and expensive recovery efforts. Conservation programs continue to target the protection of harpy eagles in Latin America and the great Philippine eagle of the Philippine Islands.

—Dwight G. Smith

See also: Beaks and bills; Birds; Endangered species; Feathers; Flight; Hawks; Molting and shedding; Nesting; Pollution effects; Respiration in birds; Wildlife management; Wings.

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EARS

Types of animal science: Anatomy, physiology
Fields of study: Anatomy, physiology

Although there is no standard structure identifying the variety of hearing organs found in the animal kingdom, an ear can be considered as any organ which has developed primarily for the purpose of hearing and which has the perception of sound as its principal function. Considering their usefulness, it is surprising that ears developed only in arthropods (crabs and insects) and in vertebrates. The simplest type of ear senses danger, detects prey, and helps locate mates. More complex ears are used in social communication and for detecting emotional expressions, such as the cries of a distressed infant.

Principal Terms

BASILAR MEMBRANE: the flexible partition connected to the cochlea along which are attached neural hair cells

CERCAL ORGANS: tufts of hair supplied with nerves, located on insects' abdomens, which respond to aerial sounds

COCHLEA: the vertebrate neural organ which transduces sound waves into nerve impulses

OSSICLES: the small bones of the middle ear

OTOLITH: a dense mineral frame supported by sensory hair cells immersed in aqueous fluid; used in the auditory system of lower animals to detect acceleration

TYMPANIC MEMBRANE: eardrum or other surface which serves the purpose of converting sound waves into mechanical vibration

Sound is vibration in a gas, liquid, or solid medium capable of being perceived by an ear when activating an auditory mechanism. For land-dwelling animals the medium is air, although some creatures also hear surface vibration transmitted through their skeletons. Aquatic life hears vibrations propagated through water, but sea mammals also perceive airborne sounds.

Due to the variety of structures and physical operating principles that exist among animals to detect sound, the ear will be defined, by its functional specialization, as an organ developed primarily for the purpose of hearing, with the reception of sound as its principal function. Although the primitive ears found in many lower life forms only faintly resemble the complicated hearing organs of higher vertebrates, they may be justifiably termed "ears" if the mechanism evolved to allow sound perception.

Invertebrate Ears

Only a few of the millions of insect species are known to possess organs capable of detecting sound. These include grasshoppers and crickets, cicadas, the waterboatman, moths, and mosquitoes. The ears of invertebrates are located on various parts of their bodies: Crickets and katydids have ears on the first walking legs; grasshoppers' ears are on the first segment of the abdomen; while the waterboatman hears through its first thorax segment. Moths have uncomplicated ears located either on the first segment of the abdomen or the rear part of the thorax; mosquitoes hear through sensors associated with their antennae. Insects can produce and perceive a variety of different highly species-specific sounds for communication and mating. Although not sensitive to pitch, information is conveyed by changes in intensity, duration, and sound patterns.

One of several different structures may serve as the hearing organ of insects: tympanal membranes, cercal organs, or antennae. The auditory system of grasshoppers and crickets is anatomically connected to the respiratory system, which conducts air from openings in the thorax to the muscles of the legs. Tympana, very thin membranes located on the forelegs or on the abdomen, are found on the body surface of a respiratory tube. Impinging sound waves cause the tympana to flex, which in turn induces tension changes in the attached scolophores, highly specialized sensory structures that transmit nerve impulses to the central nervous system. Moths have simple tympanal organs containing only two or four scolophores, while the highly developed auditory mechanism of cicadas may contain over a thousand sclorophores. The grasshopper ear, with about one hundred sclorophores, has a tympanic membrane hidden beneath the base of the wing cover.

Roaches and certain crickets respond to a wide range of sound frequencies by means of cercal organs located at the tip of the abdomen. The mosquito ear, located at the base of the antenna where an expanded sac contains many scolophores, is stimulated when the antenna shaft vibrates. The stimulation is greatest when the antenna is pointed toward the source of sound, which enables mosquitoes to determine the direction of sounds. For male mosquitoes, the frequency region which responds with the greatest intensity is the same as the hum of the female's vibrating wings, which enables him to find her when mating.

The bodies of spiders contain many slitlike openings, called lyriform organs, one of which (located on the next to last segment of each of the eight legs) is close to the joint between this segment and the last leg segment (tarsus). The tarsus is the sensing element which transmits vibrations to the lyriform organ. The small leg segments respond to the changing velocity of oscillating air particles, enabling some species to hear over a frequency range from 20 hertz to 45,000 hertz.

Fish and Amphibians

Although fish can detect very low frequency compression waves as bodily vibration, this is not considered hearing, since no ear is employed. For ears, diverse species utilize different mechanisms, either singly or in combination. These include the lateral line organ, otolith detectors, and the swim bladder. The lateral line organ is a line of sensory hair detectors, spaced along each side of the fish, that responds to water flow. These sensors are inefficient acoustic detectors because sound waves produce little relative motion between the fish and its environment, but the organ's extension along the body suggests that it locates the direction of a sound. Primitive fish, such as sharks, react to sounds in water with two mechanisms: macular organs, which give information about the orientation of the head, and the lateral-line apparatus.

It is in the bony fishes that an organ of hearing first appears among the vertebrates. Because fish flesh has a density close to that of water, however, sound detection becomes problematic; the waves tend to pass right through the fish's body. Consequently, accessories to hearing, such as the otolith detector, developed to make the fish ear more effective. The dense minerals of this detector respond sluggishly to incoming waves, resulting in an out-of-phase vibration with the surrounding tissue; the relative motion stimulates the hair cells, enabling fish to hear, albeit inefficiently. In some species the efficiency is increased by means of an air sac, a discontinuity whose surface oscillation, responding to incoming vibration, is detected by special receptors. The frequency of greatest sensitivity for most fish species is about 350 hertz, with an upper limit between 1000 and 3000 hertz.

Frogs have no visible external ears, but they possess an otic notch on either side of the skull, which houses the eardrum, and a well-developed middle ear structure. The eardrum consists of a disk of skin-covered cartilage connected to the oval window by a bony rod. When the eardrum vibrates, this rod transmits the vibration to the fluids of the inner ear, which in turn stimulates sensory hair cells similar to those found in other vertebrates. Experiments indicate that bullfrogs are capable of hearing frequencies between 50 and 3,500 hertz.

Salamanders, lacking the otic notch, eardrum, and middle-ear cavity of frogs, transmit sound through the forelimb and shoulder blade to a muscle that passes from the shoulder blade to a bony structure connected to the inner ear.

Reptiles

Lizards are the lowest form of vertebrate possessing cochlea in which different regions respond to different frequencies of sound, thus enabling pitch differentiation. Studies have shown that most lizards have good auditory sensitivity over a range from 100 to 4,000 hertz. As with frogs, a lizard has no visible outer ear, but possesses a tympanic membrane connected to the oval window of the inner ear through a two-part ossicular chain. This chain consists of a bony part ending in a stirrup at the oval window and a cartilage structure embedded into the tympanic membrane. Although the inner ear contains a basilar membrane and hair cells which are stimulated when the fluid of the inner ear vibrates, the form of the basilar membrane is different from that of frogs. Among lizards, hair cell stimulation by two or more different arrangements within the same cochlea is not uncommon; one method provides greater sensitivity, while the parallel system is more resistant to possible damage from very loud sounds.

Image Not Available

Although snakes evolved from primitive lizards, the fact that they show no external ear and their seeming indifference to aerial sound has led to the supposition that they are deaf and only perceive vibrations transmitted through the ground. Actually, snakes can perceive aerial sounds through a device consisting of a thin bony plate, detached from the skull but held in place by ligaments, which vibrates in response to sound waves. A bony structure transmits this vibration through a stirruplike plate to the oval window. Because this mechanism is somewhat inefficient, snakes can perceive only low-frequency tones lying in the range from about 100 to 700 hertz. By the relative intensity of sound in each ear, snakes can localize the direction of a sound.

The turtle's ear is not a degenerate organ as is sometimes assumed; its hearing acuity is quite good in the low-frequency range. A plate of cartilage on each side of the head serves as a tympanic membrane. The ossicular chain consists of a two-element bony structure, ending in a stirrup which covers the oval window. As the stirrup moves inward and outward in response to a sound wave, it causes the fluid in the otic capsule (the inner ear) to move back and forth, thus activating the hair cells. This rather bulky mechanism is quite effective at low frequencies, but the sensitivity to sound decreases rapidly as frequency increases. Experiments indicate that the turtle's ear can respond to aerial sounds having frequencies between 100 and 1,200 hertz, with the greatest sensitivity for tones below 500 hertz.

Crocodile and alligator ears, while obviously reptilian, have several unusual features. A short, external passageway with a closeable earlid leads to a tympanic membrane on the surface of the middle ear. The left and right middle ear cavities are connected by an internal air channel, enabling sound entering one ear to reach the other. A typical reptilian ossicular chain connects the tympanic membrane to the oval window at the entrance to the otic capsule. The inner ear is highly developed, containing approximately eleven thousand sensory hair cells (seven times as many as found in the most sophisticated lizard ear). Studies indicate that crocodilian ears respond to frequencies between 20 and 15,000 hertz.

Birds and Mammals

Avian ears are similar to reptilian ears, but the longer and more sensitive cochlea gives birds an enhanced ability to discriminate pitch. The outer ear consists of a short tube, with a muscle to partially close the opening. The eardrum of songbirds consists of two separate membranes, an outer (which protects the inner), and an inner membrane attached to the ossicular chain. As in lizards, the ossicular chain consists of a cartilaginous structure at the eardrum connected to a bony column ending in a stirrup. The inner ear is similar to that of crocodiles, with a basilar membrane enclosed within the cochlea. Studies of the hearing of small birds indicate a hearing range from about 100 hertz to above 12,000 hertz, with the greatest sensitivity in the low and middle frequencies. It is believed that certain species use echolocation when flying in the dark; owls are known to locate prey solely by means of auditory cues.

The ear of mammals is typically composed of three parts: an outer ear, a middle ear, and an inner ear. The outer ear is the visible portion (pinna) and ear canal, which terminates in the tympanic membrane, or eardrum. The middle ear is a small chamber containing three small bones (auditory ossicles), the hammer, anvil, and stirrup. The hammer is attached to the eardrum and transmits vibration through the anvil to the stirrup. The stirrup's footplate covers the oval window—the entrance to the inner ear. The inner ear (cochlea), re-

Echolocation

Echolocation is the use, by certain species, of self-generated reflected sounds to "see" their environment. This animal sonar is found in whales, dolphins, shrews, and a few birds, but is particularly well developed in bats. They emit short bursts of high-frequency sound well above the range of human hearing and decode the echoes returning from nearby objects. Their perceived sonic environment enables them to navigate, track prey, avoid predators, and perhaps to communicate. The echolocation pulses of bats are produced by vibrating membranes in the larynx and are emitted via the nose or mouth. The ultrasonic signals spread out in a cone-shaped region from the bat's head. When the signals encounter an object, the sound is reflected, scattered, absorbed, or reradiated. The returned signals are received by the bat's large external ears and transmitted through the middle ear to the inner ear, both of which are particularly sensitive to high-frequency sounds. In addition, the bat's auditory complex is acoustically isolated from the skull, enhancing its ability to determine the direction of a sound source by minute differences in the waves perceived by each ear. Typically, the region of maximum sensitivity of hearing for bats corresponds exactly with the most prominent frequencies of the emitted echolocation signals. The prominent frequencies may range from 12,000 hertz to more than 150,000 hertz.

Acoustic orientation is also important for mammals that inhabit deep or murky waters. Both dolphins and whales use echolocation for navigating and for finding food in the dark, or when visibility is low.

sembling a snail's shell, is a fluid-filled chamber which transforms mechanical vibrations into nerve impulses, which are sent to the brain. The cochlea is divided lengthwise into two compartments, separated by a slightly flexible fluid-filled duct. On the duct's lower surface is the basilar membrane, containing thousands of hair cells, which create nerve impulses when stimulated. Aerial sounds cause the tympanic membrane to vibrate; this vibration is transmitted to the fluid of the inner ear by the ossicular chain. The vibrating cochlear fluid induces traveling waves on the basilar membrane, flexing the hair cells, causing them to send nerve impulses to the brain. The brain decodes this information as sound; the frequency information is encoded by the place along the basilar membrane responding to the vibration, while the loudness is proportional to the number of nerve firings per second.

The sensitivity and hearing range vary among species, as they are dependent upon the size and mass of the moving parts. Dogs and cats can perceive frequencies as high as 40,000 hertz, and bats can detect sounds above 150,000 hertz. Adult human ears are capable of perceiving sound waves having frequencies between 16 hertz and 16,000 hertz; chimpanzees and monkeys can hear frequencies above 30,000 hertz. The delicacy and precision of pitch discrimination, dependent upon the number and distribution of hair cells along the basilar membrane, are most highly developed in primates.

In the course of adapting to the sea, marine mammals have eliminated or greatly reduced the size of their pinna and acquired a movable flap to close the outer ear when diving. Seals have remarkably acute underwater hearing, responding to frequencies up to 160,000 hertz, without sacrificing the ability to hear airborne sounds. The whale, however, has sacrificed aerial hearing for increased underwater discrimination. The external ear opening is a pinhole, the eardrum serves no useful purpose, and the bones of the middle ear are too massive to respond well to high frequencies. Underwater sounds pass through the tissues of the head directly to the middle and inner ear, the fat-filled cavity of the lower jaw helping funnel low-frequency sounds. The ossicle mass functions like the otolithic organ of fish; inertia causes the ossicles to vibrate out of phase with the surrounding tissues when sound energy is present. This relative motion is conducted to the cochlear fluid through the stirrup and excites the hair cells of the inner ear. The middle and inner ear are housed within a heavy solid complex, which is not connected directly to the skull but supported by air sacs connecting to the respiratory tract. These sacs acoustically isolate each ear from the other, and isolate both ears from sounds produced by the animal itself. Because they use echolocation, cetaceans have acute hearing and can perceive sounds up to at least 100,000 hertz; the bottle-nosed dolphin can hear to about 150,000 hertz.

—George R. Plitnik

See also: Anatomy; Beaks and bills; Bone and cartilage; Brain; Claws, nails, and hooves; Digestive tract; Endoskeletons; Exoskeletons; Eyes; Fins and flippers; Hearing; Immune system; Kidneys and other excretory structures; Lungs, gills, and tracheas; Muscles in invertebrates; Muscles in vertebrates; Nervous systems of vertebrates; Noses; Physiology; Reproductive system of female mammals; Reproductive system of male mammals; Respiratory system; Sense organs; Skin; Tails; Teeth, fangs, and tusks; Tentacles; Vocalizations; Wings.

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ECHINODERMS

Type of animal science: Classification
Fields of study: Anatomy, invertebrate biology, physiology

Echinoderms are radially symmetrical, free-moving marine organisms, such as starfishes, sea urchins, brittle stars, sea cucumbers, and sea lilies.

Principal Terms

BILATERAL SYMMETRY: an arrangement of body parts of an organism down a central axis which, when divided down the midline, produces right and left mirror images

CALCAREOUS: a material composed primarily of calcium compounds

MADREPORITE: a fine-meshed sieve that opens from the sea water into the water vascular system of the echinoderms

METAMORPHOSIS: the transformation of a larval form into an adult form

RADIAL SYMMETRY: an arrangement of body parts of an organism like the pieces of a pie around an imaginary central axis

The echinoderms represent a biological puzzle for zoologists. Biologists generally agree that bilateral symmetry is adaptive for free-moving animals and radial symmetry is adaptive for sedentary animals, but the echinoderms are free-moving yet exhibit radial symmetry. Since the echinoderm larval stages are bilaterally symmetrical, they obviously evolved from bilateral ancestry; however, the larvae metamorphose into radially symmetrical adults. The echinoderms live in marine environments and include a varied group that is considerably different from all other members of the animal kingdom. Echinoderms include the starfishes, sea urchins, brittle stars, sea cucumbers, and sea lilies. A calcareous skeleton is present in all members of the phylum, and their name is derived from the presence of external spines or protuberances.

General Characteristics of the Echinoderms

Because of the tremendous diversity in this group of animals, a complete description of all echinoderm characteristics is beyond the scope of this article. Externally, the arms or rays are joined at the center to form a disc that bears the madreporite. Many echinoderms are protected from predators by a spiny skeleton made up of calcareous plates just below the epidermis. Many of the plates bear tubercles (bumps) and spines. In addition, predators are often discouraged by the presence of pedicellariae (tiny pincers) scattered over the body. When stimulated, these snap vigorously and remain shut for several days on anything they catch.

The mouth is in the center of the ventral surface and is surrounded by a membranous area, the peristome. The mouth opens directly into a large cardiac stomach, which in turn opens into a smaller pyloric stomach. A small intestine extends upward from the pyloric stomach and ends at an anus in the middle of the upper surface of the disc. Five gastric glands extend out of the rays and open into the pyloric stomach. When feeding, the cardiac stomach everts through the mouth and spreads over the food. A fluid containing digestive enzymes is secreted and rapidly breaks down the food materials. The nervous system is composed of a nerve ring around the mouth and five radial nerves to the lower epidermis. Other nerve fibers are located in the walls of the digestive tract and inside the upper body wall. The nervous system exhibits reciprocal inhibition. The nerve centers on one side of the body inhibit those on the other side, permitting the animal to move in a coordinated manner in one direction.

The circulatory system is composed of circular and radial vessels filled with a fluid similar to that of the body cavity and which is very different from sea water. The vessels lie above the nervous system and are enclosed in their own body cavity. Some of these vessels have been observed to contract. A pair of gonads is located in the base of each ray, with one on each of the gastric glands. These gonads hang free in the body cavity except where they are attached by a short duct to a reproductive pore opening externally between the bases of adjacent rays.

Representative Echinoderms

Most starfish (class Asteroidea) have five rays and a relatively small disc, but in some species the body is pentagonal rather than star-shaped and the disc is large relative to the rays. The animals in one genus, *Leptasterias*, have six rays, while the number of rays in other starfishes may be as high as twenty-five or fifty. In general, if the number of rays is greater than seven, the number will be variable within a species. When the number exceeds five, the embryo develops five rays first and the others later. Most starfishes eat only small bivalves and other organisms that are swallowed whole. Many of the larger species, ranging from one to three feet in diameter, feed primarily on other echinoderms.

Sea lilies (class Crinoidea) are echinoderms that attach to the ocean floor by a stalk. The mouth is directed upward, and the anus is located to one side. The rays generally branch to form graceful patterns. Ciliated grooves flanked on both sides by tube feet without suckers extend out of the mouth along the upper surfaces of all the rays and branches. Food is trapped and swallowed when tiny organisms and food particles are pushed against the ciliated groove by the action of the tube feet. Movement in sea lilies is restricted to spreading and folding together of the branches and postural changes of the body. In the feather stars, the larvae attach and

Echinoderm Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Echinodermata
Subphylum: Pelmatozoa
Classes: Crinoidea (sea lilies and sea feathers), Heterostella (extinct), Cystidea (extinct), Blastoidea (extinct), Edrioasteroidea (extinct)
Subphylum: Eleutherozoa (stemless unattached echinoderms)
Classes: Holothuroidea (sea cucumbers; armless, poorly developed skeleton); Echinoidea (sea urchins and sand dollars; armless, well-developed skeleton); Asteroidea (starfishes; arms, well-developed skeleton, locomotion with tube feet); Ophiuroidea (brittle stars; arms, flexible skeleton, locomotion with prehension); Concentricycloidea (sea daisies; armless, disc-shaped with marginal skeleton); Ophiocistioidea (extinct)
Orders: Holothuroidea (five living orders); Echinoidea (three living orders, five extinct orders); Asteroidea (three living orders, five extinct orders); Ophiuroidea (two living orders); Concentricycloidea (one living order); Ophiocistioidea (one extinct order)

Geographical location: Found all over the world

Habitat: Marine, from the shoreline to the ocean depths

Gestational period: Varies among species, but most species lay eggs within a few days after fertilization; eggs usually hatch within a few days to a few weeks after being deposited

Life span: Varies among species; can be as short as a year and up to several years

Special anatomy: Body unsegmented with radial, pentamerous (five or more radiating areas) symmetry; no head or brain and few specialized sensory organs; endoskeleton of calcareous ossicles with spines; a unique water vascular system that extends from the body surface as a series of tube feet; excretory system is absent; development through free-swimming bilateral larval stages that metamorphose into radial adult grow a short stalk like that of the sea lilies, but later break loose. The general anatomy and method of feeding is unchanged, but the feather stars differ from the sea lilies in their locomotion. Feather stars can crawl through vegetation using the rays as prehensile organs, and they can swim by raising and lowering the ten arms more than one hundred times per minute.

Echinoderms, such as starfish, are unusual in that they are radially symmetrical yet are capable of movement. Most animals that move are bilaterally symmetrical. (PhotoDisc)

Sea cucumbers (class Holothuroidea) creep or burrow in the mud or sand. Since the calcareous plates are small, the body is soft and flexible. The body is elongated between the mouth and anus, but one side usually becomes the permanent lower side, causing the radial symmetry to be imperfect. While five rows of tube feet extend from mouth to anus, often only three of the rows have suckers and are used for locomotion. A circle of branched tentacles form from the tube feet near the mouth. Sea cucumbers are notable for their ability to throw away their viscera. When environmental conditions are unfavorable, the sea cucumber contracts violently and ejects the entire digestive system, which can later be regenerated.

The skeletons of the echinoids (class Echinoidea) form rigid boxes. Five grooves with tube feet radiate from the mouth up around the sides and end near the anus. The tube feet on the upper surface are often long and filamentous and apparently used for respiration, while the lower tube feet usually have suckers and are utilized in locomotion. Sea urchins possess numerous long spines, some of which are used to aid the tube feet in walking. The urchins move about slowly, using their five sharp teeth to scrape and chew whatever they encounter. The sand dollars are a group of much-flattened echinioids. They usually creep about slowly on their short lower spines under the surface of the sand.

Brittle stars (class Ophiuroidea) possess slender rays attached to a circular disc. Each ray is composed of a row of large cylindrical skeletal pieces joined together by short, powerful muscles. Each ray is very supple, and the tube feet are poorly developed. Brittle stars move by pulling or pushing on surrounding objects, and thus slither like a snake. Most brittle stars feed on debris and mud, but some capture prey with their prehensile rays and bring it to the mouth, which opens into a simple saclike stomach. Undigested remains are eliminated through the mouth because no other digestive organs are present.

The group commonly called sea daisies (class

The Echinoderm Water Vascular System

One of the unique characteristics of the echinoderms is the presence of a water vascular system. This system is primarily utilized for locomotion and food gathering, but it also has respiratory and excretory functions. A prime example of this system is illustrated in the starfishes. Starfishes move slowly on a multitude of tube feet, delicate projections that end in suckers. Each tube foot is connected to a radial canal by a small lateral canal. The five radial canals join to form a circular canal, and from this a stone canal leads upward to the madreporite. The tube feet project from deep grooves along the lower surface of each ray. The tube feet are arranged in two longitudinal rows, which are staggered to look like a double row. Each tube foot operates as an independent hydraulic mechanism. The foot cavity extends inward through the body wall and expands inside the body as a bulb or ampulla. When the muscles lining the ampulla contract, the fluid in the cavity is forced into the foot, which expands to create suction. A suction cup at the end of the foot sticks tightly once it is pressed against a smooth surface. The foot is released when longitudinal muscle fibers contract and lift the edges of the sucker. The tube feet work synchronously to produce a creeping motion. Each foot elongates in the direction of motion, attaches to the bottom, and then is swung under the body so as to propel the body forward.

Concentricycloidea) is a class of echinoderms discovered in 1986 off the coast of New Zealand. They have no arms, and the tube feet are located around the periphery of the disc rather than in grooved areas, as in other echinoderms. Only two species have been identified. One has a small, saclike stomach but no intestine or anus, and the other lacks any digestive organs. This latter species apparently absorbs nutrients from the environment.

—D. R. Gossett

See also: Circulatory systems of invertebrates; Clams and oysters; Digestive tract; Endoskeletons; Invertebrates; Jellyfish; Marine animals; Mollusks.

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ECOLOGICAL NICHES

Type of animal science: Ecology
Field of study: Evolutionary science

An ecological niche is the physical space in which an animal lives and all the interactions with the other living organisms and components of its environment. Ecological niches are important in the preservation of organisms that are vulnerable to certain activities of human beings.

Principal Terms

COMMUNITY: all the populations of plant and animal species living and interacting in a given habitat or area at a given time

ENVIRONMENT: all the external conditions that affect an organism or other specified system during its lifetime

FOOD PYRAMID: diagram representing organisms of a particular type that can be supported at each trophic level from a given input of solar energy in food chains and food webs

HABITAT: place or type of place where an organism or community of organisms naturally thrives

ORGANISM: any form of life

TROPHIC LEVEL: a level in a food chain or food web at which all organisms consume the same general types of food

The idea of the niche probably had its first roots in ecology in 1910. At that time, Roswell Johnson wrote that different species utilize different niches in the environment. He theorized that individuals of a particular species are only in certain places because of food supply and environmental factors that limit their distribution in an area. Later, in 1924, Joseph Grinnel developed his concept of niche that centered on an organism's distribution having limits set on it by climatic and physical barriers. At the same time, Charles Elton was defining his own idea of niche. His description of niche involved the way an organism makes its living—in particular, how it gathers food.

Trophic Levels

For many years, ecologists focused on Elton's definition and referred to niche in terms of an organism's place in the food pyramid. The food pyramid is a simplified scheme in which organisms interact with one another while obtaining food. The food pyramid is represented as a triangle, often with four horizontal divisions, each division being a different trophic level.

The base of the food pyramid is the first trophic level and contains the primary producers: photosynthetic plants. At the second trophic level are the primary consumers. These are the herbivores, such as deer and rabbits, which feed directly on the primary producers. Secondary consumers are found at the third trophic level. This third trophic level contains carnivores, such as the mountain lion. The members of the uppermost trophic level are the scavengers and decomposers, including hyenas, buzzards, fungi, and bacteria. The organisms in this trophic level break down all the nutrients (such as carbon and nitrogen) in the bodies of plants and animals and return them to the soil to be absorbed and used by plants.

It should be noted that no ecosystem actually has a simple and well-defined food pyramid. Many organisms interact with more organisms than those at the adjacent trophic levels. For example, a coyote could be considered to belong to the third trophic level with the carnivores, but the coyote also occasionally feeds on fruits and other primary producers. Basically, all living things are dependent on the first trophic level, because it alone has the capability to convert solar energy to energy found in, for example, glucose and starch. The food pyramid takes the geometric form of a triangle to show the flow of energy through a system.

Photosynthetic plants lose 10 percent of the energy they absorb from the sun as they convert solar energy into glucose and starch. In turn, the herbivores can convert and use only 90 percent of the energy they obtain by eating plants. Hence, less energy is found at each higher trophic level. Because of this reduction in energy, fewer organisms can be supported by each higher trophic level. Consequently, the sections of the pyramid get smaller at each higher trophic level, representing the decreasing levels of energy and number of members.

Interrelationships Among Organisms

Through the years, two concepts of niche have evolved in ecology. The first is the place niche, the physical space in which an organism lives. The second is the ecological niche, and it encompasses the particular location occupied by an organism and its functional role in the community.

The functional role of a species is not limited to its placement along a food pyramid; it also includes the interactions of a species with other organisms while obtaining food. For example, the methods used to tolerate the physical factors of its environment, such as climate, water, nutrients, soils, parasites, and the like, are all part of its functional role. In other words, the ecological niche of an organism is its natural history: all the interactions and interrelationships of the species with other organisms and the environment.

The study of the interrelationships among organisms has been the focus of ecological studies since the 1960's. Before this time, researchers had focused on the food pyramid and its effect on population changes of merely a single species. One example, the classic population study of the lynx and the snowshoe hare of Canada, originally focused on the interactions of the species in the food pyramid. It was discovered that the lynx had a ten-year population cycle closely following the population cycle of its prey, the snowshoe hare. The lynx population appeared to rise, causing a decline in the population of the snowshoe hare. In the investigations that followed, however, studies diverted the focus from the food pyramid to other elements of the niche of the two species. For example, the reproductive nature of the hare provided a contradiction to the simple predator-prey explanation. The hare has a faster rate of reproduction than the lynx. It seemed impossible that the significantly lower population of lynx could effectively place sufficient predator pressure on the hare to cause its drastic decline in numbers. Therefore, it appeared that the population dynamics of the hare and lynx was regulated by more than simply a predator-prey relationship.

Later studies of the lynx and hare suggested that the peaks and dives in the two populations may also be a factor of parasites of the hare that are carried by the lynx. A rise in the lynx population increases the carriers of parasites of the hare. Therefore, it is thought that, although the hare has a much greater reproduction rate than the lynx, the population of hares will still decline because of the combination of predation by the lynx and the increased frequency of parasites of the hare. This study involved looking at more than one dimension of the ecological niche of a species and broke away from concentrating on only the interactions between organisms in the food pyramid.

Niche Overlap

The goal of understanding how species interact with one another can also be better accomplished by defining the degree of niche overlap, the degree of the sharing of resources between two species. When two species use one or more of the same elements of an ecological niche, they exhibit interspecific competition. It was once believed that interspecific competition would always lead to survival of only the better competitor of the two species. That was the original concept of the principle of the competition exclusion law of ecology:

No two species can utilize the same ecological niche. It was conjectured that the weaker competitor would either migrate, begin using another resource not used by the stronger competitor, or become extinct. It is now believed that the end result of two species sharing elements of ecological niches may not always be exclusion.

Ecologists theorize that similar species do, in fact, coexist, despite the sharing of elements of their ecological niches, because of character displacement, which leads to a decrease in niche overlap. Character displacement involves a change in the morphological, behavioral, or physiological state of a species without geographical isolation. Character displacement occurs as a result of natural selection arising from competition between one or more ecologically similar species. Examples might be changes in mouth sizes so that they begin to feed on different sizes of the same food type, thereby decreasing competition.

Species Specialization

The more specialized a species, the more rigid it will be in terms of its ecological niche. A species that is general in terms of its ecological niche needs will be better able to find and use an alternative for the common element of the niche. Since a highly specialized species cannot substitute whatever is being used, it cannot compete as well as the other species. Therefore, a specialized species is more likely to become extinct.

For example, a panda is a very specialized feeder, eating mainly bamboo. If a pest is introduced into the environment that destroys bamboo, the panda will probably starve, being unable to switch to another food source. On the other hand, the coyote is a generalized feeder. It has a broad variety of food types that make up its diet. If humans initiate a pest-control program, killing the population of rabbits, the coyote will not fall victim to starvation, because it can switch to feeding predominantly on rodents, insects, fruits, and domesticated animals (including cats, dogs, and chickens). Hence, species with specialized ecological niche demands (specialists) are in greater danger of extinction than those with generalized needs (generalists). Although this fundamental difference in survival can be seen between specialists and generalists, it must be noted again that exclusion is not an inevitable result of competition. Many cases of ecologically similar species coexist.

When individuals of the same species compete for the same elements of the ecological niche, it is referred to as intraspecific competition. Intraspecific competition has the opposite effect of interspecific competition: niche generalizations. In increasing populations, the first inhabitants will have access to optimal resources. The opportunity for optimal resources decreases as the population increases; hence, intraspecific competition increases. Deviant individuals using marginal resources may slowly begin to use less optimal resources that are in less demand. That can lead to an increase in the diversity of ecological niches used by the species as a whole. In other words, the species may become more generalized and exploit wider varieties of niche elements.

Representing a situation on the opposite end of the spectrum from that of two organisms competing for the same dimension of an ecological niche is the vacant niche theory. This ecological principle states that when an organism is removed from its ecological niche, space, or any other dimension of the niche, another organism of the same or similar species will reinvade.

Field Research

Theoretical studies of ecological niches are abstract, since humans are limited to three-dimensional diagrams, and there are more than three dimensions to an ecological niche. This multidimensionality is referred to as the *n*-dimensional niche. This abstract *n*-dimensional niche can be studied mathematically and statistically, but ecology is mainly a field science. Therefore, the focus of techniques is on those used for field research of the ecological niche.

Research that attempts to describe all the elements of the *n*-dimensional ecological niche would require extensive observations. Yet, ecological niches are difficult to measure not only because of the plethora of data that would have to be collected but also because of the element of change in nature. The internal and external environment of an organism is always dynamic. Nothing in life is static, even if equilibrium has been established.

These constant fluctuations create daily and seasonal changes in space and ecological niches. Therefore, because of the constant fluctuations, any merely descriptive field observations would not be reliable depictions of an organism's ecological niche. Ecologists must also resort to quantitative data of measurable features of an organism's ecological niche. For example, the temperature, pH, light intensity, algae makeup, predators, and activity level of the organism are measurable features of an ecological niche in a pond community. The difficulty is in the collection of each of the necessary measurements making up an ecological niche. The ecologist would have to limit the data to a manageable number of specific dimensions of the niche based on conjecture and basic intuition. Such limitations often lead to incomplete and disconnected measurements that can at best only partially describe a few of the dimensions of the ecological niche.

Ecologists realize that complete observations and measurements of all the dimensions of an organism's ecological niche are unattainable. The focus in understanding how a species interacts with its community centers on determining the degree of niche overlap between any two species—in other words, the level of competition for niche space and resources. Studies of this niche overlap are typically limited to dimensions that can be quantitatively measured. Yet, there is still the problem of deciding which of the dimensions are involved in the competition between the two species. Again, the ecologist must usually rely on inherent knowledge about the two species in question. Often, researchers investigating niche competition measure no more than four ecological niche dimensions to determine the niche overlap in an attempt to understand how two individuals competing for the same space, resources, or other ecological niche features can coexist.

Field methods for observations and quantitative measurements of elements of ecological niches, niche overlap, and niche competition are probably endless. To name a few, describing an organism's niche may involve fecal samples to determine its diet, fecal samples of possible predators to identify its primary predator, animal and plant species checklists of its space niche along

Image Not Available

with soil components, climatic trends, and the like. Niche competition and overlap often can be studied first in the laboratory under controlled situations. One method might involve recording the population dynamics of the species as different elements in the ecological niche are manipulated to determine which is the better competitor and what is the resource that is most responsible for limiting the population size.

Niche and Community

The shift in meaning and study from merely space and trophic level placement in the food pyramid to ecological niche of *n* dimensions has been beneficial for the field of ecology. This focus on community ecology is obviously much more productive for the goal of ecology, the understanding of how all living organisms interact with one another, and with the nonliving elements in the environment.

Perhaps more important is the attempt to describe niches in terms of community ecology, which can be essential for some of humankind's confrontations with nature. For example, it becomes more and more apparent that synthetic chemicals are often too costly and too hazardous to continue using for control of crop pests and carriers of diseases. The goal is to control pests effectively with biological controls. Biological controls can involve the introduction of natural predators of the undesirable pest or the introduction of a virus or bacteria that eliminates the pest and is harmless to humans and wildlife.

The success of a biological control is directly proportional to the knowledge of the pest's *n*-dimensional ecological niche and the other organisms with which it comes in contact. A classic example of the havoc that can result from manipulations of nature without adequate ecological information is when Hawaii attempted to use biological controls to eradicate a population of snakes, which humans had accidentally introduced. The biological control used was the snake's natural predator, the mongoose. One very important dimension of the ecological niche of both species was ignored. One species was active only at night, while the other was active only during the day. Needless to say, this particular venture with a biological control was not a success.

Another relevant function of community-oriented studies of ecological niches involves endangered species. In addition to having aesthetic and potential medicinal values, an endangered organism may be a keystone species, a species on which the entire community depends. A keystone species is so integral to keeping a community healthy and functioning that if the species is obliterated, the community no longer operates properly and is not productive.

Habitat destruction has become the commonest cause of drastic population declines of endangered species. To enhance the habitat of the endangered species, it is undeniably beneficial to know what attracts a species to its particular preferred habitat. This knowledge involves the details of many of the dimensions of its ecological niche integral to its population distribution. Another common cause of endangering the survival of a species is when an introduced organism or exotic species competes for the same resources and displaces the native species. Solving such competition between native and introduced species would first involve determining niche overlap.

It is often stated that an ounce of prevention is worth a pound of cure. Thus, the researching and understanding of all the dimensions of ecological niches are integral components of preventing environmental manipulations by humankind that might lead to species extinction. Many science authorities have agreed that future research in ecology and related fields should focus on solving three main problems: species endangerment, soil erosion, and solid waste management.

This focus on research in ecology often means that studies of pristine communities, those undisturbed, will be the most helpful for future restoration projects. Although quantitative and qualitative descriptions of pristine areas seem to be unscientific at the time they are made, because there is no control or experimental group, they are often the most helpful for later investigations. For example, after a species has shown a drastic decline in its population, the information from the observations of the once-pristine area may help to uncover what niche dimension was altered, causing the significant population decrease.

—*Jessica O. Ellison*

See also: Adaptations and their mechanisms; Clines, hybrid zones, and introgression; Coevolution; Communities; Competition; Demographics; Ecology; Evolution: Animal life; Food chains and food webs; Groups; Habitats and biomes; Mark, release, and recapture methods; Migration; Population analysis; Population fluctuations; Population genetics; Predation; Urban and suburban wildlife.

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ECOLOGY

Type of animal science: Ecology
Fields of study: Evolutionary science, systematics (taxonomy)

Ecology is the study of the relationships of organisms to their environments. By examining those relationships in natural ecosystems, principles can be discovered which may help humankind understand its own role on this planet.

Principal Terms

ADAPTATION: a genetic (intrinsic) feature of an organism which, through natural selection, enhances its fitness in a given environment

COMMUNITY: all the populations that exist in a given habitat

ECOSYSTEM: the biological community in a given habitat, combined with all the physical properties of the environment in that habitat

ENVIRONMENT: all the forces and things external to an organism that directly affect it

FITNESS: the contribution of an organism to future generations; the perpetuation of its genes through reproduction

HABITAT: the place where an organism lives; for example, a pond or forest

NATURAL SELECTION: a change in the genetic makeup of a population as a result of different survival and reproduction rates (fitness) among its members

NICHE: the role of an organism in its environment; the sum of all factors that define its existence (temperature, energy requirements, and so on)

POPULATION: all the individuals in a habitat which are of the same species

RESOURCE: a requirement for life, such as space for living, food (for animals), or light (for plants), not including conditions such as temperature or salinity

Ecology is the study of how organisms relate to their natural environments. The two principal concerns of ecologists are the distribution and abundance of organisms: Why are animals, plants, and other organisms found where they are, and why are some common and others rare? These questions have their roots in the theory of evolution. In fact, it is difficult (and not often worthwhile) to separate modern ecological matters from the concerns of evolutionary biologists. Ecology can be divided according to several levels of organization: the individual organism, the population, the community, and the ecosystem.

Environment and Natural Selection

An ecologist views organisms as consequences of past natural selection brought about by their environments. That is, each organism represents an array of adaptations that can provide insight into the environmental pressures that resulted in its present form. Adaptations of organisms are also revealed by other features, such as the range of temperature an organism can tolerate, the amount of moisture it requires, or the variety of food it can exploit. Food and space for living are considered resources; factors such as temperature, light, and moisture are conditions which determine the rate of resource utilization. When ecologists have discovered the full range of resources and conditions necessary for an organism's existence, they have discovered its niche.

Many species, such as many insects and plants, have a large reproductive output. This compensates for high mortality imposed by natural selection. Other species, such as large mammals and birds, have fewer offspring. Many of these animals care for their young, thus increasing the chances that their offspring will survive to reproduce. These are two different strategies for success, based upon the principle that organisms have a finite energy budget. Energy acquired from food (animals) or sunlight (plants) must be partitioned among growth, maintenance, and reproduction. The greater the energy allocated to the care of offspring, for example, the fewer the offspring that can be produced.

The concept of an energy budget is a key to understanding evolutionary strategies of organisms, as well as the energetics of ecosystems. The amount of energy fixed and stored by an organism is called net production; this is the energy used for growth and reproduction. Net production is the difference between gross production (the amount of energy assimilated) and respiration (metabolic maintenance cost). The greater the respiration, the less energy will be left over for growth and reproduction. Endothermic animals, which physiologically regulate their body heat (mammals and birds), have a very high respiration rate relative to ectotherms (reptiles, amphibians, fish, and invertebrates), which cannot. Among endotherms, smaller animals have higher respiration rates than larger ones, because the ratio of body surface area (the area over which heat is exchanged with the environment) to volume (the size of the "furnace") decreases with increasing body size.

Demography and Population Regulation

Although single organisms can be studied with regard to adaptations, in nature most organisms exist in populations rather than as individuals. Some organisms reproduce asexually (that is, by forming clones), so that a single individual may spawn an entire population of genetically identical individuals. Populations of sexually reproducing organisms, however, have the property of genetic variability, since not all individuals are identical. That is, members of a population have slightly different niches and will therefore not all be equally capable of living in a given environment. This is the property upon which Charles Darwin's theory of natural selection depends: Because not all individuals are identical, some will have greater fitness than others. Those with superior fitness will reproduce in greater numbers and therefore will contribute more genes to successive generations. In nature, many species consist of populations occupying more than a single habitat. This constitutes a buffer against extinction: If one habitat is destroyed, the species will not become extinct, because it exists in other habitats.

Two dynamic features of populations are growth and regulation. Growth is simply the difference between birth and death rates, which can be positive (growing), negative (declining), or zero (in equilibrium). Every species has a genetic capacity for exponential (continuously accelerating) increase, which will express itself to varying degrees depending on environmental conditions: A population in its ideal environment will express this capacity more nearly than one in a less favorable environment. The rate of growth of a population is affected by its age structure—the proportion of individuals of different ages. For example, a population which is growing rapidly will have a higher proportion of juvenile individuals than one which is growing more slowly.

Populations may be regulated (so that they have equal birth and death rates) by a number of factors, all of which are sensitive to changes in population size. A population may be regulated by competition among its members for the resource that is in shortest supply (limiting). The largest population that can be sustained by the available resources is called the carrying capacity of the environment. A population of rodents, for example, might be limited by its food supply such that as the population grows and food runs out, the reproductive rate declines. Thus, the effect of food on population growth depends upon the population size relative to the limiting resource. Similarly, parasites that cause disease spread faster in large, dense populations than in smaller, more diffuse ones. Predators can also regulate populations of their prey by responding to changes in prey availability. Climate and catastrophic events such as storms may severely affect

Of particular concern in the study of ecology is the question of population size in relation to available resources. (Digital Stock)

populations, but their effect is not dependent upon density and is thus not considered regulatory.

Interactions Between Species

Competition occurs between, as well as within, species. Two species are said `to be in competition with each other if and only if they share a resource that is in short supply. If, however, they merely share a resource that is plentiful, then they are not really competing for it. Competition is thought to be a major force in determining how many species can coexist in natural communities. There are a number of alternative hypotheses, however, which involve such factors as evolutionary time, productivity (the energy base for a community), heterogeneity of the habitat, and physical harshness of the environment.

Predator-prey interactions are those in which the predator benefits from killing and consuming its prey. These differ from most parasite-host interactions in that parasites usually do not kill their hosts (a form of suicide for creatures that live inside other creatures). Similarly, most plant-eating animals (herbivores) do not kill the plants on which they feed. Many ecologists classify herbivores as parasites for this reason. There are exceptions, such as birds and rodents that eat seeds, and these can be classified as legitimate predator-prey interactions. Predators can influence the number of species in a community by affecting competition among their prey: If populations of competing species are lowered by predators so that they are below their carrying capacities, then there may be enough resources to support colonization by new species.

In many cases, the interaction between two species is mutually beneficial. Mutualism is often thought to arise as a result of closely linked evolutionary histories (coevolution) of different species. Termites harbor protozoans in their guts that produce an enzyme which can break down cellulose in wood. The protozoans thus are provided with a habitat, and termites are able to derive nourishment from wood. Some acacia trees in the tropics have hollow thorns which provide a habitat for ants. In return, the ants defend the trees from other insects which would otherwise damage or defoliate them.

Communities of organisms are composed of many populations that may interact with one another in a variety of ways: predation, competition, mutualism, parasitism, and so on. The composition of communities changes over time through the process of succession. In terrestrial communities, bare rock may be weathered and broken down by bacteria and other organisms until it becomes soil. Plants can then invade and colonize this newly formed soil, which in turn provides food and habitat for animals. The developing community goes through a series of stages, the nature of which depends on local climatic conditions, until it reaches a kind of equilibrium. In many cases this equilibrium stage, called climax, is a mature forest. Aquatic succession essentially is a process of becoming a terrestrial community. The basin of a lake, for example, will gradually be filled with silt from terrestrial runoff and accumulated dead organic material from populations of organisms within the lake itself.

Ecosystems

Ecosystems consist of several trophic levels, or levels at which energy is acquired: primary producers, consumers, and decomposers. Primary producers are green plants that capture solar energy and transform it, through the process of photosynthesis, into chemical energy. Organisms that eat plants (herbivores) or animals (carnivores) to obtain their energy are collectively called consumers. Decomposers are those consumers, such as bacteria and fungi, that obtain energy by breaking down dead bodies of plants and animals. These trophic levels are linked together into a structure called a food web, in which energy is transferred from primary producers to consumers and decomposers, until finally all is lost as heat. Each transfer of energy entails a loss (as heat) of at least 90 percent, which means that the total amount of energy available to carnivores in an ecosystem is substantially less than that available to herbivores.

As with individual organisms, ecosystems and their trophic levels have energy budgets. The net production of one trophic level is available to the next-higher trophic level as biomass (mass of biological material). Plants have higher net productivity (rates of production) than animals because their metabolic maintenance cost is lower relative to gross productivity; herbivores often have higher net productivity than predators for the same reason. For the community as a whole, net productivity is highest during early successional stages, since biomass is being added more rapidly than later on, when the community is closer to climax equilibrium.

In contrast to the unidirectional flow of energy, materials are conserved and recycled from dead organisms by decomposers to support productivity at higher trophic levels. Carbon, water, and mineral nutrients required for plant growth are cycled through various organisms within an ecosystem. Materials and energy are also exchanged among ecosystems: There is no such thing in nature as a "closed" ecosystem that is entirely self-contained.

Descriptive, Experimental, and Mathematical Ecology

The science of ecology is necessarily more broadly based than most biological disciplines; consequently, there is more than one approach to it. Ecological studies fall into three categories: descriptive, experimental, and mathematical.

Descriptive ecology is concerned with describing natural history, usually in qualitative terms. The study of adaptations, for example, is descriptive in that one can measure the present "value" of an adaptive feature, but one can only conjecture as to the history of natural selection that was responsible for it. On the other hand, some patterns are discernible in nature for which hypotheses can be constructed and tested by statistical inference. For example, the spatial distribution (dispersion) of birds on an island may be random, indicating no biological interaction among them. If the birds are more evenly spaced (uniform dispersion) than predicted assuming randomness, however, then it might be inferred that the birds are competing for space; they are exhibiting territorial exclusion of one another. Such "natural experiments," as they are called, depend heavily upon the careful design of statistical tests.

Experimental ecology is no different from any other experimental discipline; hypotheses are constructed from observations of nature, controlled experiments are designed to test them, and conclusions are drawn from the results of the experiments. The basic laboratory for an ecologist is the field. Experiments in the field are difficult because it is hard to isolate and manipulate variable factors one at a time, which is a requisite for any good experiment in science. A common experiment that is performed to test for resource limitation in an organism is enhancement of that resource. If food, for example, is thought to be in short supply (implying competition), one section of the habitat is provided more food than is already present; another section is left alone as a control. If survivorship, growth, or reproductive output is higher in the enhanced portion of the habitat than in the control area, the researcher may infer that the organisms therein were food-limited. Alternatively, an ecologist might have decreased the density of organisms in one portion of the habitat, which might seem equivalent to increasing food supply for the remaining organisms, except that it represents a change in population density as well. Therefore, this second design will not allow the researcher to differentiate between the possibly separate effects of food level and simple population density on organisms in the habitat.

Mathematical ecology relies heavily upon computers to generate models of nature. A model is simply a formalized, quantitative set of hypotheses constructed from sets of assumptions of how things happen in nature. A model of population growth might contain assumptions about the age structure of a population, its genetic capacity for increase, and the average rate of resource utilization by its members. By changing these assumptions, scientists can cause the model population to behave in different ways over time. The utility of such modeling is limited to the accuracy of the assumptions employed.

Modern ecology is concerned with integrating these different approaches, all of which have in common the goal of predicting the way nature will behave in the future, based upon how it behaves in the present. Description of natural history leads to hypotheses that can be tested experimentally, which in turn may allow the construction of realistic mathematical (quantitative) models of how nature works.

All-Encompassing Nature

People historically have viewed nature as an adversary. The "conquest of nature" has traditionally meant human encroachment on natural ecosystems, usually without benefit of predictive knowledge. Such environmental problems as pollution, species extinction, and overpopulation can be viewed as experiments performed on a grand scale without appropriate controls. The problem with such experiments is that the outcomes might be irreversible. A major lesson of ecology is that humans are not separate from nature; we are constrained by the same principles as are other organisms on the earth. One object of ecology, then, is to learn these principles so that they can be applied to our portion of the earth's ecosystem.

Populations that are not regulated by predators, disease, or food limitation grow exponentially. The human population, on a global scale, grows this way. All the wars and famines in history have scarcely made a dent in this growth pattern. Humankind has yet to identify its carrying capacity on a global scale, although regional famines certainly have provided insights into what happens when local carrying capacity is exceeded. The human carrying capacity needs to be defined in realistic ecological terms, and such constraints as energy, food, and space must be incorporated into the calculations. For example, knowledge of energy flow teaches that there is more energy at the bottom of a food web (producers) than at successively higher trophic levels (consumers), which means that more people could be supported as herbivores than as carnivores.

The study of disease transmission, epidemiology, relies heavily on ecological principles. Population density, rates of migration among epidemic centers, physiological tolerance of the host, and rates of evolution of disease-causing parasites are all the subjects of ecological study.

An obvious application of ecological principles is conservation. Before habitats for endangered species can be set aside, for example, their ecological requirements, such as migratory routes, breeding, and feeding habits, must be known. This also applies to the introduction (intentional or accidental) of exotic species into habitats. History is filled with examples of introduced species that caused the extinction of native species. Application of ecological knowledge in a timely fashion, therefore, might prevent species from becoming endangered in the first place.

One of the greatest challenges we face is the loss of habitats worldwide. This is especially true of the tropics, which contain most of the earth's species of plants and animals. Species in the tropics have narrow niches, which means that they are more restricted in range and less tolerant of change than are many temperate species. Therefore, destruction of tropical habitats, such as rain forests, leads to rapid species extinction. These species are the potential sources of many pharmaceutically valuable drugs; further, they are a genetic record of millions of years of evolutionary history. Tropical rain forests also are prime sources of oxygen and act as a buffer against carbon dioxide accumulation in the atmosphere. Ecological knowledge of global carbon cycles permits the prediction that destruction of these forests will have a profound impact on the quality of the air.

—Lawrence E. Hurd

See also: Adaptations and their mechanisms; Biodiversity; Biogeography; Coevolution; Communities; Competition; Demographics; Ecological niches; Ecosystems; Habitats and biomes; Mark, release, and recapture methods; Population analysis; Population fluctuations; Population growth; Predation; Reproductive strategies; Symbiosis; Systematics; Wildlife management.

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Hutchinson, G. Evelyn. *The Ecological Theater and the Evolutionary Play*. New Haven, Conn.: Yale University Press, 1969. The author, arguably the father of modern ecology, writes lucidly and incisively about the interplay between ecology and evolution.

His approach is strongly historical, and his accounts of "the naturalist as art critic" are both informative and entertaining. Hutchinson's philosophy of science, well detailed herein, has influenced generations of ecologists and evolutionary biologists.

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Pianka, Eric R. *Evolutionary Ecology*. 6th ed. San Francisco: Benjamin/Cummings, 2000. An introductory text covering the whole spectrum of evolutionary ecology, starting with the environment and working up to complex animal and human communities.

Ricklefs, Robert E. *Ecology*. 4th ed. New York: Chiron Press, 1999. This is one of the best general texts in the field; it covers more ground more thoroughly than many other texts do. Suitable for a college-level course, it requires some background in general biology and genetics at the college level. The writing style is clear enough, however, that even the reader with less background can glean much from Ricklefs's discussion of adaptations of organisms to their environments.

ECOSYSTEMS

Type of animal science: Ecology
Fields of study: Conservation biology, ecology, environmental science, wildlife ecology

The ecosystem is the fundamental concept in ecology. It is viewed by ecologists as the basic unit of nature, consisting of the complex of interacting organisms inhabiting a region with all the nonliving physical factors that make up their environment. Ecologists study structural and functional relationships of ecosystem components to be able to predict how the system will respond to natural change and human disturbance.

Principal Terms

BIOMASS: the weight of organic matter, often expressed in terms of grams per square meter per year

CONSUMERS: animals, fungi, and bacteria that get energy by feeding on organic matter

FOOD CHAIN: an abstract chain representing the links between organisms, each of which eats and is eaten by another

FOOD WEB: a network of interconnecting food chains representing the food relationships in a community

PHOTOSYNTHESIS: the process by which green plants and algae use sunlight as energy to convert carbon dioxide and water into energy-rich compounds such as glucose

PRIMARY PRODUCTION: the energy assimilated by green plants and stored as organic tissue

PRODUCERS: green plants and chemosynthetic organisms that can produce food from inorganic materials

RESPIRATION: the release of chemical energy to do work in plants and animals; a reversal of the photosynthetic process

TROPHIC LEVEL: a feeding level on the pyramid of numbers, consisting of all the kinds of animals that feed at comparable levels on food chains

The ecosystem is essentially an abstract organizing unit superimposed on the landscape to help ecologists study the form and function of the natural world. An ecosystem consists of one or more communities of interacting organisms and their physical environment. Ecosystems have no distinct boundaries; thus the size of any particular ecosystem should be inferred from the context of the discussion. Individual lakes, streams, or strands of trees can be described as distinct ecosystems, as can the entire North American Great Lakes region. Size and boundaries are arbitrary because no ecosystem stands in complete isolation from those that surround it. A lake ecosystem, for example, is greatly affected by the streams that flow into it and by the soils and vegetation through which these streams flow. Energy, organisms, and materials routinely migrate across whatever perimeters the ecologist may define. Thus, investigators are allowed considerable latitude in establishing the scale of the ecosystem they are studying. Whatever the scale, though, the importance of the ecosystem concept is that it forces ecologists to treat organisms not as isolated individuals or species but in the context of the structural and functional conditions of their environment.

Development of the Ecosystem Concept

Antecedents to the ecosystem concept may be traced back to one of America's first ecologists, Stephen Alfred Forbes, an eminent Illinois naturalist who studied food relationships among birds, fishes, and insects. During the course of his investigations, Forbes recognized in 1880 that full knowledge of organisms and their response to disturbances would come only from more concentrated research on their interactions with other organisms and with their inorganic (nonliving) physical surroundings. In 1887, Forbes suggested that a lake could be viewed as a discrete system for study: a microcosm. A lake could serve as a scale model of nature that would help biologists understand more general functional relationships among organisms and their environment. Forbes explained how the food supply of a single species, the largemouth bass, was dependent either directly or indirectly upon nearly all the fauna and much of the flora of the lake. Therefore, whenever even one species was subjected to disturbance from outside the microcosm, the effects would probably be felt throughout the community.

In 1927, British ecologist Charles Elton incorporated ideas introduced by Forbes and other fishery biologists into the twin concepts of the food chain and the food web. Elton defined a food chain as a series of linkages connecting basic plants, or food producers, to herbivores and their various carnivorous predators, or consumers. Elton used the term "food cycle" instead of "food web," but his diagrams reveal that his notion of a food cycle—that it is simply a network of interconnecting food chains—is consistent with the modern term.

Elton's diagrams, which traced various pathways of nitrogen through the community, paved the way for understanding the importance of the cycling of inorganic nutrients such as carbon, nitrogen, and phosphorus through ecosystems, a process that is known as biogeochemical cycling. Very simply, Elton illustrated how bacteria could make nitrogen available to algae at the base of the food chain. The nitrogen then could be incorporated into a succession of ever larger consumers until it reached the top of the chain. When the top predators died, decomposer organisms would return the nitrogen to forms that could eventually be taken up again by plants and algae at the base of the food chain, thus completing the cycle.

Elton's other key contribution to the ecosystem concept was his articulation of the pyramid of numbers, the idea that small animals in any given community are far more common than large animals. Organisms at the base of a food chain are numerous, and those at the top are relatively scarce. Each level of the pyramid supplies food for the level immediately above it—a level consisting of various species of predators that generally are larger in size and fewer in number. That level, in turn, serves as prey for a level of larger, more powerful predators, fewer still in number. A graph of this concept results in a pyramidal shape of discrete levels, which today are called trophic (feeding) levels.

Ecosystems in Twentieth Century Thought

Although the basic concept of an ecosystem had been recognized by Forbes as early as 1880, it was not until 1935 that British ecologist Arthur G. Tansley coined the term. Though he acknowledged that ecologists were primarily interested in organisms, Tansley declared that organisms could not be separated from their physical environment, as organism and environment formed one complete system. As Forbes had pointed out half a century earlier, organisms were inseparably linked to their nonliving environments. Consequently, ecosystems came to be viewed as consisting of two fundamental parts: the biotic, or living components, and the abiotic, or nonliving components.

No one articulated this better than Raymond Lindeman, a limnologist (freshwater biologist) from Minnesota who in 1941 skillfully integrated the ideas of earlier ecological scientists when he published an elegant ecosystem study of Cedar Bog Lake. Lindeman's classic work set the stage for decades of research that centered on the ecosystem as the primary organizing unit of study in ecology. Drawing on the work of his mentor, G. Evelyn Hutchinson, and Charles Elton, Arthur Tansley, and other scientists, Lindeman explained how ecological pyramids were a necessary result of energy transfers from one trophic level to the next.

By analyzing ecosystems in this manner, Lindeman was able to answer a fundamental ecological question that had been posed fourteen years earlier by Elton: Why were the largest and most powerful animals, such as polar bears, sharks, and tigers, so rare? Elton had thought the relative scarcity of top predators was due to their lower rates of reproduction. Lindeman corrected this misconception by explaining that higher trophic levels held fewer animals not because of their reproductive rates but because of a loss of chemical energy with each step up the pyramid. It could be looked upon as a necessary condition of the second law of thermodynamics: Energy transfers yield a loss or degradation of energy. The predators of one food level could never completely extract all the energy from the level below. Some energy would always be lost to the environment through respiration, some energy would not be assimilated by the predators, and some energy simply would be lost to decomposer chains when potential prey died of nonpredatory causes. This meant that each successive trophic level had substantially less chemical energy available to it than was transferred from the one below and, therefore, could not support as many animals.

Ecologists soon expanded the principle of Elton's pyramid of numbers to model other ecosystem processes. They found, for example, that the flow of chemical energy through an ecosystem could be characterized as an energy pyramid; the biomass (the weight of organic material, as in plant or animal tissue) in a community could be plotted in a pyramid of biomass. Collectively, such pyramidal models became known as ecological pyramids.

Rachel Carson's book Silent Spring *brought the dangers facing the earth's ecosystems to public consciousness and was one of the contributing factors to the growth of environmentalism in the late twentieth century.* (Library of Congress)

Energy Production and Transmission

Lindeman subdivided the biotic components of ecosystems into producers, consumers, and decomposers. Producers (also known as autotrophs) produce their own food from compounds in their environment. Green plants are the main producers in terrestrial ecosystems; algae are the most common producers in aquatic ecosystems. Both plants and algae are producers that use sunlight as energy to make food from carbon dioxide and water in the process of photosynthesis. During photosynthesis, plants, algae, and certain bacteria capture the sun's energy in chlorophyll molecules. (Chlorophyll is a pigment that gives plants their green color.) This energy, in turn, is used to synthesize energy-rich compounds such as glucose, which can be used to power activities such as growth, maintenance, and reproduction or can be stored as biomass for later use. These energy-rich compounds can also be passed on in the form of biomass from one organism to another, as when animals (primary consumers) graze on plants or when decomposers break down detritus (dead organic matter).

The energy collected by green plants is called primary production because it forms the first level at the base of the ecological pyramid. Total photosynthesis is represented as gross primary production. This is the amount of the sun's energy actually assimilated by autotrophs. The rate of this production of organic tissue by photosynthesis is called primary productivity. Plants, however, need to utilize some of the energy they produce for their own growth, maintenance, and reproduction. This energy becomes available for such activities through respiration, which essentially is a chemical reversal of the process of photosynthesis. As a result, not all the energy assimilated by autotrophs is available to the consumers in the next trophic level of the pyramid. Consequently, respiration costs generally are subtracted from gross primary production to determine the net primary production, the chemical energy actually available to primary consumers.

Measuring Ecosystem Productivity

The carrying capacity for all the species supported by an ecosystem ultimately depends upon the system's net primary productivity. By knowing the productivity, ecologists can, for example, estimate the number of herbivores that an ecosystem can support. Consequently ecosystem ecologists have developed a variety of methods to measure the net primary productivity of different systems. Productivity is generally expressed in kilocalories per square meter per year when quantifying energy, and in grams per square meter per year when quantifying biomass.

Production in aquatic ecosystems may be measured by using the light and dark bottle method. In this technique two bottles containing samples of water and the natural phytoplankton population are suspended for twenty-four hours at a given depth in a body of water. One bottle is dark, permitting respiration but no photosynthesis by the phytoplankton. The other is clear and therefore permits both photosynthesis and respiration. The light bottle provides a measure of net production (photosynthesis minus respiration) if the quantity of oxygen is measured before and after the twenty-four-hour period. (The amount of oxygen produced by photosynthesis is proportional to the amount of organic matter fixed.) Measuring the amount of oxygen in the dark bottle before and after the run provides an estimate of respiration, since no photosynthesis can occur in the dark. Combining net production from the light bottle with total respiration from the dark bottle yields an estimate of gross primary production.

Other studies have concentrated on quantifying the rate of movement of energy and materials through ecosystems. Investigations begun in the 1940's and 1950's by the Atomic Energy Commission to track radioactive fallout were eventually diverted into studies of ecosystems that demonstrated how radionuclides moved through natural environments by means of food-chain transfers. This research confirmed the interlocking nature of all organisms linked by the food relationship and eventually yielded rates at which both organic and inorganic materials could be cycled through ecosystems. As a result of such studies, the Radiation Ecology Section at Oak Ridge National Laboratory in Tennessee became established as a principal center for systems ecology.

Ecologists sometimes extend the temporal boundaries of their studies by utilizing the methods of paleoecology (the use of fossils to study the nature of ecosystems in the past). Research of this type generally centers on the analysis of lake sediments, whose layers often hold centuries of ecosystem history embodied in the character and abundance of pollen grains, diatoms, fragments of zooplankton, and other organic microfossils.

More general trends in the methods of studying ecosystems include a continuing emphasis on quantitative methods, often using increasingly sophisticated computer modeling techniques to simulate ecosystem functions. Equally significant is a trend toward a "big science" approach, modeled on the Manhattan Project, which employed teams of investigators working on different problems related to nuclear fission in different parts of the country. The well-known international biological program, the Hubbard Brook Project in New Hampshire, and continuing projects on long-term ecological research all serve as examples of ecosystem studies that involve teams of researchers from a wide range of disciplines.

Responding to Disturbance

One of the practical benefits of studying ecosystems derives from naturalist Stephen Forbes's suggestion, made in 1880, that the knowledge from biological research be used to predict the response of organisms to disturbance. When disturbance is caused by natural events such as droughts, floods, or fires, ecologists can use their knowledge of the structure and function of ecosystems to help resource managers plan for subsequent recolonization and succession of species.

The broad perspective of the ecosystem approach becomes particularly useful in examining the effects of certain toxic compounds because of the complexity of their interaction within the environment. The synergistic effects that sometimes occur with toxic substances can produce pronounced impacts on ecosystems already stressed by other disturbances. For example, after the atmosphere deposits mercury on the surface of a lake, the pollutant eventually settles in the sediments where bacteria make it available to organisms at the base of the food chain. The contaminant then bioaccumulates as it is passed on to organisms such as fish and fish-eating birds at higher trophic levels. Synergistic effects occur in lakes already affected by acid deposition; researchers have found that acidity somehow stimulates microbes to increase the bioavailability of the mercury. Thus, aquatic ecosystems that have become acidified through atmospheric processes may stress their flora and fauna even further by enhancing the availability of mercury from atmospheric fallout. The complexity of such interactions demands research at the ecosystem level, and ecosystem studies are prerequisite for prudent public policy actions on environmental contaminants.

—*Robert Lovely*

See also: Biodiversity; Biogeography; Chaparral; Coevolution; Communities; Convergent and divergent evolution; Deserts; Ecological niches; Ecology; Endangered species; Extinction; Fauna: Africa; Fauna: Antarctica; Fauna: Arctic; Fauna: Asia; Fauna: Australia; Fauna: Caribbean; Fauna: Central America; Fauna: Europe; Fauna: Galápagos Islands; Fauna: Madagascar; Fauna: North America; Fauna: Pacific Islands; Fauna: South America; Food chains and food webs; Forests, coniferous; Forests, deciduous; Grasslands and prairies; Habitats and biomes; Lakes and rivers; Marine biology; Mountains; Paleoecology; Plant and animal interactions; Rain forests; Reefs; Savannas; Swamps and marshes; Symbiosis; Tidepools and beaches; Tundra; Urban and suburban wildlife; Wildlife management; Zoology; Zoos.

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EELS

Type of animal science: Classification
Fields of study: Anatomy, ethology, marine biology, physiology, zoology

Eels are a variety of fishes possessing an elongate, snakelike body form. Eels inhabit both freshwater and marine environments, and some eel species move back and forth between the two environments at different stages of their life cycles. Although eels are not the most charismatic of aquatic organisms, their life histories make them some of the most fascinating and poorly understood marine animals.

Principal Terms

GUANINE: a chemical deposited in the skin of freshwater eels as they return to the marine environment

LEPTOCEPHALUS: the larval form of most eel species, bearing little resemblance to the adult eel

SARGASSO SEA: an area in the southwestern North Atlantic Ocean noted for large accumulations of sargassum weed; the breeding ground for North American and European freshwater eels

Eel is the name given to any fish that possesses an elongated, snakelike or ribbonlike body form. Although many eels are closely related to each other as members of the order Anguilliformes, other eel-like fishes are not closely related to this order, an example of convergent evolution of body form.

Freshwater Eels

The most commonly encountered and familiar eels are the freshwater eels of North America (*Anguilla rostrata*) and Europe (*Anguilla anguilla*). Both species are members of the same family, the Anguillidae. For many years the life cycle of these eels, which are commonly encountered in freshwater ponds and streams, remained shrouded in mystery, and egg-bearing females and early juveniles were never encountered. In the last half of the twentieth century, however, the story of the eel's life cycle has become better known, and it is a remarkable tale. All of the eels in North America and Europe are spawned in an area of the southwestern North Atlantic that is known as the

Moray eels lurk in holes and crevices of coral reefs, waiting for fish to swim past. (Digital Stock)

Sargasso Sea. From there the larval eels, which are known as leptocephalus larvae, are carried by the North Atlantic currents including the Gulf Stream, to the shores of North America and Europe. The leptocephali bear little resemblance to the adult eels; they are long, ribbonlike, and transparent. Upon arrival at the coastlines of North America and Europe, the eels metamorphose into the more familiar eel-like adult form and penetrate freshwater rivers and streams. Eels also have been shown to travel through underground streams into seemingly isolated ponds and lakes. They spend most of their adult lives in such freshwater systems.

Upon reaching sexual maturity, the eels return to the Atlantic Ocean, and during this journey they undergo another metamorphosis. Guanine deposits in the skin give the eels a silvery appearance, as opposed to their usual dark olive color, the eyes enlarge, and their physiology changes in order to cope with the new demands of living in the ocean depths. Upon entering the ocean, the eels become deep-water fishes, and are very rarely seen as they return to spawn in the Sargasso Sea. How these fish manage to navigate to, and locate, their spawning grounds in the Sargasso Sea from freshwater ponds and streams while traveling in the ocean's depths is completely unknown. For years, there has been speculation among scientists that the two species of North American and European freshwater eels are members of the same species and are randomly scattered by the ocean's currents to North America and Europe. Recent genetic studies have suggested, however, that the two groups may at least be separate breeding populations if not actually separate species. Nevertheless, much remains to be learned about the life histories of these remarkable animals.

Eel Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Superclass: Gnathostomata
Class: Osteichthyes
Subclass: Actinopterygii
Superorder: Teleosteii
Order: Anguilliformes
Suborder: Anguilloidei
Families: Anguillidae (freshwater eels, one genus, two species); Muraenidae (moray eels, four genera, six species); Moringuidae (spaghetti eels, two genera, four species); Synaphrobranchidae (cutthroat eel); Congridae (conger eels, four genera, four species); Nemichthyidae (snipe eels, two genera, two species); Myrocongridae, Muraenesocidae (pike eels, one genus, three species); Heterocongridae (garden eel); Ophichthyidae (snake eels, two genera, three species); Illyophidae; Simenchelyidae (snubnosed eel); Serrivomeridae (two genera, two species); Cyemidae (deepwater eel)

Geographical location: Worldwide, in temperate and tropical freshwater and marine systems

Habitat: Highly variable, from freshwater ponds and streams to open ocean, coral reefs, and ocean bottom

Gestational period: None; as in most bony fishes, fertilization is external and the larval eels develop as plankton in the water column

Life span: Variable and frequently unknown

Special anatomy: Elongate, snakelike or ribbonlike body forms; pelvic fins and supporting skeleton are generally not present and pectoral fins and skeletal pectoral girdle are also missing in some forms; typically have dorsal, caudal, and anal fins fused together to form a single fin extending along the dorsal surface, around the tail, and onto the ventral surface; gill opening is typically small and located low on the body; body form is specialized for squeezing into cracks or crevasses, burrowing on soft bottom substrates, and occasionally for a pelagic existence, swimming in the open waters of the ocean

Moray Eels

Another type of eel commonly encountered by divers and snorkelers is the moray eel, a member of the family Muraenidae. These eels typically inhabit holes and crevasses in coral reefs. They lack pectoral fins and are often brightly colored and patterned. Some species, such as *Gymnothorax*, have impressive, fanglike teeth and feed on reef fishes; others have blunt, crushing teeth and feed primarily on invertebrates. Although morays have a sinister reputation, in general they are inoffensive to humans and will bite only if provoked by the intrusion into their burrows of fingers, which they may mistake for an octopus. At some dive sites, resident moray eels have been semi-tamed and are hand-fed and handled; however, such treatment occasionally results in the handlers being bitten. Studies have demonstrated that morays are hermaphroditic, starting their mature life as males and later becoming females. A few species are synchronous hermaphrodites, possessing both male and female reproductive organs at the same time.

—John G. New

See also: Deep-sea animals; Fish; Hermaphrodites; Lakes and rivers; Marine animals; Marine biology; Metamorphosis; Migration; Reproductive strategies.

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ELEPHANT SEALS

Type of animal science: Classification
Fields of study: Anatomy, conservation biology, ecology, marine biology, physiology, zoology

Elephant seals are carnivorous marine mammals that spend time on land and in the ocean. There are two distinct species: the northern and the southern elephant seal. Both species have claws on their front flippers and both lack external ears. A trunklike nose anatomically differentiates the males. Blubber provides buoyancy and insulation. Elephant seals swim using their rear flippers.

Principal Terms

CARNIVORE: an animal that eats flesh
ESTRUS: a time during which females are receptive to mating
HAREM: a group of breeding females controlled by a single male
SHEDDING: a process through which organisms lose and replace their external covering; in elephant seals this involves loss of hair and portions of worn-out skin

Elephant seals are the largest seals on earth. Male northern elephant seals attain a mature length of thirteen to sixteen feet, and may weigh between 4,500 and 6,000 pounds. Males of the southern species are larger and heavier than their northern cousins, and may reach a length of twenty feet, and weigh as much as 8,700 pounds. Females of both species are smaller. Their weight varies according to certain conditions. Adult elephant seals are gray in color, which is more pronounced in the females. They have no fur, but have areas covered with short, firm hairs.

An adult male has a large, trunklike extension of the nasal canal. This organ plays a vital role in the behavior and communication of these animals. The trunk, which can be described as short, baglike, and fleshy, hangs downward and is longer in the northern species of elephant seals. The skull is large and serves as a point of attachment for powerful muscles that move the trunk. Adult males have huge canine teeth.

Reproduction, Behavior, and Communication

Elephant seals communicate by producing loud barks and snorts with their trunks and mouths. These noises are often highly specific within isolated groups. Several different dialects have been identified. Elephant seals reach sexual maturity rapidly. Females give birth and mate in specific breeding grounds. Males are competitive and battle with raised heads, facing each other. They use their canine teeth as weapons. Dominant males

Image Not Available

Elephant Seal Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Carnivora
Suborder: Pinnipedia
Family: Phocidae
Genus and species: Mirounga angustirostris (northern elephant seal), *M. leonina* (southern elephant seal)

Geographical location: Northern species inhabit the Pacific coastline from Mexico as far north as Alaska, and the waters of the northeastern Pacific Ocean; southern species inhabit specific areas of the southwestern Atlantic Ocean, the Kerguelen Islands in the southern Indian Ocean, and Macquarie Island off the coast of New Zealand

Habitat: Marine waters or coastal shores of temperate or subarctic seas

Gestational period: About eleven months, which includes a delayed implantation of the fertilized ovum

Life span: Twelve to twenty years; females generally live longer than males

Special anatomy: Massive size; presence of large, trunklike extension of the nasal cavity in the males; hind flippers for swimming

mate with a large harem of females that may number between forty and fifty. Pups are born on land and have a black fur coat at the time of birth. They are suckled for three weeks before they are abandoned. Females enter estrus and mate again immediately after weaning their last pup. Most mature females become pregnant every year.

Because of the value of their oil, both elephant seal species were hunted to near extinction. Successful reproduction and protection against hunting have enabled elephant seal populations to recover, but have left the northern elephant seal population with a limited gene pool. It is unknown how this lack of genetic diversity will affect the survival and future of this species.

Alternating between land and sea, a single elephant seal may travel up to thirteen thousand miles in one year. The migratory cycle starts toward the end of winter, after females give birth and conceive again. Females leave their breeding grounds and are soon followed by the males. Elephant seals search for food in specific foraging sites for about three months. Since they do not eat while on land, they dive continuously to great depths for their preferred diet of squid or bottom-dwelling fish. Once they haul themselves out of the sea onto land, it is time to shed. Shedding can take several weeks. When shedding is completed, the seals return to the ocean for up to eight months and search for food. Elephant seals are the most migratory marine mammals on earth.

—*Paul J. Frisch*

See also: Endangered species; Gene flow; Marine animals; Migration; Seals and walruses; Teeth.

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ELEPHANTS

Type of animal science: Classification
Fields of study: Anatomy, behavior, ecology, physiology

Found in parts of Africa and Asia, the elephant is the largest land animal, anatomically differentiated by tusks, a trunk, and a massive head. Elephants are herbivores, with distinct behavioral and physical characteristics.

Principal Terms

BROWSER: feeding on shoots and leaves
GRAZER: feeding on grasses and pasture
JACOBSON'S ORGAN: a sense organ in the mouth, which detects reproductive chemical signals
MUSTH: aggressive rutting behavior during mating
TEMPORAL GLAND: located between the eyes and the ears, and active during reproduction

Although all elephants have a number of similarities, African elephants are different from Asian elephants. The highly muscular trunk is common to both and is described as a modified nose. Elastic, cartilaginous tissue cushions the soles of the feet, making elephants silent walkers that can move up to twenty-five miles per hour. Elephants lose body heat through their ears.

Adult African elephants can weigh up to 1,500 pounds. They have large ears and two fingerlike lips at the tips of their trunks. Anatomically, the African elephant has a concave back, with shoulders that rise above the head. In this species, both sexes have tusks.

Adult Asian elephants can weigh eleven thousand pounds. They have smaller ears and one lip at the tip of the trunk. Anatomically, the Asian elephant has a convex back with shoulders that lie below the bulbous head. In this species, some males have tusks. Easier to domesticate than the African variety, Asian elephants are used for transport and logging. Their trunks have a characteristic flexibility and a greater range of motion that makes them more suitable for such activities. Asian elephants are an endangered species, and African elephants are a threatened species, because of destruction to their habitat and illegal poaching for their valuable ivory tusks.

Diet

The elephant is a herbivore that consumes up to four hundred pounds of vegetation per day. Large molars chew vegetation, which may take up to nineteen hours to digest. Molar teeth do not all erupt at once; when one molar wears down, it is replaced by a new one. This replacement happens six times, and after that the elephant may starve to death.

The trunk serves to siphon up gallons of water to facilitate digestion and ensure hydration. These animals are unselective browsers that use their tusks to chisel away tree bark and, in the process, often uproot trees. Over time, these destructive habits can transform the ecology of the environment.

Protection, Defense, and Communication

Elephants use their tusks for defense and sharpen them on tree bark. An aggressive elephant will fan out its ears, kick sand, sway from side to side, and trumpet and scream when angry and excited. Males travel with female herds until puberty. At approximately twelve years of age, males leave female herds and form smaller male herds. Mature males join a herd when a female is in heat. Older males are solitary.

A matriarch leads the herd, which is mainly female. Males in musth and females in heat advertise their condition by producing infrasonic rumbles not audible to humans. Since elephants have poor eyesight and hearing, these sounds allow for long-distance coordination of mating.

Reproduction and Birth

Elevated testosterone levels cause notable physical changes in elephants. The male secretes fluid down the sides of his face from the temporal glands. He also dribbles urine that often stains the insides of his hind legs. The male is now ready to mate: He is in a musth state. The male in musth is hostile and aggressive toward other males, viewing them as competitive suitors in his quest to mate successfully. Meanwhile, the female's urine emits a distinct odor that invites the male's advances. A male interprets a female's readiness to mate through his Jacobson's organ. Females mate once every three to five years. A female will exhibit aggressive behavior, including

Elephant Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Proboscidae
Family: Elephantidae (modern elephants)
Genus and species: Loxodonta africana (African elephant), *Elephas maximus* (Asian elephant)

Geographical location: African elephants are abundant south of the Sahara desert; Asian elephants occur in India, Sri Lanka, and south and east to Sumatra

Habitat: Mostly forest and savanna biomes, which are never far from water

Gestational period: Twenty-two months

Life span: Sixty years in the wild; eighty years in captivity

Special anatomy: Gray coloration; massive head with trunk and tusks; large, flaplike ears

Elephant herds are led by matriarchs and are composed of females and prepubertal males. (Corbis) fighting to kill, when aggressors threaten her calves.

Elephants also grieve the death of the aggressor soon after they have killed it. They may cover the dead animal with leaves and sand. This is noteworthy, as such behavior is rare in the animal kingdom.

Elephants are extremely intelligent mammals. Aggressive and defensive, protective and devoted to their young, elephants are majestic herbivores with muscular, serviceable trunks and magnificent ivory tusks.

—William P. Carew

See also: Death and dying; Domestication; Emotions; Endangered species; Fauna: Africa; Fauna: Asia; Herds; Hyraxes; Intelligence; Mammalian social systems; Mating; Noses; Teeth, fangs, and tusks.

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ELK

Types of animal science: Behavior, classification, ecology
Fields of study: Ecology, wildlife ecology, zoology

Elk, also known as wapiti, are members of the mammal order Artiodactyla. They are noted for their large antlers.

Principal Terms

ANTLERS: outgrowths from the skull, composed entirely of bone, shed after breeding season
HERBIVORE: an animal that feeds on plants for its diet
MANE: long, thick hair growing from the neck
PIEDMONT: area at the base of mountains
PELAGE: a mammal's fur coat
PREDATOR: an animal that preys on other animals for its food
RUT: activities associated with bull elk mating behaviors
UNGULATE: mammals with cloven hooves
VELVET: a hairy skin richly endowed with blood vessels that covers developing antlers

Elk are the largest members of the red deer group of the Artiodactyla. This order has more than two hundred other species including pigs, peccaries, wild boars, warthogs, hippos, cows, goats, sheep, moose, caribou, giraffes, camels, pronghorns, llamas, and deer. Antarctica and Australia are the only continents without any members of Artiodactyla. The fossil record of Artiodactyla dates back at least fifty million years. Female elk (cows) weigh about 360 kilograms at maturity, while males (bulls) weigh about 450 kilograms. Elk calves weigh about 15 kilograms at birth and add 30 kilograms within the next two weeks. Calf survival is highly variable; researchers have reported a range of eighteen to seventy calves at six months for every one hundred cows. The environment and the available nutrition influence all of the average weights above.

Physical Characteristics

As in many of the deer species, calves have creamy colored spots on their reddish-brown pelage. Bulls are distinctly different from cows in their winter coat color. During the winter, bulls have a dark colored mane, in vivid contrast to their cream colored coats, whereas cows are somewhat darker and lack the mane.

Elk Facts

Classification:
Kingdom: Animalia
Phylum: Chordata
Class: Mammalia
Order: Artiodactyla
Family: Cervidae (deer)
Genus and species: Cervus elaphus (red deer, twelve subspecies), *Cervus canadensis* (American elk or wapiti, thirteen subspecies); *Alces alces* (moose or European elk, six subspecies)
Geographical location: Across North America and Eurasia
Habitat: Grasslands, piedmonts, forests, and mountain ranges
Gestational period: 7.5 to 8.5 months
Life span: Up to twenty years
Special anatomy: Four-chambered stomachs; bulls have antlers that can weigh more than thirteen kilograms

Bull elk begin growing antlers in mid to late May, with full antler development finished by August, when velvet rubbing begins. Rubbing the velvet from the antlers, gives an elk a highly polished rack. In aspen trees stands, elk leave scars on the tree trunks at about head height during the removal of the velvet. Antler lengths have been recorded at as much as 150 centimeters. Elk antlers are branched and have tines (points) at their ends. March is the usual month for shedding of the antlers. No good correlation exists between age of the bull and number of tines.


Unlike some other horned species, the number of tines on a bull elk's antlers is not connected with its age. (PhotoDisc)

After copulation, which usually occurs in September and October, a cow delivers one calf seven months later. Although twins are produced, it is uncommon. Mature cows have an extremely high pregnancy rate, averaging 90 percent in some cases, although older cows (more than eight years old) appear to be less fertile. The decline in fertility may be related to nutritional status. First-year bulls can be fertile but it is more common for bulls in their third year to be the ones participating most in mating events. Bulls mate with more than one cow in their harems, which they defend from other bulls during the rutting season. Presently there is insufficient evidence to support declining bull fertility with increasing age.

Lifestyle

Foraging habits of elk are similar to those of other ungulates. Elk adapt their diet according to the seasons. Some elk populations migrate between spring and winter habitats in search of a better environment and food resources. Other populations do not migrate, remaining in their selected habitat year around because there is adequate forage and cover. During the winter season, dried grasses and shrub branches and shoots are eaten. In the spring and summer, new shoots of grasses and other plants, such as aspens, oaks, and willows are selected. In certain areas of national forests in the southwest, areas are fenced off to prevent elk from grazing on young aspens.

Although wildlife experts have reported that elk can live more than twenty years, most do not. At birth the sex ratios are reported to be one male for every female, but this changes dramatically as elk attain adult status (thirty males per one hundred females). Wolves and mountain lions are the primary predators of elk.

Elk are social animals, tending to form loose congregations that are segregated by sex most of the year. Herds of elk are not constant; individuals tend to move about, leaving one herd and joining another. During the rutting season, bugling by the bull elk can be heard. In addition to bugling, other behaviors used by males during the rutting season to establish harems and territory include antler rubbing, digging with the forelimbs, posturing with head and neck, and lowering of the ears.

—Sylvester Allred

See also: Antelope; Deer; Fauna: North America; Herbivores; Herds; Horns and antlers; Migration; Moose; Reindeer; Ungulates; Wildlife management.

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EMBRYOLOGY

Types of animal science: Development, reproduction
Fields of study: Cell biology, developmental biology, embryology, reproduction science

Embryology is the study of the development of animals, from the formation of gametes until birth, hatching, or metamorphosis.

Principal Terms

CLEAVAGE: cell division in the early embryo that, unlike division in adults, involves little or no growth between divisions

FERTILIZATION: the process by which the egg and sperm unite to form the zygote

GAMETES: the haploid cells, ova and spermatozoa, that fuse to form the diploid zygote

GASTRULA: the stage of development during which the endoderm (gut precursor) and the mesoderm (muscle and connective tissue precursor) are internalized

HAPLOID: having only one of each kind of chromosome

ZYGOTE: the single cell formed when gametes from the parents (ova and sperm) unite, a one-celled embryo

For thousands of years, humans have wondered how they and other organisms came to be. By 340 B.C.E., Aristotle had described the development of the chicken in the egg, but since most early embryos are too small to be seen by an unaided eye, his and later descriptions of development started with larger, more formed embryos. That did not change very much until the late 1600's, when development of the microscope gave a glimpse of life too small to be seen unmagnified. By the early eighteenth century, the developmental patterns of many organisms had been observed and described. There was, however, still much disagreement about how the early stages progressed. The majority of scientists believed in the theory of preformation, which said that a preformed embryo was present in the gametes. There were two main factions among the preformationists. The ovists believed that inside the egg was a tiny, fully formed organism that was stimulated to grow by the seminal fluid. Their opponents, the spermists, believed that the fully formed miniature organism was in the sperm and was nourished in its growth by the ovum. Thus seventeenth and eighteenth century drawings of sperm and of eggs often show fully formed bodies within. By the end of the eighteenth century, more and more scientists were deserting preformation in favor of the theory of epigenesis, first proposed by Caspar Wolff in 1789, which stated that development occurs through growth and remodeling of embryonic cells. Karl Ernst von Baer, who had published a collection of his observations and the observations of others, proposed that general features that are common to large groups of taxonomically related organisms appear earlier in development than more specialized features of individual species. After Darwin published his evolutionary theories, Müller, Haekel, and other proponents of Baer's law and of evolution proposed that the embryonic development of an organism (ontology) mirrored its evolution (phylogeny). Although this has been shown not to apply to all organisms or to all developmental sequences, it can be seen in the development of many embryos.

During the late nineteenth and early twentieth centuries, scientists' understanding of embryonic development increased dramatically as they began applying recently discovered knowledge in evolution, genetics, and cell biology to embryology. Edwin Ray Lankester and Hans Speeman were two prominent scientists who studied comparative embryonic development at that time. Also at that time, the new science of experimental embryology began as Wilhelm Roux and G. Schmidt manipulated the cells of amphibian embryos and began to discover how and why development occurred. Today, new discoveries in biology and chemistry are applied to the study of embryonic development.

Gametogenesis

The formation of gametes, eggs and sperm, is usually considered the beginning of embryology. In sperm formation, two things need to occur, reduction of chromosomes to the haploid state and maturation of the cytoplasm. During the first part of spermatogenesis, immature cells, called spermatogonia, form four haploid cells, called spermatids, by meiosis. Spermatids then go through a maturation process in which they become streamlined and motile. They also develop an acrosome that has enzymes needed to penetrate the egg. Like sperm, eggs must become haploid and mature, but both the timing and maturation are quite different. Maturation of the cytoplasm often begins before meiosis. All the cytoplasm of the early embryo comes from the egg, so immature ova are aided by various helper cells that increase each ovum's cytoplasm and add food stores, called yolk. The amount of yolk varies considerably, from mammals that have no yolk, to birds that have huge amounts. Depending on the species, meiosis can begin at any time during cytoplasmic maturation and can be a continuous process or have one or more pauses. In sea stars and many other organisms, meiosis is complete before fertilization, while in others, such as nematodes, the egg matures fully and is released by the ovary before any meiosis begins. Sperm penetration then triggers the onset of meiosis.

Fertilization and Development

Once sperm have reached the egg, the acrosomal enzymes must digest the various protective layers that surround the egg, and recognition structures on the surface of the sperm must be complementary to recognition structures on the egg cell membrane. The sperm's nucleus then enters the egg and fuses with the haploid egg nucleus. This forms a diploid cell called the zygote. Interestingly, when a sperm first penetrates the egg, the polarity of the cell changes and chemicals are released by the membrane, which make it impossible for other sperm of that species to enter the same egg.

Following fertilization, a period known as cleavage begins. During this time, cells divide rapidly with little or no growth between cell divisions. Cells become smaller and more numerous. At the end of cleavage, a structure called the blastula is formed. In some animals, such as echinoderms, amphibians, and nonvertebrate chordates, the blastula is a hollow ball of cells. In higher vertebrates, the blastula is a flat, dish-shaped structure, often called the blastodisc. In mammals, the blastula is called a blastocyst, and consists of a hollow ball of cells, called the trophoblast, and a group of internal cells, called the inner cell mass. During gastrulation, surface cells become internalized to form the three germ layers—ectoderm, mesoderm, and endoderm—that are seen in most animal embryos. A second internalization, this time of some ectodermal cells, forms the beginning of the central nervous system. After this neurulation, the various body organs begin to form from the three germ layers. As these changes progress, cells become less general and more specialized, a process called differentiation. Once the major organs have differentiated, the embryo matures and grows, a process usually called gestation. The time it takes for embryonic development varies considerably. In chickens and small rodents, the process takes about three weeks; in humans, it takes approximately nine months, while in elephants, the process can take almost two years. Some organisms emerge in very immature states that require more development. Amphibians and arthropods hatch as feeding larvae that must grow before they begin a metamorphosis that leads to the adult. Marsupials are also born at a very immature stage and must complete their embryonic development inside the mother's pouch.

—Richard W. Cheney, Jr.

See also: Asexual reproduction; Breeding programs; Cleavage, gastrulation, and neurulation; Cloning of extinct or endangered species; Copulation; Courtship; Determination and differentiation; Development: Evolutionary perspective; Estrus; Fertilization; Gamatogenesis; Hermaphrodites; Hydrostatic skeletons; Mating; Parthenogenesis; Pregnancy and prenatal development; Reproduction; Reproductive strategies; Reproductive system of female mammals; Reproductive system of male mammals; Sexual development.

Sir Edwin Ray Lankester

Born: May 15, 1847; London, England
Died: August 15, 1929; London, England
Fields of study: Anatomy, embryology, evolutionary science, marine biology
Contribution: Lankester elucidated the structures and developmental anatomy of many marine organisms and was also a champion of Darwin's theories of evolution.

From childhood, Edwin Ray Lankester was exposed to some of the greatest scientific minds of his day. His father, Edwin Lankester, was an eminent physician, numbering among his friends Charles Darwin and Thomas Henry Huxley, who were frequent visitors to the Lankester home. These men first exposed the younger Lankester to scientific thought, and he became their ardent disciple. After completing his university studies, Edwin Ray Lankester trained in Vienna, Leipzig, and Naples, before becoming a fellow at Oxford. He was a professor at University College, London (1874-1890), and at Oxford (1890-1898). During this time he continued his studies on animal development. He was the first to show that movement of cells through the primitive streak was by delamination (a movement of individual cells) and not by invagination (a term he coined for the inward migration of a layer of cells). He also coined the terms blastopore, for the opening formed during gastrulation, and stomadeum, for the embryonic region that gives rise to the mouth. While he was at University College, he was the prime mover in the founding of the Marine Biological Laboratory at Plymouth.

He left his professorship at Oxford in 1898 to become director of the natural history division of the British Museum, from which post he retired in 1907 to devote more time to his writing. He was a prolific writer, who wrote both for his scientific colleagues and for the popular press. He made biology, especially evolution and natural history, accessible to the nonscientist in weekly newspaper columns that were later collated and published in book form. Another of his books, *Extinct Animals* (1905), was the first book to introduce dinosaurs to the general public. He despised what he thought was quackery and was one of the first scientists to dismiss spiritualists and mediums as quacks. He was also vehemently opposed to the Lamarkian idea of the inheritance of acquired characteristics. Because of his tenacity in debate, he was often likened to a bulldog.

In 1911, a partial human skeleton was discovered near Piltdown in Sussex. Although the cranium was quite human in appearance, the lower jaw was more apelike. Many crude stone tools and bone fragments of extinct animals were also found in the same area. Lankester and many other scientists thought that this might be the skeleton of a species ancestral to modern humans. Sadly, the man who exposed spiritualists and Lamarkism had himself fallen for a hoax. Many years after its discovery, the Piltdown man skull was shown to be a composite of parts of a human cranium and a juvenile orangutan's jawbone that had been modified to look a bit more human. Lankester never knew of his mistake. He died in 1929, long before the hoax was unmasked.

—Richard W. Cheney, Jr.

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EMOTIONS

Types of animal science: Behavior, evolution
Fields of study: Developmental biology, ethology, evolutionary science

The idea that animals experience a wide range of emotions continues to be a controversial concept among scientists. Although it is a popular belief supported by numerous anecdotal reports, scientific researchers often stringently dismiss such evidence as signs of anthropomorphism.

Principal Terms

- AMYGDALA: subcortical brain structure related to emotional expression
- ANTHROPOMORPHISM: attributing human characteristics to animal behavior
- DOPAMINE: neurotransmitter involved in movement and reward systems
- FIELD OBSERVATIONS: observing behavior in naturalistic settings
- LIMBIC SYSTEM: brain structures related to the regulation of emotions
- OXYTOCIN: hormone involved with pleasure during bonding
- PRIMARY EMOTIONS: emotions related to innate motivations
- SECONDARY EMOTIONS: emotions with a strong social component

In attempting to prove the existence and extent of emotions in animals, researchers have struggled with the question of how to identify and measure feelings in various species. For many scientists, it is nonsense to speak of animal emotions without the capacity to objectively define and measure them. Such scientists have an aversion to the nonscientific tendency to ascribe humanlike characteristics to animals. Anthropomorphism is the term used to describe this tendency.

Defining and Communicating Emotions

Defining emotions can be difficult even in humans. Psychologists view emotions as organized psychological and physiological reactions to change in one's relationship to the world. An emotion is a positive or negative transitory experience that is felt with some intensity. Emotional reactions are partly subjective experiences and partly objectively measurable patterns of behavior and physiological arousal. The subjective experiences can include how a person appraises a situation and what actions result from that appraisal. For example, when a student receives a passing grade on an extremely difficult exam, she may experience joy after appraising the situation as a success. Even with this appraisal, however, humans cannot decide to experience joy or some particular emotion. The subjective aspects of emotions are triggered by the thinking self and felt as happening to the self. Objective aspects of emotions include learned and innate physiological responses and expressive displays. The expressive displays include smiles, frowns, and squinting of the eyes. The innate physiological responses are biological adjustments needed to perform the actions generated by the emotional experience. For example, if anger develops in a person, heart rate increases in order to supply additional oxygen to the muscles.

Since animals do not have the capacity of speech, any inner states cannot be expressed directly to a scientific observer. Consequently, field observations of behavior are often used to infer emotions in animals. There are problems, however, in assessing emotions through behavioral manifestations. It becomes difficult or impossible to attribute an emotion to an act with many possi-

The Mirror Test

In order to determine whether animals have the capacity for self-awareness, researchers commonly utilize the mirror test. The mirror test involves a basic procedure to test for self-consciousness. In one basic procedure, after an animal is anesthetized, patches of a bright dye are placed on different parts of the face. After awakening, the animal's reflection is shown in a mirror. If the subject touches the dyed parts of its face, self-consciousness is inferred. Many animals, including primates, elephants, birds, and dolphins, have been tested with this procedure. Only chimpanzees, orangutans, and humans have consistently shown the results indicative of self-recognition. Researchers concluded that most species cannot conceive of a self. Correctly identifying one's own reflection indicates senses of identity and of personal awareness. Without this capacity an animal would not be able to identify or model the mental states of other creatures or sympathize when witnessing the suffering of another animal. Humans routinely make inferences about what other people are feeling because of this capacity for self-awareness. Apparently, only a few other primates have the rudimentary capacity for self-consciousness, yet even those who pass the mirror test do not show a consistent pattern of being able to empathize with others. In general, some researchers have been critical of the mirror test, stating that chimpanzees may have clever minds, but they are blank minds. Chimpanzees may be able to learn, memorize, and problem solve sufficiently to pass the mirror test, but be unable to utilize their situation to take into account the experiences of others.

ble motivations. If a dog chews on the shoes of an owner who is out on a date, does this indicate jealously, anger, boredom, or merely a poorly trained pet?

Historically, animals have been seen from a mechanistic perspective as being without the capacity for humanlike emotions. Behaviorism dictated that instincts and patterns of reinforcement in the environment provided the motivation for the behavior of animals. For centuries, Christian religions also promoted the idea that animals lacked humanlike emotions. The role of animals was to serve the needs of humans. The concept of "speciesism" suggested that only humans were capable of emotions because of their special place in creation. Charles Darwin was one of the first scientists to study animal emotions, and to utilize field observations to ascribe emotions to animals. In his book, *The Expression of the Emotions in Man and Animals* (1872), Darwin stressed the communicative aspects of emotion. Positive inner states were expressed through a signal for sociability, while aggressiveness indicated a desire for isolation. He believed that species developed special social signals to indicate how they would react to a social encounter. Yet the behavioristic view of animals continued to dominate the debate about animal emotions. Over a hundred years later, Jane Goodall, in her book *The Chimpanzees of Gombe: Patterns of Behavior* (1986), was criticized by the scientific community for suggesting that chimpanzees had personalities and experienced excitement and joy.

Primary and Secondary Emotions

Today even the most critical scientists accept the fact that many animals experience a core group of emotions that are similar to those found in humans. Making the distinction between primary and secondary emotions, there exists some agreement about the basic emotions of fear and aggression. The primary emotions, such as fear, involve instinctual tendencies that are essential to survival. Fear permits escape from dangerous situations or predators. The fight-or-flight response is an instinctual pattern of behavior found in response to danger. The primary emotions, which are instinctual or hardwired into many species, can be demonstrated quite easily. When a specific stimulus is presented to an animal, a predictable response takes place. For example, if the shadow of a hawk is projected on the ground among a group of chickens, the birds will respond with "fear" and attempt to get under cover.

It is the realm of secondary emotions that creates the most controversy between those with opposing views about the extent of animal emotions. Expressions of love, grief, or jealousy may be commonplace among humans, but it is debatable whether they can be inferred in animals. Grief is commonly reported during field observations of various animals. The behaviors of elephants, chimpanzees, sea lions, and geese suggesting grief in response to the loss of a mate or offspring have been well documented. The dolphin who carries a dead baby around for several days is inferred to be experiencing both grief and love. Love has been attributed to animals such as swans or geese because of lifelong bonds that are established with a mate. Critics of these interpretations point out that animals may behave as if they are grieving or in love, yet there is no way of knowing whether this is an accurate reflection of their inner states. A central issue about the capacity of animals to experience a wide range of secondary emotions involves the ability to show self-consciousness. If an animal is able to be aware of its own inner states, it would then have the capacity to infer the mental states of others. With self-awareness comes the capacity for sympathy and empathy.

The Biology of Emotions

The scientists examining the biology of emotions have discovered some similarities between the brains of humans and animals that help to explain the basic primary emotions. Emotions seem to arise from the parts of the brain that are located below the cortex and are part of the limbic system. These regions of the brain have remained intact across many species throughout evolution. So far, the amygdala has been identified as the central site of emotion. This almond-shaped structure is at the center of the brain. Neuroscientists have found that rats will show a pattern of fear when a particular section of the amygdala is stimulated. If the amygdala is damaged, a rat will not show the normal behavioral responses to danger, such as freezing or running away. The rat with a damaged amygdala also will not demonstrate the accompanying physiological reactions to danger, such as increased heart rate or blood pressure. Research with humans has highlighted the amygdala's critical role in the learning of emotional associations and the recognition of emotional expressions in other individuals. Magnetic resonance imaging studies have shown that the amygdala shows activation to fearful stimuli. In humans, the brain is also involved in the control of emotional facial expressions. Smiles that occur spontaneously as a result of genuine happiness are involuntary. The extrapyramidal motor system, which depends on subcortical areas, governs involuntary smiles and fear reactions.

The chemistry of the brain also plays an important part in animal and human emotions. The neurotransmitter dopamine is released in copious amounts during periods of pleasure and excitement. Researchers have found that rats experience an increase of dopamine when engaging in activities that appear to suggest play. Research has also shown that if dopamine production is blocked in rats through the administration of a dopamine-blocking agent, the rat's play activity disappears. The effects of the hormone oxytocin have been studied in small mammals and appear to be related to sexual activity and bonding behaviors. In humans, oxytocin is released in mothers who are nursing their infants and is considered to aid in the mother-child bond. Researchers have investigated the role of oxytocin in bonding among voles. If a female vole is injected with oxytocin, the animal will quickly select a mate. When a female vole is given a drug to block oxytocin, however, mate selection never takes place.

Many scientists contend that it is illogical to believe that emotions appear suddenly in humans. If evolution takes place through the process of natural selection, the emotions found in humans would be present in early evolutionary ancestors. The similarities in brain anatomy and chemistry between animals and humans would then support the idea that some basic emotions exist in various species. Darwin believed that some facial expressions in humans are universal. These expressions are genetically determined and evolved as the most effective at telling others something about how a person is feeling. Research with infants shows the innate capacity to grimace in pain or to smile in pleasure. For the most basic emotions, people in all cultures show similar facial responses to similar emotional situations. For example, anger is linked with a facial expression recognized by almost all cultures. Perhaps it is this line of reasoning from the evolutionary context that provides the strongest support for the existence of a wide range of emotional reactions in animals.

—Frank J. Prerost

See also: Apes to hominids; Brain; Communication; Evolution: Historical perspective; Hormones and behavior; Instincts; Learning; Offspring care; Pair-bonding; Nervous systems of vertebrates; Reproductive strategies; Rhythms and behavior; Territoriality and aggression.

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ENDANGERED SPECIES

Types of animal science: Ecology, evolution
Fields of study: Conservation biology, genetics, population biology, reproduction science, systematics (taxonomy), wildlife ecology, zoology

Endangered species are those varieties of plants and animals that are in immediate danger of becoming extinct.

Principal Terms

ECOSYSTEM: a biological community and the physical environment contained in it

ENVIRONMENT: the physical, chemical, and biological conditions of the region in which a plant or animal lives

EXTINCTION: the complete destruction of a species

HABITAT: the place in which a plant or animal lives

SPECIES: a group of similar individuals that can breed among themselves and produce offspring

According to the U.S. Fish and Wildlife Service, 529 plant species and 432 animal species in the United States are in immediate danger of extinction. Another 192 species of plants and 40 species of animals are designated as threatened, meaning likely to become endangered in the near future. Globally, the International Union for Conservation of Nature and Natural Resources (IUCN) places more than two thousand species on its list of endangered and vulnerable species. About five species are added to the IUCN list every month. The International Council for Bird Preservation has announced that 1,029 of the 9,040 species of birds are endangered. Fish, especially freshwater fish, are among the most immediately threatened types of animals. About one-fourth of the number of species worldwide are in a state of dangerous decline.

Causes of Species Endangerment

The destruction of species is caused in four major ways: Humans have hunted other species out of existence; habitats, the environments in which plants or animals grow and develop, have been destroyed; new species, such as rats, cats, goats, or ground-covering plants, have been introduced into regions and displaced native species; and nonnative plants and animals have introduced diseases into environments, killing the existing species. For much of history, hunting was the major cause of species extinction. However, hunting has become less of a factor because governments and conservation authorities have imposed strict controls on the practice. In the second half of the twentieth century, habitat destruction and invasion by exotics (nonnative plants and animals) and the diseases they carry caused the most damage. Most biologists agree that whatever the factors involved, the rate of extinction has increased rapidly since the 1950's.

Some people have argued that the destruction of a single species of fish, bird, or flower would make little or no difference to the future of human life or the earth. They also suggest that extinctions have always taken place, even before human beings existed, and therefore are simply part of the natural process of existence. Who, for instance, would really want to have "saved" the dinosaurs? We should be glad they are gone. At least ten million species exist, so who would miss a few dozen or a few hundred of them? These arguments omit an important point. Individual species each inhabit a small part of an entire ecosystem, a community of plants and animals that are closely associated in a chain of survival. For example, plants absorb from the soil chemicals and minerals that are essential to their health. Animals then eat the plants—grasses, fruits, leaves, or flowers—and digest the nutrients they need for energy. Other animals, meat eaters (carnivores), then eat these plant eaters and get their energy from them. If a single species is removed from this chain, the whole ecosystem can suffer unknown and perhaps terrible consequences.

The death of an entire species constitutes a loss that cannot always be measured in economic terms. The American biologist William Beebe made the point that any species that is lost diminishes the quality of life for everyone:

> The beauty and genius of a work of art may be reconceived, though its first material expression can be destroyed; a vanished harmony may yet inspire the composer, but when the last individual of a race of living things breathes no more, another heaven and another earth must pass before such a one can be again.

Deaths of entire species grew more frequent in the 1900's.

How Species Are Lost

One example of this loss was the passenger pigeon, a bird so numerous in the 1820's that John James Audubon, the famous American painter and collector, wrote that the flapping of wings of flocks numbering in the hundreds of millions on the Great Plains sounded like the roar of thunder. More than nine billion of the pigeons were alive in 1850, yet slightly more than sixty years later, exactly one bird, Martha, survived, in the Cincinnati Zoo, where she had been taken in 1912. The population fell from nine billion to one in little more than half a century, then to zero when Martha died on September 1, 1917. People had found these pigeons delicious to eat and easy to kill. They formed hundreds of hunting parties, killing more than fifty thousand birds a week. No one dreamed the passenger pigeon could ever be exterminated.

The same fate almost befell the American bison, often called the buffalo. Before the coming of railroads and white settlers in the 1860's and 1870's, the bison numbered more than 100 million. Native Americans hunted the bison, eating their flesh and using the skins for clothing and shelter, but they killed only what they needed. The settlers, however, saw the bison as a problem that needed to be solved. Huge herds of bison crossed railroad tracks, forcing passenger trains to stop, and the animals interfered with farming, knocking down fences and trampling grain fields. Railroad companies and the U.S. Army sent out hunting parties to get rid of the bison. By 1890 fewer than one thousand bison survived in a herd that had managed to escape far into northern Canada. The extermination ended only after this small herd was given protection by the Canadian government.

Stories of other near extinctions are numerous and frightening but demonstrate that action can be taken to save some if not all of the endangered species. Whales, which had been hunted since the 1600's, faced possible extinction until action was taken to reduce hunting in the 1970's. Whales were easy to kill and provided oil and bone. Whale oil was the major substance burned in lamps until the electric light largely replaced oil-burning lamps in the 1880's. Europeans hunted the Atlantic whale, called the right whale because it was the "right" one to kill, into virtual extinction by the 1860's. When the right whale became too hard to find, hunters turned to the Pacific right whale and then the bowhead whale before action was taken by the world community to save remaining whales.

Greed and Ignorance

Human greed has brought death or near death to many species. The desire for fur coats has killed nearly all jaguars, snow leopards, and various species of fur seals. Pribilof Island fur seals were hunted nearly into extinction in the late 1800's. A treaty between the United States, Canada, and Russia established limits on killing the species in its remote northern Pacific island habitat, but enforcement has proved difficult, and thousands of seals have been slaughtered despite international protection.

The belief that some animals are nuisances has led to the near extinction of wolves, grizzly bears, cougars, and coyotes. These predators have been poisoned and shot by the thousands and have become endangered species as a result. Attempts to kill insects with pesticides in order to control the spread of disease and improve crop yields were successful but had an unfortunate side effect. Chemicals from the pesticides worked their way into ecosystems, killing millions of other forms of life. In the 1950's, dichloro-diphenyltrichloroethane, or DDT, was used to kill malaria-carrying mosquitoes, but the chemical infested the whole food chain. It entered plants that were eaten by animals and affected birds, fish, and butterflies. Pesticide poisoning also diminished the numbers of the bald eagle and peregrine falcon, which started to come back only after rigid controls on pesticides were established.

Events on the island of Madagascar, a large island in the Indian Ocean off the east coast of Africa, demonstrate most fully the deadly consequences of habitat destruction. About 180 million years ago, the island was attached to the African continent, then was split off after a series of geological catastrophes and ended up 250 miles to the east. The split occurred just at the time mammals were emerging as a class of animals in Africa. One mammal species, the monkeylike lemur, became isolated on Madagascar and increased abundantly. Other animals caught on the island included several kinds of giant birds, including one that weighed a thousand pounds and stood ten feet tall. The island was isolated for millions of years, allowing hundreds of species found nowhere else in the world to evolve in the diverse island ecosystems. Madagascar had deserts, rain forests, dry forests, and seashores. About 99 percent of its reptiles, 81 percent of its plants, and 99 percent of its frogs were unique and tied specifically to the island's food chain. About nine thousand years ago, the Malagasy people began to arrive on the island. They hunted, fished, began to grow crops, and in the process destroyed more than 90 percent of the forests that covered Madagascar. Dozens of species died as a result, including the giant elephant bird, which was gone by 1700. Ten out of thirty-one species of lemur had died out by 1985. The loss of Madagascar's forests caused terrible erosion, which resulted in flooding and the destruction of more trees. Madagascar's entire ecological system is now threatened, and hundreds of unique species are listed as endangered. Only major restrictions on farming and habitat destruction can save these animals.

The United States' Endangered Species Preservation Act

The implications of species and habitat destruction were first described in books such as Rachel Carson's *Silent Spring* (1962). Carson, a biologist with the U.S. Department of Interior, wrote about the effects of DDT and insecticides on birds and other animals. Her book inspired Congress to pass the Endangered Species Preservation Act in 1966. This law authorized the secretary of the interior to protect certain fish and wildlife through the creation of a National Wildlife Refuge System. Congress strengthened the law in 1969 by restricting importation of threatened species and adding more domestic species to the list of those deserving protection.

The U.S. Department of the Interior published its first list of endangered species in 1967. The list included seventy-two native species of animals, including grizzly bears, certain butterflies, bats, crocodiles, and trout. No plants were on this list. In 1973, President Richard M. Nixon signed into law an Endangered Species Act that gave the secretaries of the interior and of commerce responsibility for creating a list of endangered animals and plants, or species in immediate danger of extinction. Another list would include species threatened with extinction, or those likely to become endangered in the foreseeable future. Once an animal or plant was on either of the lists, no one could kill, capture, or harm it. Penalties for violators were increased, and international or interstate trade of listed species was prohibited. Fines

Recoveries from Near Extinctions

In the wild, herds of American bison (*Bison bison*) were decimated to extinction east of the Mississippi River by 1830, and in the west by 1897. When the American Bison Society formed in 1905, only about 25 protected bison remained in Yellowstone National Park. A census of captive herds taken in 1908 indicated that 1,116 bison were held in 15 zoos and private collections. Starting in 1907 with fifteen animals from the New York Zoological Park, captive bison were relocated to newly established reserves. By 1933, the bison herds numbered 4,404 animals. Today, bison are once again common in their western range.

Likewise, the European bison, or wisent (*Bison bonasus*), became extinct in the wild in the 1920's. The International Society for the Protection of Wisent was founded in Europe in 1923. The Frankfurt Zoo staff, and later the Warsaw Zoo staff, established a studbook for wisent in 1932. Cooperative breeding programs among European zoos increased wisent herds in captivity, which were then used to restock the wild forests. Another animal saved from extinction by European zoos was the Przewalski's horse (*Equus caballus przewalskii*). When the Polish general for whom the horse is named found the last herd in western Mongolia in the 1870's, he brought some of the horses back to Poland. From this initial captive stock, zoos bred enough horses to release them back into their natural habitats in the wild.

The Catholic missionary Armand David, who also collected natural history specimens for the natural history museum in Paris, found a herd of Père David's deer (*Elaphurus davidianus*) at a Chinese royal game park in 1865. Not sure of what they were, he obtained some living deer and brought them back to the London and Berlin Zoos. While the captive herds were increasing at European zoos, the wild herd in China had died out by 1920, due to flooding of the park by the nearby Yellow River in 1894, and decimation of the herd for food during the Boxer Rebellion of 1900. To further increase the deer population, the eleventh Duke of Bedford gathered the European animals onto his Woburn Abbey estate between 1893 and 1895. This propagation effort increased the herd to 88 animals in 1914 and 255 by 1948. By 1986, there were some 1,500 deer in England, and some were sent back to China to repopulate their natural habitat, including the park where the last herd was originally found.

Arabian oryx (*Oryx leucoryx*) were hunted to extinction on or about October 18, 1972. However, this possibility was anticipated by the Fauna Preservation Society, which captured four animals before the last remaining herd was gone. A captive propagation program began at the Phoenix Zoo, in Arizona, and in 1975 the herd had increased to forty-five. Some of these were sent to other zoos to form additional herds. By 1986, there were 172 oryx in thirteen American collections, six European collections had another 30 animals, and ten collections in the Middle East had 528 oryx. Reintroduction of the oryx to its native habitat began in 1978 and has achieved good success; however, hunting has again become a problem. Nevertheless, despite a need for improved conservation education and protection, the Arabian oryx remains in the wild.

—Vernon N. Kisling, Jr.

up to ten thousand dollars could be imposed for knowingly violating the act and one thousand dollars for unwittingly violating it.

A separate provision of the law mandated that federal agencies could not engage in projects that would destroy or modify a habitat critical to the survival of a threatened or endangered plant or animal. This provision became a very important tool in the battle to save species. Friends of wildlife used it to block highway and dam projects, at least until government officials could prove that construction would have no major impact on a fragile ecosystem. The law even called for affirmative measures to aid in the recovery of listed species. The secretaries of the interior and of commerce were required to produce recovery plans detailing steps necessary to bring a species back to a point where it no longer needed protection.

Poaching

Poaching is the illegal hunting, trapping, or taking possession of nongame wildlife. Many animals are killed so that their body parts can be sold. Others are trapped and sold as pets. Poaching poses a major problem for protecting and sustaining wildlife populations throughout the world. In some areas, it is causing a devastating effect on some of the wildlife, particularly endangered species.

Trophy heads of bighorn sheep, elk, moose, deer, goats, and bears all fetch high prices, as do the fetuses, antler velvet, hooves, and tails of deer, elk, and caribou, the feathers of eagles, hawks, and other birds of prey, and the hides, gallbladders, paws, genitals, claws, and teeth of bears. An adult grizzly bear can be worth up to $15,000 on the black market. Its gallbladder can be worth $1,000 or more, a paw worth $500, and a large claw worth $300. The bile from the gallbladder is highly valued in traditional Asian medicines. Paws are culinary treats in some Asian communities.

The demand for its gallbladders has pushed the Asiatic black bear to the brink of extinction. A dramatic decline has also occurred in recent years with the California black bear. Canada's estimated 300,000 black bears are not yet endangered, but it is estimated that 40,000 black bears are poached for body parts in Canada every year.

Numerous animal populations in Africa, particularly tigers, rhinos, and elephants, have severely diminished due to poaching. There are only a few hundred tigers left. Some African countries have declared war on poachers to save the rhinoceros from extermination. Approximately 600,000 African elephants, over half of the population, were killed during the 1970's and 1980's for their ivory tusks. Some African countries have called for eased restrictions on a global ivory trading ban enacted in 1989, so that they can sell their stockpiled tusks to raise funds for domestic conservation programs. If allowed, this could send a dangerous signal to poachers that elephant ivory is again in demand on the world market.

India's elephant population is teetering on the brink of extinction due to rampant poaching and brutal training methods. Unlike African elephants, only male Asian elephants have tusks, and fewer than eight hundred are left in India. As a result of ivory poaching, the Indian male elephant population is dropping by 10 percent every year.

Image Not Available

Poaching has greatly contributed to many animal species becoming rare and vulnerable to extinction. Some of these include whale sharks, giant pandas, orangutans of Indonesia, leatherback turtles, Chinese river dolphins, giant tortoises in the Galápagos, blue crabs, and mountain gorillas of central Africa. As members of a species become rare, they get the dubious distinction of being listed as a threatened or endangered species, which only makes them more valuable to poachers.

—Alvin K. Benson

Money was appropriated for states to design recovery programs, and most states established plans of their own to deal with local crises.

A major threat to the 1973 law arose in 1978 during the Tellico Dam controversy. The Tennessee Valley Authority, a federal government agency, proposed building a hydroelectric dam on the Tennessee River in Loudon County, Tennessee, in the late 1970's. Shortly after plans were made public, a scientist from the University of Tennessee discovered a three-inch-long fish, the snail darter, that was unique to that area. Building the dam, a $250 million project, would destroy that snail darter's habitat and eliminate the fish. Environmentalists successfully argued in federal court that the dam had to be abandoned. The U.S. Supreme Court supported the ruling of the lower court, arguing that when Congress passed the law, it had intended that endangered species be given the highest priority regardless of the cost or other concerns involved. However, in 1981, Congress enacted a special exemption that excluded "economically important" federal projects from the act. A federal judge then found the Tellico Dam to be without economic importance, and construction was again halted. Congressmen friendly to dam interests then slipped an amendment directing completion of the dam onto an unrelated environmental bill, which passed, and Tellico was constructed. However, the principle of protection remained intact, and the 1973 act remained in force. The snail darter apparently survived, too, as scientists found it living in a river not far from the spot where it was originally discovered.

International Trade Bans

The 1973 act also made the United States a partner in the Convention on International Trade in Endangered Species of Wild Flora and Fauna. This treaty came out of a conference in Washington, D.C., attended by representatives from eighty nations. It created an international system for control of trade in endangered species. Enforced by the International Union for Conservation of Nature and Natural Resources (IUCN) headquartered in Switzerland, the convention has more than one hundred members. The IUCN publishes a series of lists in its *Red Data Book* designating three categories of species. Category one consists of those in immediate danger and therefore absolutely banned from international hunting and trading. Animals and plants in categories two and three are not immediately threatened but require special export permits before they can be bought and sold because their numbers have been seriously reduced.

This convention has a major flaw, a loophole that can be exploited by any member. A nation can make a "reservation" on any listed species, exempting itself from the ban on trade. Japan has been the most frequent user of the reservation, exempting itself from controls on the fin whale, the hawksbill turtle, and the saltwater crocodile, all on the IUCN's most endangered list. Unless this loophole is closed, the IUCN can do little to save extremely threatened species.

Successes in Restoring Endangered Species

Several species in the United States—the California condor, the black-footed ferret, whooping cranes, and a bird called the Guam rail—have been saved from extinction because of the 1973 Endangered Species Act. The road to extinction has also been reversed for the brown pelican, found in the southeastern states, the American alligator, which had been hunted almost to death in Florida, and the perigrine falcon in the eastern states. Other species, however, such as the dusky seaside sparrow and the Palos Verdes butterfly, have totally disappeared.

The spotted owl, found in parts of the rain forest in Oregon and Washington, has attracted a good deal of attention because of efforts to save it. The case of the owl points to the most difficult questions raised by the act: Which comes first, the welfare of the plant or animal or the economic needs of people? Each pair of spotted owls needs six to ten square miles of forest more than 250 years old in which to hunt and breed. The owls also need large hollow trees for nesting, plus large open fields in which to search for mice and other small animals. A suitable ecosystem that meets all these needs is found only in parts of twelve national forests in the region. At the same time, loggers in the areas need jobs. The two interests, the lumber industry and environmentalists, collide, and it is left to the courts to determine which interest will prevail or whether a compromise can be arranged.

Outside the United States, the future of endangered species appears much grimmer. Scientists at IUCN think several hundred thousand species will disappear by the end of the second decade of the twenty-first century. Many of these species have never even been identified or named. The most endangered habitats in the world are the tropical rain forests, which have been reduced by half, nearly 3.5 million square miles, during the twentieth century. About 43,000 square miles is destroyed each year, mainly to provide farms and cattle ranches. The most threatened large animal species in these forests are the large cats, including tigers, jaguars, and leopards; fifteen of the twenty-five species of cats that live in the forests are on the most endangered list. One solution to forest destruction has been the creation of large wildlife refuges. Several African nations have created one or more of these, but there are limits to the amount of land available for conservation efforts. Another solution is the establishment of more wildlife zoos. Several zoos have successful programs for saving species on the very edge of extinction. However, capacity is limited, and the very small numbers of animals in a zoo's herd create problems of interbreeding and the handing down of recessive genes.

For many species, it is too late to do very much, so scientists and biologists divide populations into three groups: those that can survive without help, those that would die whatever help was provided, and those species that might survive with help and would certainly die without it. Environmentalists focus their efforts on the plants and animals that fall into the third category. Resources are limited, however, and much work needs to be done, or extinctions will take place at a pace as yet unseen in the history of living things.

—Leslie V. Tischauser

See also: Biodiversity; Breeding programs; Cloning of extinct or endangered species; Demographics; Ecological niches; Ecology; Ecosystems; Extinctions; Genetics; Habitats and biomes; Mammals; Natural selection; Paleoecology; Paleontology; Plant and animal interactions; Pollution effects; Population analysis; Population fluctuation; Population genetics; Rain forests; Wildlife management; Zoos.

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ENDOCRINE SYSTEMS OF INVERTEBRATES

Type of animal science: Physiology
Fields of study: Anatomy, biochemistry, invertebrate biology

Many invertebrates have endocrine systems almost as complex as vertebrate endocrine systems. In most invertebrate phyla, the principal source of hormones is neurosecretory cells. Neurosecretory hormones have been found in all the larger invertebrate phyla.

Principal Terms

BUDDING: a form of asexual reproduction that begins as an outpocketing of the parental body, resulting in either separation from or continued connection with the parent, forming a colony

DIAPAUSE: a resting phase in which metabolic activity is low and adverse conditions can be tolerated

MOLT: the process of replacing one exoskeleton with another

NEURONS: cells specialized for the conduction of electrical signals and the transmission of information (nerve cells)

NEUROSECRETORY CELLS: specialized neurons capable of manufacturing and releasing hormones (neurosecretions or neurosecretory hormones) and discharging them directly into circulation

PHOTOPERIOD: the measure of the relative length of daylight as it relates to the potential physiological responses that exposure to daylight evokes

TARGET ORGAN: a specific body part that a particular hormone directly affects

TROPHIC HORMONE: a hormone that stimulates another endocrine gland

The endocrine systems of many invertebrates are nearly as complicated as vertebrate endocrine systems. The principal source of hormones in most invertebrate phyla is neurosecretory cells. These hormonal mechanisms have been found in arthropods, annelid worms, mollusks, and echinoderms. The physiological processes that are affected are generally fundamental, long-term ones that include such biological phenomena as growth, regeneration, reproduction and development, and certain metabolic processes.

The subkingdom of animals made up of all vertebrates and most invertebrates (protozoa and sponges are not included) is called the Metazoa, which is defined by the presence of nervous and endocrine systems in the animals in the group. These systems coordinate the activities of the animal so it can function as a whole. The nervous system is important in rapid communication, such as contraction of muscles for movement, while the endocrine system controls long-term processes within the body, such as the growth of organs or maintenance of appropriate metabolic concentrations. Chemical messengers released by the endocrine systems have to travel to specific target organs to exert their effects. The means of travel is the circulatory system. Because it takes time for the chemicals to accumulate to effective concentrations, they must be stable enough to remain in the body without undergoing chemical changes and without being excreted. These chemical messengers—hormones—are, then, well suited to working over long periods of time. The nervous and endocrine systems do not work independently of one another, however. It is probable that most animals' central nervous systems are strongly affected by hormones much of the time.

Neurosecretory Cells

In 1928, German chemist Ernst Scharrer hypothesized that certain nerve cells have qualities of both nerve and endocrine gland cells. These neurosecretory cells are neurons which are cellularly like gland cells, but are widespread within the invertebrate body. They receive nervous impulses, but rather than communicating through synapses with other neurons or effector cells, they terminate close to the circulatory system and release substances which travel to act on organs or upon endocrine glands. These neurosecretory substances, therefore, are themselves hormones. Neurosecretory cells are usually found in clusters within the central nervous system. Extending from the cell bodies are axons that terminate in swollen knobs associated with blood spaces. Terminals that are aggregated into a body are called neurohemal organs. Neurosecretory material is produced by the cell bodies, transported down the axons, and stored in the swollen knobs. Release is accomplished by exocytosis.

To be classified as a neurosecretory cell, three criteria must be met: The cell must have the structural features of a neuron (cell body and axonlike fibers); the axons must not synapse with other cells but end in close association with an area of body fluid (generally a blood vessel or sinus, the combination making a neurohemal organ); the neuron must contain membrane-bound vesicles within the cytoplasm. There are, in addition, two physiological criteria: Destruction of these clustered cells, or the areas or organs where they are found, produces an alteration of existing internal conditions within the organism that can be restored by replacing the removed organ or injecting an extract from it; implantation of an organ thought to be neurosecretory into a normally functioning animal brings about a change in internal state by either prompting or inhibiting the occurrence of certain events.

Neurosecretions in invertebrates may influence behavior or target another endocrine gland by trophic neurosecretions or trophic hormones. For example, in many insects neurosecretions from neurosecretory cells in the brain exert a trophic effect on the prothoracic glands, which then produce and release the hormone ecdysone that controls molting, the developmental sequence of insects. There are other examples of how hormonal release is dependent on and dictated by the nervous system. Most animals respond developmentally to environmental changes, such as seasonal variations throughout the year. If unfavorable conditions develop, the animal may compensate by going into dormancy or migrating, or may overcome the conditions by other changes in habit or physiology. Even brief fluctuations, such as a temporary shortage of food or the absence of suitable mates, may dramatically affect development. The mating act in a female insect may speed up the development of her eggs; the changing day length may control when metamorphosis begins in annelids. Stimulation of sense organs sets up nervous messages that result in changes in the amounts of circulating hormones, which generate these “new” responses.

The Roles of Invertebrate Hormones

Invertebrate hormones play as many roles as there are invertebrate phyla. In the less highly organized invertebrates, endocrine glands are apparently absent; hormonal coordination depends on neurosecretions. Hormones released in the plant hydra are believed to come from the hypostomal region (the nerve ring around the oral opening) and from actively growing areas and are thought to regulate growth, regeneration, and the development of sexuality. Little is known about substances termed “wound hormones” in planarians, but their presence in wounded tissues has been inferred, even though their site of production is unclear.

All annelids possess neurosecretory cells in the brain that control growth, reproduction, and maturation. In nereids, reproductive body forms releasing eggs and sperm are controlled by at least one brain neurohormone, and normal reproductive development appears to depend on the gradual withdrawal of brain neurohormones with increasing age. Regeneration, too, is probably controlled by neurohormones.

In starfish and sea urchins, spawning of eggs is preceded by release of a "shedding hormone" found only in the radial nerves. This hormone, known as gonad-stimulating substance, also stimulates the manufacture and secretion of a second substance by the gonads called meiosis-inducing substance (MIS). MIS causes the follicle cells to pull away from the gametes so the gametes can be expelled more easily; it induces meiosis within the oocytes, and, after diffusing into the coelomic fluid, stimulates muscle contractions which cause spawning.

Many mollusks have neurons resembling neurosecretory cells that change their apparent secretory activity with conditions such as reproductive state. In a few cases, evidence has been found for neurosecretory control of reproduction, water balance, or heart function. Cephalopods such as squid, however, are one of the few classes of animals that possess endocrine glands. The cephalopod brain is connected to the optic lobes by short optic stalks bearing optic glands. As the animal matures, the size of these glands increases. These glands function in the control of reproductive development. Glands on the gills, called mesodermal branchial glands, are also endocrine organs and are thought to function similarly to vertebrate adrenal glands.

Certainly the best-studied invertebrate system is that of insects. Insects possess discrete clusters of neurosecretory cells, well-developed neurohemal organs, and even nonneural endocrine glands. The insect endocrine system has four major components: the corpora cardiaca, a group of neurosecretory cells in the brain, the corpora allata, and the thoracic glands. The corpora cardiaca, closely associated with the heart, store and secrete hormones from the brain as well as producing their own inherent hormones. Along with the brain's neurosecretory cells, they compose the cerebral neurosecretory system. Molting is controlled by hormones called ecdysteroids produced under the brain's direction. Secretion of these ecdysteroids stimulates the release of ecdysone from the prothoracic gland. Ecdysone, also called the molting hormone, stimulates the development of adult structures but is held in check by juvenile hormone (JH), which favors the development of juvenile characteristics. During juvenile life, JH predominates and each molt yields a larger juvenile. High levels of JH are released by the corpus allatum during early stages of life. Its major function, then, is to ensure that when molting is triggered by ecdysone secretion, the next larval stage results. When the final stage is reached, ecdysone production dramatically falls, but sufficient levels are produced to induce a molt that will result in the adult stage. Similar systems are found in the crustaceans.

Because invertebrates make up about 95 percent of the species in the animal kingdom, one might anticipate a great diversity of invertebrate endocrine mechanisms. Eventually, this expectation may be confirmed; but knowledge of endocrine systems in many invertebrate groups is, for the most part, incomplete. What is known is that in most groups of invertebrates, neurosecretory systems are distinctly more prominent than nonneural endocrine glands, which occur in very few cases.

Refinement of Study Techniques

Until the 1960's, the search for hormonal regulators in invertebrates was largely unsuccessful because early experiments on gonad transplantation from insects of one sex to those of the other and injection of vertebrate hormones into invertebrates yielded negative results. Strides made in the last twenty-five years are mostly the results of refinements of microscopic, operative, and analytical techniques, both chemical and physical. Arthropods have provided the most accessible material for study, and more is known about the phenomenon in crustaceans and insects than in any other group. The range of investigation is expanding, however, and neurosecretion in invertebrates is not only accepted but recognized as widespread among them.

Many problems are generally associated with determining the functions of the neurosecretory system. The classical experimental method involves removal of the suspected endocrine gland

and then reimplanting it at another location in the body. If the effects of removal are reversed and normal conditions return when the organ is relocated, then a hormonal mechanism is probably involved. The problem arises, however, because removing a neurohemal organ will leave behind the cut ends that may continue to release hormones, perhaps in an uncontrolled manner. A new neurohemal organ may be rapidly regenerated so that the effects of lessened amounts of neurosecretory hormones cannot be observed. In addition, reimplanting the organ may produce several hormones in the animal in abnormal concentrations or proportions. Hormonal deficiency may not be obvious immediately because hormones stored outside the neurohemal organ may be secreted or leached out for some time after the organ's removal. Yet another problem encountered is the lack of distinct neurohemal organs; instead, scattered neurosecretory cells may be found throughout the nervous system. It is therefore difficult to determine the exact function of the mechanisms because of the virtual impossibility of removing and testing these individual cells. In these cases, the neurosecretory nature of the cells is deduced based on their structural and chemical similarity to those whose function has been already verified in other animals.

Typical of the early work on insect growth hormones was the work done in the 1930's in England by Vincent B. Wigglesworth on the metamorphosis of a bloodsucking insect named *Rhodnius*. This insect goes through five immature stages, each separated by a molt, until it reaches adulthood. During each of these stages, it engorges and stretches its abdomen by ingesting a blood meal. This filling meal apparently stimulates the release of hormones that cause molting at the end of a specified time interval following the meal. Usually, the final molt (to adulthood) occurs about twenty-eight days after the blood meal. If the insect is decapitated during the first few days after its meal, molting does not occur, even though the animal may live for several months longer. Decapitation more than eight days after the blood meal does not interfere with molting, although a headless adult is produced. Wigglesworth further showed that joining the circulatory system of a later-decapitated insect to that of an earlier-decapitated insect allows both to molt into adults. It appears obvious that some stimulus passes via the blood from one insect to the other and induces molting; it is assumed that the stimulus is a hormone that is secreted about eight days after the blood meal.

Since Wigglesworth's time, studies typical of his work have shown evidence of hormonal activity and control of many other invertebrate phyla. Experimentation with insects still outweighs all other studies, however, since they are so available and easy to work with because of their size.

Comparing Vertebrate and Invertebrate Hormones

The study of invertebrate hormones began as an attempt to draw parallels between invertebrate hormones and known vertebrate hormones. Experimenters were virtually forced to look for these similarities because of legal restrictions placed on the use of vertebrates for experimental study. The end results, however, have shown that invertebrate hormones share little with vertebrate hormones.

One of the few similar hormones, in structure at least, is prothoracicotropic hormone (PTTH), isolated from the heads of adult silkworms. (PTTH stimulates the prothoracic gland to release ecdysone, which then regulates molting and growth.) Though structurally similar to vertebrate insulin, insect insulin has no functional link with vertebrate insulin.

The interaction of neurohormones and the nervous system has been studied using the lobster, tying the release of neurohormones to its behavior. By introducing neurohormones via injection, one can induce behavioral changes, such as increased aggression. By working with these crustaceans, the apparent relationship among neurohormones, the nervous system, and behavior modification may be used in observing and controlling animal behavior.

—Iona C. Baldridge

See also: Circulatory systems of invertebrates; Courtship; Endocrine systems of vertebrates; Hormones and behavior; Hormones in mammals; Invertebrates; Mating; Metamorphosis; Molting and shedding; Muscles in invertebrates; Pheromones; Regeneration; Reproduction; Reproductive strategies.

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ENDOCRINE SYSTEMS OF VERTEBRATES

Types of animal science: Development, physiology
Fields of study: Developmental biology, reproduction science

Endocrinology is a relatively young branch of physiology. It deals with chemical messengers, carried in the blood, that stimulate specific responses. The responses are agents in the control of growth, development, metabolism, osmotic and ionic regulation (hydromineral metabolism), reproduction, and control of hormone secretion itself.

Principal Terms

FEEDBACK: in endocrinology, this usually refers to one hormone controlling the secretion of another that stimulates the first, usually in the form of negative feedback, in which the second hormone inhibits the first

GLAND: a tissue composed of similar cells that produce a hormone

HORMONE: a blood-borne chemical messenger

RECEPTOR: a protein molecule on or in a cell that responds to the hormone by binding to it and initiating a series of events that compose the response

TARGET: cells that contain hormone receptors

Endocrine systems have been known only since the early twentieth century. The first known hormone was discovered around 1902 when William Bayliss and Ernest Starling discovered, in dogs, secretin, a hormone that stimulates pancreatic exocrine secretion in response to acid in the small intestine. Since that date, dozens of other hormones have been discovered, which control all aspects of growth, metabolism, and reproduction.

The endocrine system consists of glands that secrete chemical substances called hormones in response to specific signals. The hormones are secreted into the blood stream, where they travel to specific target cells or tissues, which contain specific receptors that allow the hormones to bind, initiating the response. Classically, hormones were thought to belong to two very different groups, the polypeptide (small protein) hormones and the steroid (cholesterol-like) hormones. It is now known that hormones can be composed of several different kinds of molecules, including fats (prostaglandins) and even gases (nitric oxide). Proteinlike hormones bind receptors found on external cell membranes to stimulate second messengers, such as cyclic adenosine monophosphate (cAMP), which activate enzymes and other cellular substances to produce a response. Steroid hormones enter target cells and bind intracellular receptors. The hormone-receptor complexes migrate to the nucleus and activate gene expression, which results in the response. This, like descriptions of many concepts in biology, is an oversimplification, and many hormones appear to work by a combination of the two mechanisms.

Endocrine Control Systems

The endocrine secretions are controlled by the nervous system through a complex chain of command. Receptors around the body monitor sensory signals and alert the brain, which then relays the information to specific cells in the median eminence of the hypothalamus. For example, temperature receptors in the skin detect cold and inform the brain of potential body cooling. The brain then relays the information to cells in the hypothalamus, which secrete a molecule called thyrotropin-releasing hormone into a blood vessel called the hypothalamo-hypophysial portal vessel. This blood vessel delivers the releasing hormone to the anterior pituitary gland, which in turn secretes a hormone called thyroid-stimulating hormone (TSH), or thyrotropin, into the blood. The TSH travels to the thyroid gland to stimulate the secretion of thyroid hormones, which stimulate metabolism in liver, muscle, and other cells. Heat produced as a by-product of metabolism warms the body. Some hormones are under dual control. Growth hormone (somatotropin) is stimulated by a releasing hormone called somatocrinin and inhibited by somatostatin. There are about seven anterior pituitary hormones that are controlled by similar mechanisms. Adrenocorticotropic hormone (ACTH) is controlled by corticotropin-releasing hormone. Melanocyte-stimulating hormone (MSH) and prolactin are under dual control by both releasing hormones and inhibiting hormones. The gonadotropins—follicle-stimulating hormone (FSH) and luteinizing hormone (LH)—are under the control of a single releasing hormone called gonadotropin releasing hormone. All of these control systems are subject to feedback loops which usually involve negative feedback (for example, TSH secretion being inhibited by thyroid hormone), but positive feedback loops exist (estrogen feeding back positively to stimulate LH secretion).

Hormones Controlling Growth, Development, and Metabolism

The major control of growth is carried out by somatotropin (STH) from the anterior pituitary. STH does not act directly, however. Cells in the liver respond to STH to produce somatomedin, which stimulates bone growth and muscle production. Prolactin, a protein similar to STH, stimulates breast development in female mammals. In an interesting case of hormone evolution, thyroid hormone stimulates amphibian metamorphosis (tadpole to frog transition); however, in warm-blooded vertebrates, this same hormone has evolved to stimulate metabolism for the purpose of heat production in birds and mammals. Several hormones stimulate metabolism for different reasons. Epinephrine (adrenaline), in addition to elevating blood pressure, mobilizes glucose from glycogen, in response to stress. Steroid hormones, also produced in the adrenal glands, stimulate the production of glucose from noncarbohydrate molecules (gluconeogenesis). The stimulus for this is prolonged stress, for example, starvation. These glucocorticoids, such as cortisol and corticosterone, evolved early and are very important in combating stresses resulting from migration among birds and even fish. The pancreatic hormones insulin and glucagon also effect energy metabolism. These two proteins regulate blood sugar, fat, and protein levels. After eating, insulin stimulates transport of these molecules into liver, fat, and muscle cells and then stimulates the incorporation of the simple molecules, such as glucose, amino acids, and fatty acids, into larger storage molecules, such as glycogen, protein, and fats. Glucagon has opposite actions. After a prolonged period without food intake, glucagon stimulates breakdown of complex molecules, such as glycogen and fats, into simple molecules, which are released into the blood and made available to metabolizing cells. These two hormones act independently of the pituitary and respond directly to blood-borne signals such as glucose concentration. This regulation ensures a steady delivery of nutrients to metabolizing cells in animals who only eat intermittently.

Control of Water and Salt Balance

The state of hydration and salt levels in the body are of critical importance to vertebrate animals. Dehydration has obvious severe detrimental consequences. The salt composition of body fluids is equally important. For enzymes and other proteins such as antibodies and even hormones to function properly, salt concentrations (ionic concentrations) must be maintained. For example, blood levels of sodium and potassium must be maintained at approximately 145 and 4 millimolers, respectively, in most vertebrates. These levels are lower in amphibians (100 and 2 millimolers). Water content of the body is controlled primarily by a posterior pituitary hormone called antidiuretic hormone (ADH). When the body becomes dehydrated, both concentration receptors and volume receptors in the brain trigger the secretion of ADH. This small peptide then stimulates thirst and water retention in the kidneys. In amphibians, it also stimulates water absorption by the skin and urinary bladder. A steroid hormone produced in the adrenal glands called aldosterone stimulates the kidney and large intestine to conserve sodium. The kidneys also excrete increased amounts of potassium in response to aldosterone. Aldosterone secretion is stimulated by angiotensin II. When blood sodium levels decrease, there is a consequent loss of water and thus body fluid volume. Pressure receptors in the kidneys trigger the release of renin, which initiates a complex series of enzymatic reactions in the blood leading to the appearance of angiotensin II, which stimulates the secretion of aldosterone. When blood pressure increases, aldosterone secretion decreases, sodium excretion increases, and other hormones appear which also help eliminate sodium. Pressure receptors in the heart cause that organ to secrete atrial natriuretic peptide (ANP). ANP inhibits sodium conservation in the kidneys. Increased pressure in blood vessels activates nitric oxide synthetase, which produces nitric oxide locally. Nitrous oxide increases the excretion of sodium by the kidneys.

Calcium and phosphate are also controlled by hormones. The parathyroid hormones respond

Endocrine Control of Pregnancy, Parturition, and Lactation

During an ovarian cycle, a pregnancy can occur if the ovum becomes fertilized. The events that occur during pregnancy are also controlled by hormones.

In mammals, fertilization normally occurs in the oviduct. When the fertilized embryo is implanted in the uterus, it is nourished as a result of the glandular and vascular buildup of the uterine wall. This buildup is maintained by estrogen and progesterone secreted by the corpus luteum. As the embryo grows, it begins to produce a portion of the placenta; the other portion is produced by the uterus. Cells in the embryonic chorion of the placenta produce chorionic gonadotropin, which "rescues" the corpus luteum and prevents its becoming deactivated by a prostaglandin produced by the ovary as a signal to deactivate the corpus luteum if fertilization has not occurred. During the latter stages of a pregnancy, the placenta takes over the production of estrogen and progesterone in some species. During pregnancy, chorionic gonadotropin will be present in the urine. During the last days of pregnancy, the ovary begins to produce a new hormone called relaxin. Relaxin is a very ancient hormone; it has been found in sharks and birds as well as mammals. Relaxin softens the ligaments connecting the bones in the birth canal. It also stimulates uterine contractions. The uterine contractions begin the process of labor, resulting in birth. The signal for the onset of labor is a fetal hormone, cortisol. Cortisol crosses the placenta to the maternal blood, where it causes the synthesis of another prostaglandin. The strongest support for this conclusion comes from experiments in which the adrenal glands were removed from fetal goats; the result of such in utero surgery is significantly delayed parturition (birth). This uterine prostaglandin intensifies the uterine contractions to initiate labor and thus parturition.

Following birth, the suckling of the infant at the mother's mammary glands stimulates the release of the posterior pituitary hormone oxytocin. Oxytocin stimulates contraction of muscles in the mammary glands to eject milk. Oxytocin also stimulates uterine contraction to pass the placenta (afterbirth) through the vagina. Prolactin, which stimulates mammary development during pregnancy, has nothing to do with milk ejection during lactation. Prolactin is also present in lower vertebrates that lack mammary glands. In fish, prolaction stimulates sodium conservation. In amphibians, prolactin decreases skin water permeability and increases sodium uptake across the skin. In some salamanders, prolactin initiates "water drive," which is the migration of adults back to water for reproduction. In pigeons and similar birds, prolactin stimulates the production of crop-sac milk, which the mother regurgitates to feed her young; a process remarkably similar, in effect, to lactation.

directly to blood calcium concentrations. When calcium levels are low, parathyroid hormone (PTH) is secreted into the blood to stimulate three centers. In bone, PTH mobilizes calcium to elevate blood levels of this ion. Because mobilization of bone also elevates phosphate, which can be toxic at high concentrations, the kidneys become important. PTH stimulates the kidneys to increase calcium conservation and potassium excretion. PTH also stimulates uptake of calcium in the small intestine. Vitamin D enhances the action of PTH. Working antagonistically to PTH, calcitonin, produced in the thyroid gland, responds directly to high blood calcium to move this ion into bone.

Digestive Hormones

The digestion and assimilation of food are also controlled by hormones. In meat-eating animals, beginning in the stomach, stretch and the presence of protein stimulate the secretion of gastrin into blood vessels in the wall of the stomach. This gastrin stimulates the secretion of hydrochloric acid into the lumen of the stomach to digest protein. When the partially digested food enters the small intestine for the completion of digestion and assimilation, a slightly alkaline pH is required. The walls of the small intestine detect the acidity and secrete another pair of hormones into blood vessels. Secretin travels to the pancreas and stimulates sodium bicarbonate secretion. The sodium bicarbonate travels through the common bile duct to the small intestine, where it neutralizes the acid. Gastric inhibitory polypeptide travels to the stomach to inhibit acid secretion and stomach contractions. Another peptide, cholecystokinin-pancreozymin (CCKPZ), responds to fats and proteins in the small intestine and is thus secreted into the blood. This hormone travels to the gallbladder, causing it to contract and release its bile through the common bile duct to aid digestion of fats in the small intestine. CCKPZ also stimulates secretion of a whole host of enzymes by the pancreas. These enzymes also move through the common bile duct to the small intestine to aid in the digestion of carbohydrates, fats, and protein. At least two other digestive hormones have been discovered that are not well understood at present. Motilin is secreted by the small intestine and stimulates stomach muscle contractions. Vasoactive intestinal polypeptide also is secreted by the small intestine and it, in turn, stimulates sodium bicarbonate secretion by the walls of the small intestine. Both hormones are of obvious benefit, but key details of their function, such as what triggers their secretion, are not clearly understood. It is important to realize that all of the hormones of the stomach and small intestine are secreted into the blood vessels in the walls of the organs, not into their lumens.

Reproductive Hormones

The two pituitary hormones that are involved in reproduction are called the gonadotropins, FSH and LH. These hormones are identical in males and females. The gonadal hormones differ between the two sexes. Females produce estrogens and progesterone in their ovaries. Males produce androgens (primarily testosterone) in the testes.

The mammalian menstrual cycle has two components. Both the ovarian cycle and the uterine cycle proceed simultaneously and last approximately four days in rats, sixteen days in sheep, and twenty-eight days in humans. The length and pattern of the cycle vary with species. For the sake of comparison, the human cycle is described here. The first five days of each cycle is called the menstrual period, and during this period the built-up walls of the uterus (resulting from the previous cycle) are shed and discharged through the vagina. At this time the concentrations of FSH and LH in the blood are about the same. From the close of the menstrual period until ovulation is the follicular cycle. FSH stimulates the ovaries to begin the growth and maturation of an egg-containing follicle. This follicle produces estrogen. Estrogen feeds back negatively on FSH, causing its levels in the blood to drop. At the same time, estrogen is feeding back positively on LH, causing its levels to rise.

At the midpoint of the ovarian cycle, LH peaks and causes the now mature follicle to burst and eject an egg (ovum) into the oviduct. The ruptured follicle now becomes a corpus luteum and continues to secrete estrogen, but also begins to secrete progesterone. The estrogen, and now the progesterone, stimulate the walls of the uterus to thicken and produce glandular tubes and blood vessels. This goes on for the final half of the cycle, which is called the follicular phase in the ovaries and the proliferative phase in the uterus. If fertilization of the ovum in the oviduct fails to occur during this period, a hormone, probably a prostaglandin, builds up in the corpus luteum, causing it to stop producing estrogen and progesterone. With the loss of these two steroids, the thickened wall of the uterus is shed and the menses flows during the first five days of the next cycle.

Male reproductive endocrinology is much different. The first striking difference is that, although the pituitary hormones FSH and LH are the same, the patterns of secretion are different. Instead of the cyclic peaks found in females, males secrete constant levels of gonadotrophins. FSH stimulates sperm production and maturation in the seminiferous tubules of the testes. LH stimulates testosterone secretion by the interstitial cells of the testes. Testosterone helps FSH to stimulate sperm maturation. This androgen also stimulates such primary sex characteristics as penis and epididymal growth during puberty. The epididymis is a tubular structure that stores sperm in preparation for ejaculation. Testosterone also stimulates secondary sex characters, such as the deepening of the voice and development of muscle mass that manifest during puberty in humans.

—Daniel F. Stiffler

See also: Circulatory systems of vertebrates; Courtship; Digestion; Endocrine systems of invertebrates; Fertilization; Gametogenesis; Growth; Hormones and behavior; Hormones in mammals; Kidneys and other excretory structures; Lactation; Mating; Metabolic rates; Muscles in vertebrates; Nervous systems of vertebrates; Osmoregulation; pH maintenance; Pheromones; Reproduction; Reproductive strategies; Reproductive system of female mammals; Reproductive system of male mammals; Sexual development; Thermoregulation; Vertebrates; Water balance in vertebrates.

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ENDOSKELETONS

Type of animal science: Anatomy
Fields of study: Biochemistry, developmental biology

Endoskeletons are a distinctive primary feature of most of the members of the phylum Chordata. Their evolution eventually provided vertebrates with many advantages over invertebrate animals. Study of the various types of tissues that make up endoskeletons is important to the study of both medicine and evolution.

Principal Terms

APPENDICULAR SKELETON: one of two main divisions of vertebrate skeletal systems, composed of the bones of the pelvic girdle, the shoulders, and the limbs

AXIAL SKELETON: the other main division of vertebrate skeletal systems, made up of the bones of the skull, the vertebral column, the ribs, and the sternum

CANCELLOUS BONE: spongy bone that is composed of an open, interlacing framework of bony tissue oriented to provide maximum strength in response to normal strains and stresses

CARTILAGE: a soft, pliable typically deep-lying tissue that constitutes the endoskeletons of primitive vertebrates, such as sharks, as well as the embryonic skeletons and jointing structures of adult higher vertebrates

COMPACT BONE: a dense type of bone, often termed lamellar bone, formed of a calcified bone matrix having a concentric ring organization

HAVERSIAN SYSTEMS: narrow tubes surrounded by rings of bone, called lamellae, that are found within compact bones of animals having endoskeletons; the tubes contain blood vessels and bone

OSTEOBLAST: a bone-secreting cell found in vertebrates, that is instrumental in the process of ossification

The study of endoskeletons can be approached in three basic ways. First, endoskeletons can be approached as gross structures—that is, as primarily mechanical or architectural systems. Second, they can be viewed as types of tissue—bone and cartilage—which involves study at the microscopic level. Third, endoskeletons can be considered products of the evolution of the endoskeletal organism. This area examines such factors as the organisms' development from protochordates and the intrinsic biological advantages of the endoskeleton over the exoskeleton.

The Development of Endoskeletons

The evolution of vertebrate animals, such as fishes, reptiles, and mammals, having articulating endoskeletons represents a biological quantum leap forward for the phylum Chordata. The development of endoskeletons permitted several significant structural advantages that allowed the higher chordates to compete successfully with invertebrates and eventually to become dominant in many varied ecosystems.

The evolution of endoskeletons allowed a greater degree of general body efficiency and organization. Coupled with a great increase in the rapidity, power, and control of movement with which endoskeletons and their improved musculature endowed their possessors, endoskeletons allowed vertebrates to become the highest and fastest flyers, the swiftest runners and swimmers, and the widest ranging of animals. The organizational plan of the endoskeleton of the more highly evolved vertebrates is exemplified by that of mammals. The mammalian endoskeleton is articulated in many ways, giving it a great degree of flexibility and great range of movement. Cartilaginous joints facilitate the articulations. The endoskeleton itself is typically made of bone material composed of calcium phosphate. Other than the endoskeleton proper, minor externalizations can take the form of fingernails and toenails, claws, hooves, antlers, and horn cores, as well as teeth. In these cases, materials other than bone can sometimes originate at or near the body surface or in the skin. These expressions can be present in the form of scales or plates, though this is the exception rather than the rule among this vertebrate class. All these external expressions can be considered, in a way, forms of a limited exoskeleton.

Axial and Appendicular Skeletons

Aside from such exceptions as pangolins and armadillos among mammals, and turtles and tortoises among reptiles, exoskeletal tissue does not usually constitute an architectural structure that the animal's other organs or structures depend on for support or protection. The one exception among the various bones of the vertebrate endoskeleton is the bones of the cranium, or skull. The cranial bones are a group of hard, thick bones, usually ovoid or spheroidal in general geometry, that offer extensive protection to the brain and primary sensory organs, such as the eyes and ears. The cranium is such a universal feature among vertebrates that the subphylum is sometimes referred to as the craniates. Evolutionarily lower vertebrates tend to have larger numbers of skull bones. Some fish have as many as 180 skull bones. Higher taxonomic groups have inversely lower numbers of skull bones: Amphibians and reptiles possess between fifty and ninety-five, while mammals have thirty-five or fewer. The skull itself is a member of two fundamental divisions between which the entire endoskeleton is usually subdivided; it is part of the axial skeleton. The axial skeleton also includes the bones of the vertebral system, the ribs, and the sternum. Possession of all axial features is not universal. Some vertebrates, such as the leopard frog, do not possess ribs, while others, such as the snakes, do not have sternums.

The other endoskeletal subdivision is called the appendicular skeleton, and it is made up of the bones of the pelvic girdle, shoulders, and limbs. The components of the appendicular system exhibit a great degree of variation from vertebrate group to vertebrate group and even among species, as do those of the axial system, and reflect the many different environments and lifestyles to which their respective possessors have adapted. A case in point is the numerous variations in form and length found among limb bones. The various lengths represent adaptations to such external environmental factors as the medium through which the animals move from place to place (air, water, ground surface, and subsurface) and speed. The lower and upper limb bones themselves are connected by joints. The jointing arrangements of limb bones are highly efficient mechanical developments. Two basic types of limb joint exist: the pulley joint and the ball-and-socket joint. Pulley joints are exemplified by finger and toe joints and represent great freedom of motion in one plane. Ball-and-socket joints are exemplified by shoulder or hip joints and represent freedom of universal motion. Still another joint type is a cross between these two. Such a combination of pulley and ball joints is exemplified by the elbow joint in humans.

Histology

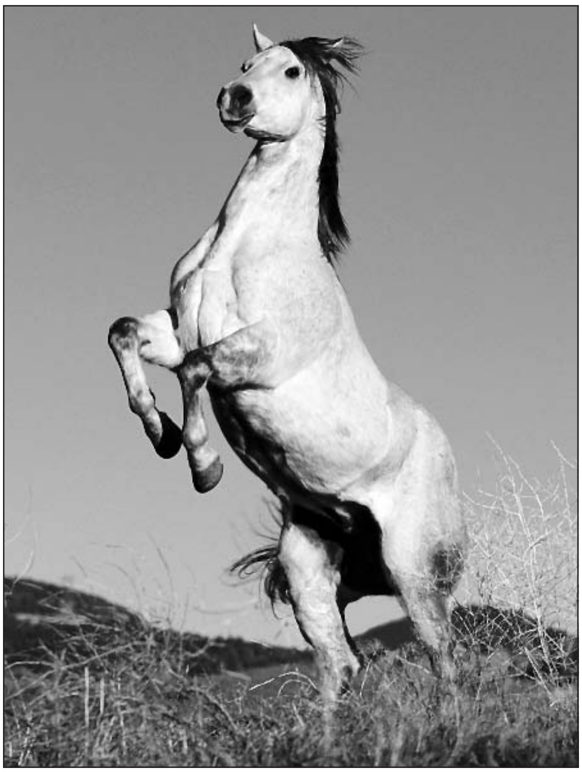
Another major approach to the study of the endoskeleton is its histology, or the fine details of tissues and how these tissues develop. Bone material itself is active metabolically—that is to say, it is alive. It can be considered not only an architecture along which the vertebrate body is arranged but also a complex and specialized connective tissue. As an organic material, it possesses a number of unique properties that are derived from the fact that it has evolved to perform its various duties efficiently for the size, weight, and arrangement of the materials of which it is composed. It is engineered like structurally reinforced concrete, having fibers of collagen, a tough, fibrous binding protein that is analagous to the function of steel rods.

The mineral calcium is analogous to the concrete in a building. Bone is formed in two different ways, depending on type. One process involves a means of growth of two bone types, termed lamellar bone (compact bone) and cancellous bone (spongy bone). Lamellar bone, sometimes also called membrane bone, develops through the process of ossification when certain cells called osteoblasts become bone-secreting. The osteoblastic cells, in association with numerous fibers of connective tissue cells, form a network in which layers of calcium mineral salts, called lamellae, are deposited. This network slowly builds up a plate that expands along its margins. As the plate thickens, some osteoblasts remain alive and are incorporated into the bone growth. At this point, they begin to have irregular shapes and are termed osteocytes. Spaces in which the osteocytes are sited are termed lacunae (cavities) and develop long, omnidirectional, branching processes, termed canaliculi. Neighboring canaliculi eventually link up and create a network through which life-supporting blood containing oxygen and food can reach the growing bone tissue. The canaliculi system grows such that no bone cell is more than 0.1 millimeter from a blood-carrying capillary. This overall arrangement is termed a Haversian system.

Cartilage tissue is another endoskeletal material that forms the adult skeletons of higher vertebrates, such as mammals, when they are still in early developmental stages. In mammals, this type of tissue is not formed directly, but rather by a replacement process. In mammalian embryos, most of the skeletal structure is initially laid down in the form of cartilage and then subsequently replaced by true bone. The process does not reach completion in the higher vertebrates until the animal is full-grown; in humans, this is as late as twenty-five or twenty-six years of age. Cartilage is not as hard or rigid as bone, but it is extremely tough and is resistant to forces of compression or extension. Under microscopic examination, it appears as a clear matrix which possesses numerous, embedded cells termed chondroblasts. These chondroblasts lie in fluid-filled voids termed lacunae. Chondroblasts secrete the matrix called chondrin, which surrounds the lacunae. Both the chondrin and the fluids act in an elastic manner and are resistant to compression and external shocks. Various types of cartilage have collagen fibers. The amounts of collagen fiber present determine the amount of extension that the cartilage can resist. The total effect of the cartilage's unique composition is to render it a good skeletal material for young, rapidly developing, vulnerable animals, such as mammal embryos.

Vertebrate Evolution

The last basic approach to the study of endoskeletons is that of examining the evolutionary development of the phylum Chordata in general and the subphylum of vertebrates in particular. The earliest history of the chordates is only very sketchily understood; the remains of early, ances-



Endoskeletons provide the interior support and locus for muscle attachment, allowing vertebrates a wide range of motion. (Corbis) tral forms of this group made poor candidates for the fossilization process because they lacked hard body parts. A line of hypothesized evolution, therefore, has been drawn through surviving marine animals called protochordates, which presently are sessile or stationary for most of their life cycles, although before attaining this current form, they were capable of locomotion. These curious animals are considered invertebrate chordates as they possess notochords, or flexible skeletal rods that run up the long axes of their bodies. Among this group are such animals as the amphioxus and the so-called sea squirts or tunicates.

Further evolved along the path that eventually led to the present diversity of endoskeleton-possessing vertebrates are animals possessing bone matter, such as the agnathan (jawless) fishes. Later fishes evolved jaws and eventually true teeth and progressed from having cartilaginous skeletons (the class Chondrichthyes) to having true, bony endoskeletons (the class Osteichthyes). These more advanced fishes eventually gave rise to the land-pioneering class Amphibia and ultimately engendered the vertebrate classes of Reptilia (reptiles), Aves (birds), and Mammalia. The reason that bone tissue evolved at all in the lower vertebrates is a subject that is still open to debate. Several rival theories exist; one holds that bone evolved simply as a more improved, harder material for exoskeletons superior to such material as calcium carbonate, the most common building material for invertebrate exoskeletons. Another suggests that bone evolved as a phosphate reserve as one component for energy storage and transfer for metabolic processes within the bodies of ancestral vertebrates. Still another theory postulates that bone materials such as dentine and enamel evolved originally simply as effective insulation for the electrosensory organs found in primitive, marine vertebrates. Other theories integrate versions of the theories above in complex, interactive arrangements.

Endoskeletal Research

Histological research of endoskeletal tissues has in the past been the most productive approach to obtaining the large body of data on bone tissues and processes that currently exists. The majority of the data accumulated with this approach has been gained in the laboratory and has involved specialized equipment and the use of techniques tailored to produce useful information on bone cells, their composition, related tissues, and the various organic processes involved. These techniques and laboratory tools and appliances were developed laboriously over the centuries. Real progress in the field had to wait until the advent of the simple microscope. Believed to be invented by the Dutch scientist Antoni van Leeuwenhoek or one of his contemporaries in the seventeenth century, the simple optical microscope—utilizing only one lens—allowed the first close-up look at living structures at or near the cellular level. Examination of Leeuwenhoek's original equipment has revealed that he was able to obtain the respectable magnification of as much as 250 times. His lenses thus allowed humans an entry into a world that had hitherto been barred to them: the world of the very small. Subsequent development in microscopes produced compound optical microscopes with several lenses working in series and an eventual exponential increase in magnifying power. Biologists quickly recognized that the new tool underscored the relation between structure and function of organic materials at the microscopic level. It is this critical concept that has been the key to unlocking the many secrets of the organic microstructures of living things, among them endoskeletons.

Hand in hand with the development of research using optical microscopes has been the preparation of histological sections. These are extremely thin, transparent shavings of organic tissues prepared in such a way as to facilitate microscopic examination. With the increased sophistication of the use of microscopy has come the perfected use of many different types of staining and dying. The use of stains and dyes has been selectively employed to highlight the different types of tissue being observed. A further refinement in microscopy has been the use of various lens filters, such as polarizing filters, that have added control of the light target to emphasize or de-emphasize various features.

Late Twentieth Century Advances

After the advent of applied nuclear physics during World War II, a new technique called autoradiography appeared; this enhanced the resources available to histological research. Autoradiography involves the introduction of radioactive substances into animals; consequently, these substances are incorporated into various tissue components. The great advantage to this technique is that it can provide direct information on how long it takes for the various tissue components to be synthesized and on how long they last.

As the spectrum of isotopic labels expanded and became refined, it became possible to label and study in great detail almost every common tissue component found in animals. The study of the most intricate or delicate endoskeletal tissues thus became realistic along with the added advantage of being able to determine the durations of the metabolic processes involved in development, decay, and replacement.

A solution to the magnification limitation of the light microscope was reached when the first electron microscope (EM) was built in 1931. Further improvements were made until the 1950's saw the widespread use of more technologically advanced devices called scanning electron microscopes (SEMs), which allow observation and SEM photography, termed electron micrography, of target objects considerably less than 1 micron in diameter.

Still newer technologies, such as the use of fiber-optic probes inserted into the living bodies of animals and humans, allow benign observation of tissues in their natural state in the midst of normal processes. Fiber optics involves the transmission of light (and therefore images) through very fine, flexible glass rods by internal reflection. Fiber-optic instruments called fiberscopes allow the viewing of extremely small, and normally dark, internal structures such as skeletal tissues.

—Frederick M. Surowiec

See also: Anatomy; Bone and cartilage; Evolution: Historical perspective; Exoskeletons; Horns and antlers; Muscles in vertebrates; Physiology; Shells; Teeth, fangs, and tusks; Vertebrates.

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MAGILL'S ENCYCLOPEDIA OF SCIENCE

ANIMAL LIFE

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MAGILL'S ENCYCLOPEDIA OF SCIENCE

ANIMAL LIFE

Volume 2
Estivation–Learning

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ESTIVATION

Types of animal science: Behavior, ecology, physiology
Fields of study: Ecology, herpetology, invertebrate biology, physiology, wildlife ecology

Estivation, like hibernation, is a dormant state that enhances an animal's ability to survive when environmental conditions are harsh. In hot, arid climates, estivating animals reduce water losses and energy requirements during long periods of drought when little water or food is available.

Principal Terms

EPIPHRAGM: covering or sealing membrane
HYGROSCOPIC: able to retain moisture
NEMATODE: a long, cylindrical worm; some are parasitic
POIKILOTHERM: cold-blooded or ectothermic; any organism having a body temperature that varies with its surroundings; in general, reptiles, amphibians, fish, and invertebrates
TORPID: dormant, numb, sluggish in action

During true estivation, metabolic processes including oxygen consumption, respiration, heart rate, and neurological activity decrease substantially, but the term is often used loosely to describe the activity of any animal that spends part of the warmer, drier season in a torpid state. Except for the environmental stimuli that trigger them, estivation and hibernation appear similar, although they differ physiologically, and occur most often in the poikilotherms. Among the animals most likely to estivate are mollusks, arthropods, fish, amphibians, and reptiles, although some small desert mammals estivate as well.

Invertebrate Estivation

A seemingly lifeless desert may be teeming with estivating life underground, waiting for seasonal rains that will awaken them to resume their life cycles. Snails, slugs, earthworms, insects, spiders, and nematodes, along with cocoons, eggs, grubs, larvae, and pupae, may all lie dormant in the soil, in building foundations and rock crevices, or under rotting logs or other vegetation. The animals are not just dormant; some of them will also be in an arrested state of sexual development called diapause. Some tropical snails can estivate for years at a time. To prepare, a snail digs a deep burrow in moist ground or under rocks. Next, it forms an epiphragm (a sealing membrane for the shell) to prevent evaporation and desiccation. Finally, its metabolism slows dramatically until it detects favorable environmental cues such as increased moisture.

Lungfish Estivation

Among the fishes, the process of estivation is best known in the air-breathing lungfishes of Africa (*Protopterus*) and South America (*Lepidosiren*). Adult fish have paired lungs and vestigial gills; in fact, they will drown if held underwater. Both abilities—to estivate and to breathe air—have contributed to their survival in areas that experience severe seasonal droughts. When the rivers, lakes, and marshes they inhabit dry up, lungfish dig burrows deep in the mud, leaving air passages to the surface. They curl up inside and wait out the arid conditions until rain fills up their burrows with water. *Protopterus* secretes a mucous coating that hardens, forming a tough, cocoonlike hygroscopic chamber with only one opening, connected to its mouth. When the rains come and flood the passage, the dormant fish awakens with a cough. *Lepidosiren* burrows more deeply than *Protopterus* and plugs the entrance to its air tube with perfo-

Image Not Available

rated clay. Its burrow is somewhat larger and usually contains some water. It coats the walls with a jellylike substance to maintain moisture. During estivation, lungfish are so torpid that they make easy prey for local fisherman, who spear them in their burrows.

During estivation, energy required for reduced metabolism is provided by the breakdown of tissue protein. The waste product is urea, which is excreted in large amounts once the fish is again submerged in water. Lack of oxygen can become a problem for lungfish sealed in their burrows, but the aerobic metabolism of an estivating *Protopterus* is only 20 percent of its normal resting metabolism. Similarly, *Lepidosiren* and the swamp eel (*Synbranchus*) can survive a lack of oxygen for long periods during estivation.

Estivation in Reptiles and Amphibians

During the summer, many reptiles and amphibians estivate. Some frogs and toads insulate themselves in cocoons composed of many layers of unshed skin. The eastern spadefoot toad digs backward into sandy soil with its spade-shaped hind feet to estivate for periods of weeks; experiments indicate that the sound of rain falling rather than moisture itself may trigger the toad's arousal. The mud turtle *Kinosternon* abandons its drying pond for a burrow where it estivates up to three months. Desert tortoises of the North American Southwest spend much of their summers estivating in burrows but emerge to drink and browse after infrequent thunderstorms. In the same region, the lizard called the chuckwalla stops eating and estivates in rock crevices, emerging every third day for about an hour at sunset.

Estivation in Mammals and Birds

Among the few estivating mammals are small desert rodents, lemurs, and hedgehogs. Some ground squirrels remain dormant in their burrows from late summer, merging estivation with hibernation. They reappear in early spring to take advantage of new growth after winter rains. The round-tailed ground squirrel of southern Arizona (*Citellus tereticaudus*) avoids the hot, dry autumn by disappearing in August and September. Generally, the period of estivation coincides with the period most prone to scarcity of vegetation.

While a few birds may hibernate, it is unlikely that they estivate. They can migrate to more attractive regions, or, like many reptiles and most mammals, they cope with high temperatures by confining their activities to cooler parts of the day.

—Sue Tarjan

See also: Deserts; Hibernation; Insects; Lungfish; Metabolic rates; Respiration and low oxygen; Respiratory system.

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ESTRUS

Types of animal science: Behavior, physiology, reproduction
Fields of study: Anthropology, ethology, reproduction science

Estrus is the recurring period of sexual excitement and receptivity in female mammals. A central feature of most mammalian species' reproductive lives, it helps structure social and communicative behavior as well.

Principal Terms

COPULATION: mating; the insertion of the male's penis into the female's vagina to fertilize her ova

ESTROGENS: a group of female sex hormones which regulate the estrous cycle

ESTRUS CYCLE: the cycle of females' bodily changes related to reproductive potential

OVA: eggs released from the females' ovaries at the height of estrus

PROGESTERONE: a female sex hormone produced chiefly in the latter half of the cycle

The physiological and behavioral events which make up estrus are complex and intertwined. For successful mating to occur, it is usually necessary that male and female cooperate in the act. Estrus ensures that both sexes are impelled to do so at the same time, when the female's body is ready for a pregnancy.

During the days prior to estrus, ova in follicles ripen rapidly within the ovary. Estrogens, produced by cells in the follicle walls, increase rapidly in this phase, causing not only follicular growth but thickening of the vagina walls and the various signs of "coming into heat," and then of estrus itself. In most species, the ova spontaneously burst from their follicles at the peak of estrus and enter the oviduct, which leads to the uterus, ready to join with sperm. Females of several species, however, including the rabbit and the cat, require the added stimulus of mating for release of their ova. Once the ova are released, the ruptured follicles begin secreting progesterone in place of estrogen; this hormone prepares the uterus to support a pregnancy. This internal process is regulated through feedback connections between the ovaries and the hypothalamus in the brain. The hormonal effects which make females eager for mating also originate largely in the hypothalamus, sensitizing the nervous system to respond strongly to the presence of and stimulation by their male counterparts.

Variations Between and Within Species

External estrus signals vary greatly by species. In every case, they are largely produced by hormonal influences, and are keyed to evoke specific sexual response from the male of the species. Such signals may be visual, behavioral, auditory, or scent-based, or may possibly draw on senses imperceptible to human observers.

Visual signals are often found among social mammals. These have been most observed in primates. Chimpanzee and bonobo females show a spectacular pink swelling of their genitals during estrus, which recurs every five weeks if pregnancy does not occur. Certain monkeys develop an estrus flush on their faces as well as their buttocks.

Scent and sound signals can alert males who are not initially within sight range of the receptive female. As such, they are effective for species who do not live in groups, although these signals are not confined to such species. Urine markings are among the most common scent signals. A female black rhino in estrus leaves a long trail of scent posts, which the male follows. Other scent signals are partly airborne, like those of domestic cats and dogs. Mating calls are given by many females, such as the female gibbon's ascending call, which is then answered by the male.

Behavioral changes during estrus are almost universal, as both sexes concentrate on the quest for one or several partners. The initial stages, which may suggest female coyness to an observer, are part of the courtship process. For example, the female cheetah leads several males on a headlong run across the plain, finally selecting one with whom to mate. Pet owners notice a restlessness in their dogs and cats; female cats in heat are especially likely to roam. The penultimate female signal in many species is lordosis, an arched-back posture which allows the male to mount. Mammalian species are normally either monestrous—having a single estrus period a year—or polyestrous—with several estrus periods recurring annually. The latter situation is more common.

Environmental changes can cause variations in these patterns. Such factors include climate shifts, changes in available light, nutrition, and the presence of a new male. In monestrous mammals, the estrus period usually falls at a time when resulting births will take place in the optimal season for young animals to thrive and grow. Domestication may disrupt this pattern. For instance, a female dog typically comes into heat twice a year with no regard to seasons. Her ancestor the wolf has one estrus period a year, sometime between January and April, depending upon latitude.

The length of estrus also varies by species: It lasts four to nine days in the mare, and only fourteen hours in the rat. In a few species, such as the ferret, estrus lasts for several weeks if copulation has not occurred. There are also infrequent phenomena such as "silent heats," in which the animal ovulates but the usual external signs are absent.

Estrus, Evolution, and Ethology

Sexual reproduction provides genetic diversity and adaptability to a species. However, in order to proceed successfully, it requires a fairly complex series of events. Estrus is central in this process. It communicates to males a female's readiness at the same time that it impels that female to mate and primes her body for pregnancy. Nature plays many

The Northern Fur Seal

Estrus behavior has seldom been studied closely by biologists. More often it has been a practical concern of livestock breeders and pet owners, or subsumed in general studies of reproductive behavior. However, as part of a study of the northern fur seal, Roger L. Gentry and colleagues made detailed observations on estrous females over a six-year span.

Like many animals, the seals have a definite seasonal breeding time, typically July 7 through 14 of each year. Females come ashore and huddle in large groups on breeding beaches, where mating occurs. The seals' known sex ratio is sharply skewed, with forty or more females to each male. The male in the territory works his way through the group, mating with many females as each one reaches the peak of her receptivity. This arrangement is efficient for both sexes.

Several unusual species-specific features were discovered by Gentry's study. Fur seals go into estrus only five days after giving birth. Any resulting pregnancy enters an embryonic diapause, or delayed implantation, until the newborn seal is weaned the following fall. The actual period when female seals are receptive is brief, usually only twenty-four hours.

Unlike many other female animals, who choose mates based on status, appearance, or other traits, fur seal females seem indifferent to which male they mate with. Some are almost comatose by the time copulation occurs. Gentry concludes that female choice cannot be an evolutionary factor in this species; males are selected for reproduction solely by direct competition among themselves. The pattern seems to be an optimum one, though, for a species which spends most of its time at sea without opportunity to mate.

The Human Puzzle

Humans are unusual, but not unique, among mammals in lacking a perceptible estrus period. Did humans, or their hominid ancestors, once have estrus and lose it? Is this absence just another oddity in the amazingly wide spectrum of mammalian reproductive traits? The fossil record gives no clues, nor are they likely to be found in the future.

This silence has not kept anthropologists, ethologists, and others from speculating. The prevailing theory until the 1980's asserted that loss of estrus was essential to becoming human, because only a female's continuous sexual availability secures a monogamous pair bond and keeps the male from wandering away.

This theory has many problems. Monogamous pair bonding now appears to be a "hard-wired" trait in some species, unrelated to continual sexual contact. The bonobo, and to some extent other primate species, copulate even when the female is not in heat. Humans (and presumably their primate ancestors) are innately social animals. Without group backup, a lone prehistoric or hominid hunter would not fare well. Loss of estrus would also seem to have disruptive social possibilities. Rape, fetish obsessions because males have no instinctual guide to what is sexy, and a double standard denying that females have sexual desires—all are made possible by the lack of clear female signals.

Anthropologist Sarah Hrdy suggests that the human pattern may simply resemble that of species such as orangutans, who show no visible estrus signals. Study subjects ranging from Connecticut college women to Kalahari hunter-gatherers have reported peaks of female sexual interest around their time of ovulation.

If hominid or prehistoric human females did have full estrus, what was the evolutionary advantage or mechanism of its loss? The subject is one of those puzzles unlikely to be solved, but fascinating to speculate about.

variations on this basic theme, each connecting the species' estrous cycle to its environment and its whole life cycle.

Because the survival of young mammals requires maternal care, and often that of the father and/or other adult animals as well, estrus patterns are significant for social structure. In some species, estrus may help secure a pair bond, a polygynous herd, or bonds within a troupe or pack. It can also cause disruption, as when males battle for access to estrous females, or a new male takes over a harem and kills the young, hastening their mothers' next heat.

Humans have known of estrus ever since they first domesticated animals. Charles Darwin's *On the Origin of Species* (1859) credits estrous females' mate choices with being an evolutionary mechanism, giving many examples. Ethologists' field studies have recently described many details about species-specific estrus behavior, as well as its role in life cycles and social behavior.

However, direct estrus observations are hard to make and sometimes hard to interpret, especially in wildlife.

—*Emily Alward*

See also: Asexual reproduction; Breeding programs; Cleavage, gastrulation, and neurulation; Cloning of extinct or endangered species; Copulation; Courtship; Determination and differentiation; Development: Evolutionary perspective; Fertilization; Gametogenesis; Hermaphrodites; Hydrostatic skeletons; Mating; Parthenogenesis; Pregnancy and prenatal development; Reproduction; Reproductive strategies; Reproductive system of female mammals; Reproductive system of male mammals; Sexual development.

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ETHOLOGY

Type of animal science: Ethology
Fields of study: Genetics, neurobiology

Ethology is the study of animal behavior from the perspective of zoology. The information acquired through ethology has helped scientists better understand animals in all their variety.

Principal Terms

ADAPTATION: a structure, physiological process, or behavioral pattern that gives an organism a better chance of surviving and of reproducing

BEHAVIORAL ECOLOGY: the systematic study of the strategies animals use to overcome environmental problems and the adaptive value of those strategies

BEHAVIORISM: the school of psychology that focuses on the investigation of overt behaviors and rejects allusion to inner processes as a means of explaining behavior

COMPARATIVE PSYCHOLOGY: the branch of psychology that uses comparative studies of animals as a means of investigating phenomena such as learning and development

EVOLUTIONARILY STABLE STRATEGY: a behavioral strategy that will persist in a population because alternative strategies, in the context of that population, will be less successful

IMPRINTING: a specialized form of learning characterized by a sensitive period in which an association with an object is formed

SOCIOBIOLOGY: the scientific discipline that examines social behavior in the context of evolutionary theory

Ethology is the branch of zoology that investigates the behavior of animals. Behavior may be defined as all the observable responses an animal makes to internal or external stimuli. Responses may be either movements or secretions; however, the study of behavior is much more than a descriptive account of what an animal does in response to particular stimuli. The ethologist is interested in the how and why questions about the behaviors observed. Answering such questions requires an understanding of the physiology and ecology of the species studied. Those who study animal behavior are also interested in the ultimate or evolutionary factors affecting behavior.

The Roots of Ethology

Ethology is a young science, yet it is also a science with a long history. Prior to the late nineteenth century, naturalists had accumulated an abundance of information about the behavior of animals. This knowledge, although interesting, lacked a theoretical framework. In 1859, Charles Darwin published *On the Origin of Species*, and with it provided a perspective for the scientific study of behavior. Behavior was more central to two of Darwin's later books, *The Descent of Man* (1871) and *Expression of the Emotions of Man and Animals* (1873). By 1973, the science of ethology was sufficiently well developed to be acknowledged by the presentation of the Nobel Prize for Physiology or Medicine to Nikolaas Tinbergen, Konrad Lorenz, and Karl von Frisch for their contributions to the study of behavior. The work of these men was central to the development of modern ethology.

The experimental studies of Frisch revealed the dance language of the honeybee and ways in which the sensory perception of the bees differed from our own sensory world. An awareness of species-specific sensory abilities has provided an important research area and has emphasized a factor that must be considered in the experimental design and interpretation of many types of behavioral research.

Tinbergen studied behavior in a variety of vertebrate and invertebrate organisms. He was good both at observation of animals in their natural habitat and in the design of simple but elegant experiments. His 1951 book, *The Study of Instinct*, is a classic synthesis of the knowledge that had been gained through the scientific study of animal behavior at that time.

Konrad Lorenz is considered by many to be the founder of ethology, because he discovered and effectively publicized many of the classic phenomena of ethology. Pictures of Lorenz being followed by goslings are almost a standard feature of texts that discuss the specialized form of learning known as imprinting. In natural settings, imprinting allows young animals to identify their parents appropriately. Another contribution of Lorenz was his book *King Solomon's Ring: New Light on Animal Ways*, published in 1952. This extremely readable book raised public awareness of the scientific study of animal behavior and kindled the interest of many who eventually joined the ranks of ethologists.

Ethology and Neurobiology

Many of the features of ethological research characteristic of the work of Lorenz, Tinbergen, and von Frisch have continued to be characteristic of the field. They were concerned that the behavior of animals be understood in the context of the species' natural habitat and that both proximate and ultimate levels of explanation would be examined. Their research strategies have been supplemented by an increase in laboratory-based research and by the introduction of new types of experimental design. These developments have softened the distinctions between ethology and another field of behavioral study, comparative psychology. The focus of comparative psychology is comparative studies of the behavior of nonhuman animals. Initially, questions about learning and development were the major problems investigated in comparative psychology. Although the animals most frequently studied were primates and rodents, those doing the research were interested in gaining insight into the behavior of humans. Comparative psychology was long dominated by behaviorism, a school of thought that assumes that the ultimate basis of behavior is learning. The behaviorists employed rigorous experimental methods. Because such methods require carefully controlled conditions, behavioral research is typically laboratory based, and animals are therefore tested in surroundings remote from their natural environments. Over time, comparative psychology has broadened both the questions it asks and the organisms it studies. The boundaries between comparative psychology and ethology have been further blurred by the rising number of scientists crossing disciplinary lines in their research. Each discipline has learned from the other, and both have also profited from knowledge introduced through neurobiology and behavioral genetics.

Neurobiology investigates the structure and function of the nervous system. One area of ethology that has been directly enriched through neurobiology is the study of sensory perception in animals. The techniques developed in neurobiology allow the investigator to record the response of many individual neurons simultaneously. The neurobiologist examines phenomena such as stimulus filtering at the level of the cell. Stimulus filtering refers to the ability of nerve cells to be selective in their response to stimuli. For example, moths are highly sensitive to sounds in the pitch range of sounds made by the bats that are their chief predators. Neurobiology provides a powerful tool for understanding behavior at the proximate level.

Behavioral Genetics

Another source of information for the ethologist is behavioral genetics. Because of the evolutionary context of ethology, it is important to have an understanding of the genetic basis of behavior. If there were no genetic component in behavior, behavior would not be subject to natural selection. (Natural selection refers to the process by which some genes increase in frequency in a population while alternates decrease because the favored genes have contributed to the reproductive success of those organisms that have them.) While the ethological approach to behavior assumes that behavior patterns are the result of interactions between genes and environment, investigators often ask questions about the genetic programming of behavior.

Early ethologists performed isolation and cross-fostering experiments to discover whether behaviors are learned or instinctive. If a behavior appears in an individual that has been reared in isolation without the opportunity to learn, the behavior is considered instinctive. Observing the behavior of an individual reared by parents of a different species is similarly revealing. When behavior patterns of conspecifics appear in such cross-fostered individuals, such behaviors are regarded as instinctive. Instinctive behaviors typically are innate behaviors that are important for survival. For example, one very common instinctive behavior is the begging call of a newly hatched bird. Isolation and cross-fostering experiments are still a part of the experimental repertoire of ethologists, but behavioral genetics permits the asking of more complex questions. For example, a behavior may accurately be labeled instinctive, but it is more revealing to determine the developmental and physiological processes linking a gene or genes to the instinctive behavior.

The ethologist is also interested in determining whether behavior is adaptive. It is not sufficient to identify what seems to be a commonsense advantage of the behavior. It is important to show that the behavior does in fact contribute to reproductive success in those that practice the behavior and that the reasons the behavior is adaptive are those that are hypothesized. When behaviors are tested, they frequently do turn out to be adaptive in the ways hypothesized. This type of research, however, has provided many surprises. Research on the adaptive value of behaviors in coping with environmental problems that affect reproductive success is known as behavioral ecology; this is a major area of modern ethology.

Behavioral ecology addresses a variety of questions, in part because the process of evolution is opportunistic. For any environmental problem there are alternate solutions, and the solution a particular species adopts is dependent upon the possibilities inherent in its genes. Questions addressed include such things as whether a species is using the optimum strategy or how a species benefits from living in a group. Because alternate strategies are possible even within a species, behavioral ecologists are interested in evolutionarily stable strategies. An evolutionarily stable strategy is a set of behavioral rules that, when used by a particular proportion of a population, cannot be replaced by any alternative strategy. For example, the sex ratio present in a particular population will determine the optimum sex ratio for the offspring of any individual.

Sociobiology

Sociobiology is another major area of modern ethology. Sociobiology examines animal social behavior within the framework of evolution. Animal species vary in the degree of social behavior they exhibit; other variables include group size and the amount of coordination of activities occurring within the group. The sociobiologist is interested in a number of questions, but prominent among them are the reasons for grouping. Hypotheses such as defense against predators or facilitation of reproduction can be tested. The particular advantage or advantages gained by grouping varies among species. Two important concepts in sociobiology are kin selection and inclusive fitness.

Kin selection refers to the differential reproduction of genes that affect the survival of offspring or closely related kin. Behavior such as the broken-wing display of the killdeer is an example. The behavior carries risk but would be promoted by selection if the offspring of individuals using the display were protected from predators often enough to compensate for the risk. Inclusive fit-

As a result of imprinting in the moments immediately after hatching, baby geese automatically follow their mother in a line wherever she goes. (Corbis)

ness is the term used to recognize the concept that fitness includes the total genotype, including those genes that may lower the individual's survival as the price of leaving more genes in surviving kin. The concepts of kin selection and inclusive fitness help to address one problem raised by Darwin, the question of altruistic behavior. Ethology is a young science but a very exciting one, because there are so many questions that can be asked about animal behavior within the context of evolution.

Studying Ethology

The methods and tools of ethology cover the entire spectrum of complexity. One simple, but demanding, method is to collect normative data about a species. In its simplest form, the scientist observes what an animal does and writes it down in a field notebook. Finding and following the animal, coping with field conditions such as bad weather and rugged terrain, and keeping field equipment in operating condition add challenge and variety to this approach. The ethologist uses various techniques to get data as unbiased as possible. One of these is to choose a focal animal at random (or on a rotation) and observe the focal animal for a specific amount of time before switching observation to another member of the population. This prevents bias in which individuals and which behaviors are observed. The sampling of an individual's behavior at timed intervals is an even more effective way of avoiding bias.

When all or most of an animal's behavioral repertoire is known, a list known as an ethogram can be constructed. This catalog can be organized into appropriate categories based on function. Ethograms provide useful baseline information about the behavior of a species. For animals that are difficult or impossible to follow, radio-tracking techniques have been developed. Collars that emit radio signals have been designed for many animals. Miniaturization has made it possible for radio tracking to be used even on relatively small animals.

In field studies, animals are often marked in some way so that observers are able to follow individual animals. A number of techniques have been developed, including banding birds with colored acrylic bands. Color combinations can be varied so that each member of the population has a unique combination. Marking allows the observer to get information such as individual territory boundaries and to determine which animals interact.

Models are frequently used in experiments. For example, a model can be used to determine whether individuals in a species need to learn to identify certain classes of predators. Models were used in many of the classic experiments in ethology. Modern technology has allowed the development of much more sophisticated models. One of the most interesting is a "bee" that can perform a waggle dance (used by bees to indicate location) so effectively that its hivemates can find the food source. Whether a model is simple or sophisticated, it can provide a tool to determine the cues that trigger an animal's response.

Neurobiologists use electrodes and appropriate equipment to stimulate and record the responses of neurons. They can also stimulate specific regions of the nervous system by using tiny tubes to deliver hormones or neurotransmitters. Genetic technology has made it possible to examine the deoxyribonucleic acid (DNA) of individuals in a species. This tool can be used, for example, to determine whether females in monogamous species are completely monogamous or whether some of their offspring are fathered by males other than their mates.

Tape recorders have become very important in studies of animal vocalizations. Recorders are used in two ways. The animal's vocalizations may be recorded and the recording used to make sound spectrographs for analysis. The recordings may also be used to determine whether individuals can discriminate between the vocalizations of neighboring and nonneighboring individuals in their species. Playbacks can also be used to simulate intruders in the territory of an individual and can be applied to many other experimental situations in both field and laboratory.

The methods used by ethologists are as varied as the problems they investigate. Because the skill of the observer is still a vital link in the investigation of animal behavior, ethology remains one of the more approachable areas of scientific investigation.

Uses of Ethology

The investigation of animal behavior has a number of benefits, both practical and abstract. Some animals are pests, and knowledge of their behavior can be used to manage them. For example, synthetic pheromones have been used to attract members of some insect species. The insects may then be sampled or killed, depending upon the application. To the extent that researchers develop behaviorally based pest management strategies and reduce pesticide use, they will be promoting our own safety as well as that of other species.

It is sometimes important for humans to be able to understand the communication signals of other species and the characteristics of their sensory perception. The knowledgeable individual can recognize the cues that indicate risk that a dog might bite, for example, and can also avoid behavior that the dog will regard as threatening. Understanding the behavior of the wild animals most likely to be encountered in one's neighborhood is an important factor in peaceful coexistence.

The study of animal behavior is providing one of the more fascinating areas of evolutionary biology. Ethology has demonstrated more effectively than most fields of study how diverse the solutions to a given problem can be and has provided insight into human behavior from a biological perspective. Knowledge of animal behavior also enriches human lives simply by satisfying some of our natural curiosity about animals.

—Donna Janet Schroeder

See also: Altruism; Coevolution; Communication; Communities; Competition; Domestication; Emotions; Evolution: Animal life; Evolution: Historical perspective; Grooming; Groups; Habituation and sensitization; Hormones and behavior; Imprinting; Insect societies; Isolating mechanisms in evolution; Language; Learning; Mammalian social systems; Migration; Offspring care; Pheromones; Predation; Reproductive strategies; Rhythms and behavior; Sex differences: Evolutionary origin; Territoriality and aggression; Zoology.

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EVOLUTION: ANIMAL LIFE

Types of animal science: Evolution, fields of study
Fields of study: Developmental biology, evolutionary science, genetics, human origins, zoology

Evolution is the change in the gene pool of a population over time by such processes as natural selection, genetic drift, mutation, and migration.

Principal Terms

GENE: the basic unit of heredity

GENE FLOW: the movement of genes from one population to another

GENETIC DRIFT: change in gene frequencies in a population owing to chance

INTERBREEDING: the mating of closely related individuals, which tends to increase the appearance of recessive genes

MIGRATION: the movement of individuals, resulting in gene flow, changing the proportions of genotypes in a population

MUTATION: alteration in the physical structure of the DNA, resulting in a genetic change that can be inherited

NATURAL SELECTION: the process of differential reproduction in which some phenotypes are better suited to life in the existing environment and thus are more likely to survive

SPECIATION: the formation of new species as a result of geographic, physiological, anatomical, or behavioral factors

SPECIES: the basic category of biological classification representing a group of potentially or actually interbreeding natural populations which are reproductively isolated from other such groups

TAXON (pl. TAXA): group of related organisms at one of several levels such as the family Canidae, the genus *Canis*, or the species *Canis lupus*

Current consensus holds that the so-called big bang—the high-temperature, high-density event that marked the beginning of the universe—occurred some fifteen billion years ago, with the sun and Earth formed about four and a half billion years ago. Four billion years ago, the relatively newly created sun shone with only 70 percent of its current strength. The atmosphere had no free oxygen. No bacteria, no viruses, no plants, and no animals were in existence. Subsequently, as chemical processes are assumed to have created oxygen and an organic "soup," microbial life in the form of the simplest cells without a nucleus, prokaryotes, developed out of this primordial ooze. These bacteria were the only living organisms for about two billion years. After that time, about 1.5 billion years ago, more complex cells with nuclei, eukaryotes, appeared. Thus, in all, for some 5.5 billion years, bacteria were the only existing animal organisms.

The Beginnings of Animal Life

Eventually, the two kingdoms, the botanical and the zoological, started to diverge and millions of animals came into being, multicelled and with specialized body parts, distinguished from plants primarily but not exclusively by their methods of feeding, locomotion, and reproduction. Most of the phyla seem to have appeared during the Precambrian period, an immense span of geological time that ended about 590 million years ago. Few fossils have remained from these prehistoric times, but the most explosive period for the development of life was the Cambrian, some 590 to 505 million years ago. In a relatively short span of ten million years, all the animal phyla currently known came into being, perhaps encouraged by an increase in oxygen in the seas, where animal life began.

Eventually, animals developed a nervous system enabling them to control their movements more appropriately, as well as sense organs to help them find suitable food. At the margins, however, the dichotomy between the botanical and the animal world has remained ambiguous, since there are many microorganisms which defy clearcut classification At times, these difficult cases are known as Protista, or Protists.

In all forms of life, including the animal kingdom, no phylum has been produced by a single evolutionary event. Nor have different animal orders appeared as a result of sudden evolutionary changes. Rather, all have come about, whether in gradual or punctuated manner, by the cumulative effect of small steps in different directions. This, at least, is the theory posited by Charles Darwin's explanation of evolution.

The time line of the animal kingdom is closely connected with this evolutionary chronology. Darwin's theory of the origin of species through natural selection, nearly universally accepted in the scientific community but at times opposed on Biblical creationist grounds and in some circles of the lay community, has it that animals, like plants, have changed since the beginning of life on earth and are still evolving today. In this view, there was no sudden creation of all species. Instead, over long periods of time, new species have evolved from isolated populations of existing species. These came to occupy new niches separate from the niches of the original species. Thus, all current species are changed descendants of others that existed previously. If there are fewer apparent links between phyla than between families further down the classification ladder, the reason is that phyla have had a longer history and so have experienced more opportunities for the elimination of intermediate forms. From an evolutionary viewpoint, the difference between species down an evolutionary line are even more recent than those between families, and so on. On average, it takes about 500,000 generations for one species to evolve into another. For species to have survived in their environments—with simultaneous changes in ecology, climate, and flora—many animal forms are now more complex and efficient than their ancestors used to be.

Genes and Evolution

Life began in the seas, so for animals to live in freshwater, let alone on dry land or in the air, many obstacles had to be overcome. The impetus to conquer these inhospitable realms came from competition, according to Darwin's theory of the survival of the fittest. Those fauna that managed to surmount the problems were the ones that underwent waves of adaptive measures and evolved into new kinds of animals.

It was only in the twentieth century that it was discovered that the characteristics of a species are passed on from parents to offspring by genes. Genes provide cells for particular features, such as webbed feet. With such characteristics inherited by offspring from parents, there is a resemblance among generations. However, at times a parent may produce quite a different offspring because of genetic change. The young, in turn, may replicate this difference in their own descendants in a process known as mutation, which may occur spontaneously for unknown reasons, but also may occur due to known causes, such as exposure to radiation. At times, mutations may be useful in allowing the species to adapt better to its environment; for instance, darker moths have a better chance of survival in a forest than lighter ones because the latter are more visible to their predators than the former. Other mutations may be harmful, such as larger size that slows down a species, making its flight from danger more difficult.

Whatever the case, within a time frame of 1 to 10 million years, animals may remain the same, may evolve, or may become completely extinct, as did the dinosaurs about 60 million years ago, after being dominant for some 350 million years.

Adaptation to Environment

Natural selection leading to a new species may be accelerated when members of the original species move to a new environment, whether voluntarily or driven by the elements. Separated populations may develop different traits as they adapt to their new condition. Eventually, they will become sufficiently different to be unable to produce offspring with members of their original population. This process has repeated itself many times, over millions of years, and accounts for the large diversity in the animal world, not to mention the additional diversity consequent on artificial breeding by humans, widely observed among domesticated animals such as horses, cattle, and dogs.

Animals occupied new environments as species living in water moved to the land or later to the air. Thus, the step from fish to amphibian was essentially one from living in water for the whole life to living on land for the adult stage of the life cycle. The step from amphibian to reptile was one of increasingly proficient adaptation to land life at all stages of the life cycle.

Birds and mammals evolved in different directions from the reptiles, the first in adaptation to an arboreal and finally a flying life and the second as a further advance in the maintenance of an even and high body temperature—homeothermy—by combining an insulating external layer such as hair with a variety of physiological thermostats.

Events in geology, climate, and flora also determined the geographic distribution of species. Thus, marsupials are currently found almost entirely in Australasia and South America. The tiger exists only in India and Southeast Asia. The lion is restricted mainly to Africa. This pattern reflects the way in which these groups have evolved in relation to the physical world.

New animal groups evolve into many different forms, especially when they become dominant. For instance, when mammals came to occupy the dominant position, some became meat-eaters while others became vegetarians; some became smaller while others became larger; some became runners while others ended up as burrowers or flyers; still others returned to the water. This trend allowed the descendants of the original type to

Image Not Available

exploit a much greater range of environments and resources. Essentially, those species whose sense organs or brain morphology and functions improved the most ended up being dominant—primates in general and humans in particular.

Time Frame

The exact time of the origins of animals during earth's evolutionary history is not known because the early species were soft-bodied, at first single-celled and later multicellular life forms, that did not fossilize well. Fossils are the best material evidence of archaic times. Fossils do not appear earlier than 650 to 500 million years ago, not only because the animal life of the time was inappropriate for fossilization, but also because continued crustal shifts in the ensuing eons disturbed the very early rock formations. Accordingly, fossil evidence is unavailable for the entire early history of animals, which must consequently remain speculative. Current taxonomic interrelationships suggest the early history, and taxonomic diagrams may be regarded as presumptive evolutionary diagrams as well. However, a ball of carbon discovered in a cavity etched in a rock some 3.86 billion years old suggests that some life on earth was already possible at that time.

Knowledge is also limited by the fact that, even though over a million different species of animals have been identified, it is suspected that a similar number remain to be discovered or became extinct before such identification could be made. In the United States alone, some forty species of birds, about thirty-five species of mammals, and twenty-five other species have become extinct in the last two hundred years alone—less than a blip on earth's time scale—as a result of human activities such as the destruction of animal habitats through urbanization, the clearing of land for agricultural purposes, pollution, the introduction of new species from other parts of the world which turned out to be predatory to domestic specimens, hunting, and especially human population growth. It is widely predicted that climatic change triggered by greenhouse gases will continue, even enhance, this process, thereby endangering more animal species. Whatever the future, however, evolutionary biologists estimate that some 99 percent of all species that have ever lived on earth are now extinct.

Despite these and other caveats, here is a very approximate timetable of the evolution of animal life:

Life Form	Date of Emergence
Simplest single-celled Protozoa	3.5 billion years ago
Invertebrates evolving from Protozoa	670 to 640 million years ago
First vertebrates evolving from invertebrates	500 million years ago
First mammals	200 million years ago
Hominids (modern man) from apelike hominoids	200,000 to 25,000 years ago

Translated in terms of a single year:

January 1: Big Bang
March 22: Bacteria, the first living animals
November 9: Invertebrates
November 22: Vertebrates
December 16: Mammals
December 28: Primates, the highest order of mammals
December 31, a few minutes before midnight: Modern man, the dominant primate

Evolution of Existing and Extinct Human Species and Australopithecines

The root of the hominid evolutionary tree is still imperfectly known. The earliest australopithecine species, *Australopithecus anamensis*, is believed to be over four million years old, by which time that branch had diverged from African apelike ancestors. This species was followed by the *Australopithecus afarensis* nearly 3.5 million years ago. Much later came *Homo habilis*, called "skillful man" since they could presumably produce primitive tools, some two million years ago. They were followed by *Homo erectus*, "upright man," about one million years ago. Finally, *Homo sapiens*, "knowing man," emerged about 200,000 years ago. In the meantime, the australopithecine branch, after evolving through a number of intermediate species such as *A. africanus*, *A. aethiopicus*, and *A. robustus*, died out about one million years ago. To date, the earliest unearthed fossil, that of Lucy, a three-foot-tall female discovered in Ethiopia, is about four million years old. Modern humans are believed to have radiated out of Africa into Asia and Europe. Subsequently, cultural evolution became more prominent than biological evolution, but as modern humans evolved over the last four million years to their current condition, they developed manipulative skills, bipedalism, a change from specialized to omnivorous feeding habits, and especially, a threefold increase in cranial capacity from *H. afarensis* to *H. neanderthalensis*, together with behavior appropriate to the control of the environment.

Although humans are not the only animals capable of conceptual thought, they have refined and extended that ability until it has become their hallmark. Thus, thanks to the symbolic language of *Homo sapiens*, modern humans make possible the accumulation of experience from one generation to the next. Such cultural evolution is possessed by few, if any other animal species. It is for this reason that humans, more than other animals, have found ways to mold and change their environment according to need rather than in response to environmental demands. Because of this ability and humans' control of technology, the species has more say about their biological future than any other.

—Peter B. Heller

See also: Adaptive radiation; Apes to hominids; Clines, hybrid zones, and introgression; Coevolution; Convergent and divergent evolution; Development: Evolutionary perspective; Evolution: Historical perspective; Extinction; Extinctions and evolutionary explosions; Gene flow; Genetics; Hardy-Weinberg law of genetic equilibrium; Heterochrony; *Homo sapiens* and human diversification; Human evolution analysis; Isolating mechanisms in evolution; Natural selection; Neutral mutations and evolutionary clocks; Nonrandom mating, genetic drift, and mutation; Paleoecology; Paleontology; Phylogeny; Punctuated equilibrium and continuous evolution; Sex differences: Evolutionary origins; Systematics.

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EVOLUTION: HISTORICAL PERSPECTIVE

Type of animal science: Evolution
Fields of study: Ecology, embryology, evolutionary science, genetics, paleontology, population biology, zoology

Evolution is the process of change in biological populations. Historically, it is also the theory that biological species undergo sufficient change with time to give rise to new species.

Principal Terms

- ADAPTATION: the possession by organisms of characteristics that suit them to their environment or their way of life
- CATASTROPHISM: a geological theory explaining the earth's history as resulting from great cataclysms (floods, earthquakes, and the like) on a scale not now observed
- DARWINISM: branching evolution brought about by natural selection
- ESSENTIALISM (TYPOLOGY): the Platonic-Aristotelian belief that each species is characterized by an unchanging "essence" incapable of evolutionary change
- GENOTYPE: the hereditary characteristics of an organism
- GEOFFROYISM: an early theory of evolution in which heritable change was thought to be directly induced by the environment
- LAMARCKISM: an early evolutionary theory in which voluntary use or disuse of organs was thought to be capable of producing heritable changes
- SCALE OF BEING (CHAIN OF BEING): an arrangement of life forms in a single linear sequence from "lower" to "higher"
- UNIFORMITARIANISM: a geological theory explaining the earth's history using processes that can be seen at work today

Evolution is the theory that biological species undergo sufficient change with time to give rise to new species. The concept of evolution has ancient roots. Anaximander suggested in the sixth century B.C.E. that life had originated in the seas and that humans had evolved from fish. Empedocles (fifth century B.C.E.) and Lucretius (first century B.C.E.), in a sense, grasped the concepts of adaptation and natural selection. They taught that bodies had originally formed from the random combination of parts, but that only harmoniously functioning combinations could survive and reproduce. Lucretius even said that the mythical centaur, half horse and half human, could never have existed because the human teeth and stomach would be incapable of chewing and digesting the kind of grassy food needed to nourish the horse's body.

For two thousand years, however, evolution was considered an impossibility. Plato's theory of forms (also called his "theory of ideas") gave rise to the notion that each species had an unchanging "essence" incapable of evolutionary change. As a result, most scientists from Aristotle to Carolus Linnaeus in the eighteenth century insisted upon the immutability of species. Many of these scientists tried to arrange all species in a single linear sequence known as the scale of being (also called the chain of being and the *scala naturae*), a concept supported well into the nineteenth century by many philosophers and theologians as well. The sequence in this scale of being was usually interpreted as a static "ladder of perfection" in God's creation, arranged from higher to lower forms.

The scale had to be continuous, for any gap would detract from the perfection of God's creation. Much exploration was devoted to searching for "missing links" in the chain, but it was generally agreed that the entire system was static and incapable of evolutionary change. Pierre-Louis Moreau de Maupertuis, in the eighteenth century, and Jean-Baptiste Lamarck were among the scientists who tried to reinterpret the scale of being as an evolutionary sequence, but this single-sequence idea was later replaced by Charles Darwin's concept of branching evolution. Georges Cuvier finally showed that the major groups of animals had such strikingly different anatomical structures that no possible scale of being could connect them all; the idea of a scale of being lost most of its scientific support as a result.

The Struggle to Conceptualize Evolution

The theory that new biological species could arise from changes in existing species was not readily accepted at first. Linnaeus and other classical biologists emphasized the immutability of species under the Platonic-Aristotelian concept of essentialism. Those who believed in the concept of evolution realized that no such idea could gain acceptance until a suitable mechanism of evolution could be found. Many possible mechanisms were therefore proposed. Étienne Geoffroy Saint-Hilaire proposed that the environment directly induced physiological changes, which he thought would be inherited, a theory now known as Geoffroyism. Lamarck proposed that there was an overall linear ascent of the scale of being but that organisms could also adapt to local environments by voluntary exercise, which would strengthen the organs used; unused organs would deteriorate. He thought that the characteristics acquired by use and disuse would be passed on to later generations, but the inheritance of acquired characteristics was later disproved. Central to both these explanations was the concept of adaptation, or the possession by organisms of characteristics that suit them to their environments or to their ways of life. In eighteenth century England, the Reverend William Paley and his numerous scientific supporters believed that such adaptations could be explained only by the action of an omnipotent, benevolent God. In criticizing Lamarck, the supporters of Paley pointed out that birds migrated toward warmer climates before winter set in and that the heart of the human fetus had features that anticipated the changes of function that take place at birth. No amount of use and disuse could explain these cases of anticipation, they claimed; only an omniscient God who could foretell future events could have designed things with their future utility in mind.

The nineteenth century witnessed a number of books asserting that living species had evolved from earlier ones. Before 1859, these works were often more geological than biological in content. Most successful among them was the anonymously published *Vestiges of the Natural History of Creation* (1844), written by Robert Chambers. Books of this genre sold well but contained many flaws. They proposed no mechanism to account for evolutionary change. They supported the outmoded concept of a scale of being, often as a single sequence of evolutionary "progress." In geology, they supported the outmoded theory of catastrophism, an idea that the history of the earth had been characterized by great cataclysmic upheavals. From 1830 on, however, that theory was being replaced by the modern theory of uniformitarianism, championed by Charles Lyell. Charles Darwin read these books and knew their faults, especially their lack of a mechanism that was compatible with Lyell's geology. In his own work, Darwin carefully tried to avoid the shortcomings of these books.

Darwin's Revolution in Biological Thought

Darwin brought about the greatest revolution in biological thought by proposing not only a theory of branching evolution but also a mechanism of natural selection to explain how it occurred. Much of Darwin's evidence was gathered during his voyage around the world aboard HMS *Beagle*. Darwin's stop in the Galápagos Islands and his study of tortoises and finchlike birds on these islands are usually credited with convincing him

Comte de Buffon (Georges-Louis Leclerc)

Born: September 7, 1707; Montbard, France
Died: April 16, 1788; Paris, France
Fields of study: Anthropology, biology, botany, chemistry, geology, mathematics, paleontology, zoology
Contribution: The greatest naturalist of the eighteenth century, Buffon popularized zoology and botany through his publications. He tried to separate science from religious and metaphysical ideas and rejected teleological reasoning and the idea of God's direct intervention in nature.

Born to a noble family in Dijon, Buffon was admitted to the French Academy of Sciences in 1734 and the Académie Française in 1753. In 1739 he was appointed director (*Intendant*) of the Jardin du Roi, the royal botanical garden. Between 1749 and his death, he published (with associates) thirty-six volumes of the *Histoire Naturelle* (44 vols., 1739-1804; *A Natural History, General and Particular*, 10 vols., 1807) which took in the formation of the earth, geology, paleontology, zoology, and botany. The last eight volumes were posthumous. A master of style, his books were among the most popular in the eighteenth and early nineteenth centuries.

Buffon believed that the study of Earth was a necessary prerequisite to botany and zoology, and wrote two important texts on geology and paleontology. The first, *Théorie de la terre*, was published in 1749, the other, *Époques de la nature*, in 1778. From experiments on the cooling of globes, he estimated the age of the earth to be 85,000 years, significantly at variance with his contemporaries' estimation of an origin around 4000-6000 B.C.E. Buffon's cosmogony replaced the intervention of God by a cause whose effects are in accord with the laws of mathematics.

Buffon postulated that new varieties of plants and animals (including humans) were produced in nature by external geographical influences. Such influences could also cause degeneration. He was against classifying nature, as "... everything that can be, is." He gave "species" a purely biological definition: animals that by means of copulation perpetuate themselves and preserve their similarity. He thought families were artificial creations made by man. He therefore thought Linnaeus' classification of plants based on sexual characters was too rigid. He arranged animals in order of their utility to humans (later he rearranged them according to distinctive characteristics) and believed that some forms might have degenerated from others over time—thus, the ass might be a degenerate form of the horse. Buffon thus alluded to a form of "evolution" where physical characteristics produced by external influences could be passed down the generations.

The Comte de Buffon was perhaps the greatest naturalist of the eighteenth century, rejecting religious explanations of the state of the world in favor of scientific research. (Library of Congress)

Buffon tried to separate science from religious and metaphysical ideas, and rejected teleological reasoning and the idea of God's direct intervention in nature. His theories went against the accepted theological belief of immutability of species and he was reprimanded by the Faculty of Theology at the University of Paris for this. Buffon apologized but did not change his views.

Buffon was made a count in 1773 by Louis XV. He was greatly respected by his contemporaries and was made a member of almost every learned society in Europe.

—Ranès C. Chakravorty

that evolution was a branching process and that adaptation to local environments was an essential part of the evolutionary process. Adaptation, he later concluded, came about through natural selection, a process that killed the maladapted variations and allowed only the well-adapted ones to survive and pass on their hereditary traits. After returning to England from his voyage, Darwin raised pigeons, consulted with various animal breeders about changes in domestic breeds, and investigated other phenomena that later enabled him to demonstrate natural selection and its power to produce evolutionary change.

Darwin's greatest contribution was that he proposed a suitable mechanism by which permanent organic change could take place. All living species, he said, were quite variable, and much of this variation was heritable. Also, most organisms produce far more eggs, sperm, seeds, or offspring than can possibly survive, and the vast majority of them die. In this process, some variations face certain death while others survive in greater or lesser proportion. Darwin called the result of this process "natural selection," the capacity of some hereditary variations (now called genotypes) to leave more viable offspring than others, with many leaving none at all. Darwin used this theory of natural selection to explain the form of branching evolution that has become generally accepted among scientists.

Darwin delayed the publication of his book for seventeen years after he wrote his first manuscript version. He might have waited even longer, except that his hand was forced. From the East Indies, another British scientist, Alfred Russel Wallace, had written a description of the very same theory and submitted it to Darwin for his comments. Darwin showed Wallace's letter to Lyell, who urged that both Darwin's and Wallace's contributions be published, along with documented evidence showing that both had arrived at the same ideas independently. Darwin's great book, *On the Origin of Species by Means of Natural Selection*, was published in 1859, and it quickly won most of the scientific community to a support of the concept of branching evolution. In his later years, Darwin also published *The Descent of Man and Selection in Relation to Sex* (1871), in which he outlined his theory of sexual selection. According to this theory, the agent that determines the composition of the next generation may often be the opposite sex. An organism may be well adapted to live, but unless it can mate and leave offspring, it will not contribute to the next or to future generations.

Acceptance of Darwinism in the Twentieth Century

In the early 1900's, the rise of Mendelian genetics (named for botanist Gregor Mendel) initially resulted in challenges to Darwinism. Hugo de Vries proposed that evolution occurred by random mutations, which were not necessarily adaptive. This idea was subsequently rejected, and Mendelian genetics was reconciled with Darwinism during the period from 1930 to 1942. According to this modern synthetic theory of evolution, mutations initially occur at random, but natural selection eliminates most of them and alters the proportions among those that survive. Over many generations, the accumulation of heritable traits produces the kind of adaptive change that Darwin and others had described. The process of branching evolution through speciation is also an important part of the modern synthesis.

The branching of the evolutionary tree has resulted in the proliferation of species from the common ancestor of each group, a process called adaptive radiation. Ultimately, all species are believed to have descended from a single common ancestor. Because of the branching nature of the evolutionary process, no one evolutionary sequence can be singled out as representing any overall trend; rather, there have been different trends in different groups. Evolution is also an opportunistic process, in the sense that it follows the path of least resistance in each case. Instead of moving in straight lines toward a predetermined goal, evolving lineages often trace meandering or circuitous paths in which each change represents a momentary increase in adaptation. Species that cannot adapt to changing conditions die out and become extinct.

Studying Evolution

Evolution is studied by a variety of methods. The ongoing process of evolution is studied in the field by ecologists, who examine various adaptations, including behavior and physiology as well as anatomy. These adaptations are also studied by botanists, who examine plants; zoologists, who examine animals; and various specialists, who work on particular kinds of animals or plants (for example, entomologists, who study insects). Some investigators capture specimens in the field, then bring back samples to the laboratory in order to examine chromosomes or analyze proteins using electrophoresis. Through these methods, scientists learn how the ongoing process of evolutionary change is working today within species or at the species level on time scales of only one or a few generations.

The long-term results of evolutionary processes are studied among living species by comparative anatomists and embryologists. Extinct organisms are studied by paleontologists, scientists who examine fossils. Biogeographers study past and present geographic distributions. All these types of scientists make comparisons among species in order to determine the sequence of events that took place in the evolutionary past. One method of reconstructing the branching sequences of evolution is to find homologies, deep-seated resemblances that reflect common ancestry. Once the sequences are established, functional analysis can be used to suggest possible adaptive reasons for any changes that took place. The sequences of evolutionary events reconstructed by these scientists represent the history of life on the earth. This history spans many species, families, and whole orders and classes, and it covers great intervals of past geologic time, measured in many millions of years.

The Historical Context of Evolutionary Theory

The historical development of evolutionary theory should be viewed in two contexts: that of biological science and that of cultural history. The concept of evolution had been talked about for many years before 1859 and was usually rejected because no suitable mechanism had gained widespread acceptance. The fact that the phenomenon of natural selection was independently discovered by two Englishmen shows both that the time was ripe for the discovery and that the circumstances were right in late nineteenth century England.

Evolutionary biology is itself the context into which all the other biological sciences fit. Other biologists, including physiologists and molecular biologists, study how certain processes work, but it is evolutionists who study the reasons why these processes came to work in one way and not another. Organisms and their cells are built one way and not another because their structures have evolved in a particular direction and can only be explained as the result of an evolutionary process. Not only does each biological system need to function properly, but it also must have been able to achieve its present method of functioning as the result of a long, historical, evolutionary process in which a previous method of functioning changed into the present one. If there were two or more ways of accomplishing the same result, a particular species used one of them because found it easier to evolve one method rather than another.

Everything in biology is thus a detail in the ongoing history of life on the earth, because every living system evolves. Living organisms and the processes that make them function are all products of the evolutionary process and can be understood only in that context. As biologist Theodosius Dobzhansky once said, "Nothing in biology makes sense, except in the light of evolution."

—*Eli C. Minkoff*

See also: Adaptive radiation; Apes to hominids; Clines, hybrid zones, and introgression; Coevolution; Convergent and divergent evolution; Development: Evolutionary perspective; Evolution: Animal life; Extinction; Extinctions and evolutionary explosions; Gene flow; Genetics; Hardy-Weinberg law of genetic equilibrium; Heterochrony; *Homo sapiens* and human diversification; Human evolution analysis; Isolating mechanisms in evolution; Natural selection; Neutral mutations and evolutionary clocks; Nonrandom mating, ge-

Jean-Baptiste de Lamarck

Born: August 1, 1744; Bazentin-le-Petit, Picardy, France
Died: December 18, 1829; Paris, France
Fields of study: Evolutionary science, invertebrate biology, paleontology, zoology
Contribution: Lamarck established the division of animal life into the vertebrate and invertebrate categories, and he formulated an evolutionary theory based on the premise that acquired traits are inheritable.

Jean-Baptiste de Lamarck is best known for his theory that acquired physical traits may be inheritable. (Library of Congress)

After studying briefly for the priesthood at the Jesuit seminary in Amiens, Jean-Baptiste de Monet, chevalier de Lamarck, served as an army officer in the Seven Years' War. Following an accident in 1768, he began to study botany and medicine. In 1778, he published his three-volume *Flore français* (French plants), which was widely used as a manual of identification.

Lamarck was then employed as assistant botanist at the royal botanical gardens of Paris, and he was also appointed to the prestigious Academy of Sciences. Count Georges-Louis de Buffon engaged him as tutor to his son, which allowed him to tour European botanical gardens for two years. When the Jardin des Plantes (the National Museum of Natural History) was founded in 1793, he was placed in charge of the collection of invertebrates (a term that he coined).

During the early nineteenth century, Lamarck published numerous books about invertebrates, paleontology, and biological evolution. His *Système des animaux sans vertèbres* (1801; system of invertebrate animals) presented a systematic basis for the classification of the lower animals. His *Hydrogéologie* (1802; *Hydrogeology*, 1964) interpreted the history of the earth as a series of inundations, each resulting in organic deposits that built up the continents. The book was especially noteworthy for its recognition of the vastness of geologic time.

Lamarck was not the first to propose a theory of biological evolution, but his theory was more systematic and coherent than previous versions. He gave the clearest explanation for his theory in *Philosophie zoologique* (1809; *Zoological Philosophy*, 1873), presenting a two-part process. First, a change in the environment forced organisms to change their behavior. If particular organs were used, they would increase in size and strength; in contrast, disuse or disease would weaken and shrink organs. Second, Larmark argued that such changes would be inherited, so that the characteristics of a species would change gradually over many generations.

Lamarck's scientific work culminated in an exhaustive study, *Histoire naturelle des animaux sans vertèbres* (1815-1822; natural history of invertebrate animals).

Charles Darwin acknowledged the great contribution of Lamarck's work, and Darwin's own theory of natural selection never entirely rejected the possibility that some acquired traits might be inherited. With advancements in the science of heredity during the twentieth century, the concept of Lamarckian inheritance has been largely abandoned. Late in the twentieth century, nevertheless, Edward J. Steele and other biologists found evidence that the acquired immunities of organisms might be passed on to their offspring.

—Thomas Tandy Lewis

netic drift, and mutation; Paleoecology; Paleontology; Phylogeny; Punctuated equilibrium and continuous evolution; Sex differences: Evolutionary origins; Systematics.

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EXOSKELETONS

Type of animal science: Anatomy
Field of study: Invertebrate biology

The exoskeleton is one of the distinctive primary features of members of the phylum Arthropoda. The evolution of the exoskeleton cuticle is thought to have been important in this group's successful adaptation to many diverse environments. The exoskeleton's intricate structure has provided advantages enabling the arthropods to thrive for hundreds of millions of years.

Principal Terms

CHITIN: a cellulose-like, crystalline material that makes up 25 percent to 60 percent of the dry weight of the cuticle

CUTICLE: the outer arthropod exoskeleton consisting of several layers of secreted organic matter, primarily nonliving chitin

ENDOCUTICLE: usually the thickest layer of the cuticle, found just outside the living epidermal cell layer and made of untanned proteins and chitin

EPICUTICLE: the outermost and thinnest layer of the arthropod cuticle, composed mainly of the hardened protein cuticulin

EPIDERMIS: a living cellular layer that secretes the greater part of the cuticle and is responsible for dissolving and absorbing the cuticle during molting (also termed the hypodermis)

EXOCUTICLE: a thick middle layer in the cuticle made up of both chitin and rigid, tanned proteins termed sclerotin

INTEGUMENTARY PROCESSES: surface outgrowths from the cuticle, primarily rigid nonarticulated processes or movable articulated processes

SCLEROTIN: a hard, horny protein constituent of the exocuticle found in arthropods such as insects; it is superficially similar to vertebrate horn or keratin

The evolution of invertebrate animals possessing rigid, hard exoskeletons represented a great advance for members of the phylum Arthropoda. The development of such exoskeletons—in comparison with less solid structures, such as the hydrostatic skeleton of coelenterates—gave arthropods several distinct evolutionary advantages over other invertebrate phyla. Hydrostatic skeletons, such as those possessed by sea anemones, operate by the animal's musculature being arranged in a pattern that surrounds an enclosed volume of fluid. Contraction of any one section of the muscular system creates a fluid pressure in the central cavity that is consequently transmitted in an omnidirectional manner to the rest of the body. Arthropodic exoskeletons, on the other hand, are consistently rigid and much harder because they are composed to some extent of crystalline substances. Flexibility of movement is attained by multiple jointings in the limb system and in other appendages in the body such as feeding and sensory apparatuses.

Exoskeletons and Arthropod Success

As a consequence of two distinctive features—a hard, rigid exoskeleton and jointed appendages and other body parts—arthropods have become one of the most successful of all animal groups; indeed, it is by these two features that they are taxonomically defined. Biologists sometimes term the enhancement of the annelid (worm) body plan of segmentation by arthropod improvement "arthropodization." Because of it, the ancestors of the present immense spectrum of arthropod species successfully adapted to myriad ecological niches in the sea, on land, and in the air. Arthropod species account for more than three quarters of all known animal species. In fact, the class Insecta, one of a number of classes within the arthropod phylum, numbers at least 700,000 known species, with new species being discovered yearly, mostly in the tropics.

The immense success of arthropods is, to a great extent, the result of the advantages provided by the composition and structure of the seemingly simple surface architecture that is the arthropod exoskeleton. This exoskeleton not only provides a substantial chemical and physical barrier between the animal and the external environment, protecting the internal organs and fluids, but also allows a degree of temperature and osmotic regulation. In addition, the exoskeleton helps deter predation, provides a solid base of attachment for an internal muscular system, and offers a good site for the location of various sense organs. One of the most noteworthy evolutionary advantages of the exoskeleton is its service as a solid base of muscle attachment. The arthropod limbs act as a system of mechanical levers that is a much more efficient locomotive system than that of evolutionarily older and less sophisticated invertebrate locomotive systems such as that of the annelids. Because of exoskeletons and the structurally strong, jointed appendages that exoskeletons permit, arthropods possess an internal, muscular body wall broken down into separate muscles having an arrangement allowing contractions that are more localized in time and space than annelid or coelenterate muscle behavior. This more modular approach to the musculature allows arthropods to react to their environments to use energy more efficiently and with greater precision of movement and response. In fact, the inner surface of the exoskeleton acts as a limited type of endoskeleton, or inner skeleton, in that it provides good anchoring sites for muscle attachment, thus further increasing the leverage power of arthropod limbs and appendages.

The Parts of the Exoskeleton

The exoskeleton itself can be divided into several distinct units based on function and composition. These are composed of consecutive layers that surround the animal in an arrangement similar to a medieval knight's suit of armor. Like the armor suit, the outermost exoskeleton is, in a typical arthropod, very rigid and hard; movement is possible only because both protective systems are composed of plates or body-contoured segments that incorporate narrow, flexible jointings allowing motion. The motion is usually narrowly defined in extent and direction, and it is this quality that gives both armored humans and many arthropods their often distinctively awkward and ungainly mode of movement. The larger terrestrial beetles and marine forms such as crabs and lobsters are ready examples of this. Some arthropods are nevertheless adroit and delicate in their movements, as shown by various arthropod aerialists such as the dragonflies and butterflies.

Insects can, in many ways, be considered typical arthropods and are therefore useful as models for a discussion of the exoskeleton as found among all arthropods. All the various layers of the exoskeleton, both living and nonliving, are as a whole variously termed the integument or cuticle. These layers are the skin or surface of the animal. The innermost layer of the exoskeleton is termed the epidermis, or hypodermis, and is made of living cells. The epidermis is immediately external to a basement membrane that separates the epidermis from the inner body, with its organs and fluids. The epidermis is responsible for secreting the layers external to it, which are organic but actually nonliving material. From the epidermis outward, these layers in insects consist of the endocuticle, the exocuticle, and the epicuticle. (Some biologists use the term procuticle to describe the endocuticle and use epicuticle to mean both the epicuticle and the exocuticle.) Whatever precise terms may be employed, the general concept is that layers of material closer to the epidermis are more flexible and less chemically hardened than layers that are found closer to the actual exterior of the animal. The endocuticle is usually the thickest cuticle layer and is constituted of protein mixed with a material called chitin. Chitin is a cellulose-like, crystalline material that makes up anywhere from 25 percent to 60 percent of the dry weight of the cuticle. It has many useful properties, such as resistance to concentrated alkalies and acids. In chemical composition, chitin is a nitrogenous polysaccharide. Chitin itself can be a relatively soft and flexible material that gains hardness in the outermost arthropod exoskeleton in several ways. One way is by using the presence of a material termed sclerotin. The process of hardening through the agency of sclerotin is called sclerotinization and involves a molecular change in the organization of the protein part of the cuticle. The outermost chitin found in the exocuticle of insects, for example, is thoroughly sclerotinized, which characteristically results in a darkening of the chitin. The other method by which chitin hardens is the deposition of calcium carbonate, primarily in the form of calcite. This is the process found among marine arthropods such as the Crustacea: crabs, lobsters, and shrimp, for example. This process, called calcification, occurs among Crustacea, starting in their epicuticle, or outermost exoskeletal layer, and works inward to the exocuticle and finally the endocuticle.

Besides the darkening caused by sclerotinization, coloration of the cuticle is effected in two basic ways. One is simple pigmentation caused by the presence of colored compounds found within the cuticle itself. The other is through the presence of extremely fine parallel ridges found on the epicuticle. These ridges break normal white light into its constituent wavelengths by prismatic diffraction in the same way that raindrops create rainbows. It is by this means that the effect of spectacularly iridescent rainbow hues found on many insects' wings and bodies is achieved.

Adding to the complexity of the cuticle are great numbers of sensory organs that project from or extend through the various exoskeletal layers. Prominent among these sensory structures are tactile hairs, bristles, and spines found all over the general body surface and on limb surfaces. These sensory structures, or setae, are movable and are set into thin, flexible disks on the cuticle surface itself. When one of these projections is moved, its base mechanically stimulates one or more sensory cells, setting off stimuli to which the arthropod can respond.

The Drawbacks of Exoskeletons

While the exoskeleton has evolved wonderfully to protect the arthropod and to enhance its locomotive and sensory abilities, its overall rigid structure presents some inherent drawbacks. Perhaps chief among these is the fact that its formidable rigidity and solidity are limitations to an individual's physical growth throughout its lifetime. Growth, in fact, is probably an arthropod's single most difficult physiological problem. This is true because once formed and hardened, an exoskeleton cannot be enlarged as the animal within enlarges with time. The physiologic solution among arthropods is the process termed ecdysis, or molting.

This process is intrinsically dangerous to the arthropod, as it leaves each individual extremely vulnerable to predation during, and immediately following, molting. It has been estimated that as much as 80 to 90 percent of arthropod mortality occurs during ecdysis. The process takes place in stages. Prior to the shedding of the old exoskeleton, a new, soft cuticle is formed beneath the old one. The new cuticle has not started along either the sclerotinization or calcification process and therefore is still soft and pliable. As the new cuticle is forming, the lower section of the old cuticle is partially dissolved by corrosive fluids secreted by cutaneous glands situated below the new cuticle. Immediately prior to the shedding, also termed casting, of the old exoskeletal cuticle, the arthropod stops feeding and absorbs more than the usual amount of water and oxygen. Its body begins to swell, and the animal makes spasmodic movements to shake off the old cuticle, most of the base of which has been removed by the corrosive process. Eventually, the old exoskeleton is effectively disconnected from the arthropod's body, and the animal extricates itself from the remains. At this point, its new exoskeleton is soft and very pliable, and its movements are limited. Conse-

Image Not Available

quently, the individual is extremely vulnerable to both predation and serious damage from tearing through abrasive or sharp-edged materials in its environment. It takes some time before the animal's cuticle has hardened and thickened enough for it to resume its normal activities. In the meantime, the exoskeleton—which normally provides a great degree of protection and mobility—acts as a hindrance and danger to the arthropod.

Studying Exoskeletons

The two main approaches used to study the arthropod exoskeleton are the same types of study used by researchers in nearly all branches of the life sciences: field studies and laboratory studies. In the field approach, living arthropods are observed in nature. The specific techniques employed include both still and motion photography in various light—normal, infrared, and ultraviolet. It is important to combine the observational database with later structural analyses of specific arthropod body parts, such as exoskeletons, to ascertain how the anatomical components actually function in the natural setting. Actual physical collections are necessary for study by laboratory workers, who subject the specimens to a range of tests to determine their qualities and features in comparison with similar species and with the normal parameters that are known for previously collected members of the same species.

Specimens are often dissected—or in some cases, vivisected (disassembled while alive)—in order to record useful data such as chemical composition of exoskeletons, metabolic rates, and the estimated age of the sample. In the case of specimens raised in captivity, more precise data can be gained, as the precise age, food type, and daily or hourly intake are known with great precision.

A wide range of techniques are employed in the laboratory to analyze the structural components of exoskeletons. Among them, optical microscopy has traditionally been the primary approach. Working with dissected parts, frequently cut and chemically stained to facilitate viewing or bring out certain features selectively, researchers have used powerful microscopes capable of magnifying by a factor of many hundreds to see tiny subcomponent structures found within exoskeletal tissue. Optical microscopes have also been used to take a close look at associated cellular and noncellular organic matter, such as chitin and sclerotin. An exponential increase in magnification for study, however, has arrived with the advent of scanning electron microscopes (SEMs). These are instruments that use a beam of focused electrons to scan an object and form a three-dimensional image on a cathode-ray tube. The SEM reads both the pattern of electrons scattered by the object and the secondary electrons produced by it. This greatly enhanced ability to see smaller objects with great clarity allows scientists to see very small target sections of exoskeletal tissue, measured in microns (millionths of a meter) in circumference. Researchers can examine in minute detail the structures and interrelationships of the various layers of the arthropod cuticle.

Exoskeletons in the Fossil Record

Because the hard arthropod exoskeleton fossilizes more readily than the remains of many other animals, the evolutionary history of the phylum Arthropoda is abundantly represented in the fossil record. Much more is known about this phylum than other invertebrate phyla because of this phenomenon. Entire classes of arthropods that have left no modern descendants are known today because their substantial body armor appears in various marine strata. Examples of this are well documented in the remains of the extinct marine groups of the trilobites (similar to modern horseshoe crabs) and the eurypterids (giant "water scorpions"). In the case of the trilobites, many fossils are actually the result of cast-off exoskeletal moltings rather than the carcasses of the dead animals. This illustrates the fact that, for hundreds of millions of years, arthropods have maintained a lifestyle and evolutionary approach to physiological problems that are similar to those of modern forms. X-ray photography has been employed successfully to penetrate the hard, mineralized fossils of extinct and ancestral forms of modern arthropods, showing in good detail the internal structures of exoskeletons and other tissues. Radiographic images produced by this technique demonstrate the continuity of structure and life shared by members of this extremely successful phylum for a period extending beyond the early Cambrian period (500 million years before the present).

The exoskeleton is an evolutionary advantage shared by all arthropods. This advantage, along with their body and limb segmentation, has allowed them to move into myriad ecological niches, first in the sea and later on land, in freshwater, and finally in the air. As a phylum, arthropods are arguably the most successful of all metazoan animal phyla; they exceed all others combined in terms of the number of species, diversity, and the number of individual organisms. This ubiquity in all biomes and climates and in virtually every conceivable niche in every ecosystem makes them a force that has a constant influence on human life.

—Frederick M. Surowiec

See also: Arthropods; Bone and cartilage; Cell Types; Circulatory systems of invertebrates; Endocrine systems in invertebrates; Endoskeletons; Evolution: Historical perspective; Hydrostatic skeletons; Invertebrates; Insects; Molting and shedding; Metamorphosis; Muscles in invertebrates; Scales; Shells.

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EXTINCTION

Type of animal science: Evolutionary science
Fields of study: Conservation biology, evolutionary science, genetics, population biology

Extinction is the total disappearance (by dying out) of all members of a species. Two types of extinction are recognized by scientists: background extinction, in which a single species disappears for one or more reasons, and mass extinction, which occurs when many different species disappear in a relatively short period of time.

Principal Terms

CATASTROPHISM: a scientific theory which postulates that the geological features of the earth and life thereon have been drastically affected by natural disasters of huge proportions in past ages

FOSSIL: a remnant, impression, or trace of an animal or plant of a past geological age that has been preserved in the earth's crust

GENE: an element of the germ plasm that controls transmission of a hereditary characteristic by specifying the structure of a particular protein or by controlling the function of other genetic material

GENE POOL: the whole body of genes in an interbreeding population that includes each gene at a certain frequency in relation to other genes

SPECIES: a category of biological classification ranking immediately below the genus or subgenus, comprising related organisms or populations potentially capable of interbreeding

UNIFORMITARIANISM: a scientific theory that all processes which have affected the earth and living creatures thereon in the past are presently at work and observable by scientists

In 1796, a French naturalist, Georges Cuvier, demonstrated incontrovertibly that many species of once-living plants and animals had completely disappeared from the earth. Cuvier was also the first to recognize that many of the extinct species he identified had disappeared at approximately the same time—a mass extinction. He and his successors attributed extinctions to catastrophic events, such as the biblical Flood. The catastrophists held the field of scientific opinion concerning extinction until the publication of Charles Lyell's *Principles of Geology* (1830-1833), which proclaimed the doctrine of uniformitarianism. Lyell maintained that no processes have affected the earth (including its flora and fauna) that are not presently observable. He denied that any spectacular cataclysms had occurred.

Climate, Evolution, and Extinctions

Lyell's arguments convinced geologists, but the problem of extinctions remained: What could cause a species to die out? In 1859, Charles Darwin offered a biological explanation for extinctions that seemed to answer all questions. In *On the Origin of Species*, Darwin suggested that all life-forms engage in a perpetual struggle for survival. The best-adapted species, therefore, survive and perpetuate themselves. The less-adapted species are outcompeted and disappear. Darwin's ideas seemed to fit well with the doctrine of uniformitarianism, but the problem of mass extinctions remained. He suggested no reasons why great numbers of very different species should disappear at approximately the same time.

Although his ideas were not accepted for many years after Darwin, another scientist proposed a

Coelacanths

Bony fishes are divided into two lineages, the Actinopterygii, or ray-finned fishes, which are by far the dominant group today, and the Sarcopterygii, or lobe-finned fishes, which are now very rare although they were a much more significant group in the past. The sarcopterygians include the modern lungfish and coelacanths, as well as the extinct rhipidistians, which gave rise to the tetrapods or land animals in the Devonian period (350 million years ago). All sarcopterygians are characterized by the presence of a muscular fin base that contains a stout bony skeleton, and it is this structure that became the limbs in land animals.

Coelacanths are known from the Early Devonian era (410 million years ago) but have not been found in sediments younger than the end of the Cretaceous era (70 million years ago). They are fairly large fish, up to five feet long, with deep bodies covered by large, rough scales, paired fins that are conspicuously lobed, and symmetrical tails with small central lobes. As they were thought to be extinct, it was a great surprise when a specimen was caught off the southeast coast of South Africa in 1938. It was recognized as a coelacanth by Marjorie Courtenay-Latimer, who brought it to the attention of the ichthyologist J. L. B. Smith. He named it the following year as *Latimeria chalumnae*, after its discoverer and the Chalumna River, near the estuary of which the specimen had been caught. The next specimen was not discovered until 1952, this time almost one thousand miles farther north, in the Comoro Islands, which lie between East Africa and the northern tip of Madagascar. Since then, numerous specimens have been caught around the two main Comoro islands, and it is clear that a breeding population of these fish lives around the islands at a depth of between one hundred and five hundred meters. Because *Latimeria* lives at depth, it does not survive being caught on a line and pulled rapidly to the surface. However, in 1987, it was filmed swimming free in its natural environment by Dr. Hans Fricke, using a submersible. His film shows them moving slowly and hovering above the bottom, using the paired lobe fins in a regularly alternating pattern to scull themselves along. Although no film has been taken of *Latimeria* feeding, it is clear from stomach contents that it feeds on small fish, and its body shape indicates that it is a fast swimmer over a short distance, suggesting that it is probably an ambush predator.

No additional populations were discovered until 1997, when a specimen was recognized in a fish market in North Sulawesi, Indonesia, by Dr. Mark Erdmann. North Sulawesi is about eight thousand miles from the Comoros, with no apparent water current interactions. That this was a separate population was subsequently confirmed when a second specimen was caught, and the fish was then named *Latimeria menadoensis*. This discovery raises the hope that other populations may exist, and that although still a "living fossil," the coelacanth may be more widely distributed than previously thought.

—*David K. Elliott*

possible solution to the puzzle of mass extinctions as early as 1837. Louis Agassiz produced evidence that the earth has periodically undergone periods of extreme cold, with much of its surface covered by glaciers. Agassiz's glaciers are presently in existence, move very slowly, and thus fit well with the uniformitarian view. His glaciers might also explain mass extinction in evolutionary terms, since plants and animals that could not adapt to changing climate would be outcompeted by other species that could adapt, and, thus, the less-flexible species would disappear.

Uniformitarian views about extinction received a further boost in the twentieth century with the proposal of the theory of continental drift, which has evolved into the modern theory of plate tectonics. Scientists have demonstrated that the landmasses of the earth are in constant motion relative to one another and to the poles of the planet. Over millions of years, the present landmasses have occupied very different positions on the earth's surface, often drifting quite near the polar regions, causing massive climatic changes. In addition, scientists have demonstrated that landmasses have subsided to be covered by the seas and have risen to create dry land from ocean floors. These massive changes would also have a profound effect on flora and fauna, creating constant competition and struggle for survival.

Genetic Factors in Extinctions

Many contemporary biologists believe that background extinctions may be the result of genetic rather than strictly climatic factors. In simple terms, extinction results from an excess of deaths over births in a given species. This excess represents, in biological terms, a reduction in the characteristics of a species that allow it to adapt to its environment. Those characteristics, biologists argue, are brought about through natural selection, a process that favors the genes that give the organism an advantage in the struggle for survival. Since natural selection has produced not only the species itself but its ancestors as well, any change in environment must work against the existing organisms. In the new process of changed environment, new gene combinations will result that will produce an organism better adapted to the changed environment. If, however, these genetic changes do not occur rapidly enough, adaptation will not take place and the species will become extinct.

Another possibility results if an organism is too well adapted to its environment. The gene pool of a species usually combines those genes that work well with one another to produce a well-adapted individual. Some biologists have observed a tendency within the gene pools of some species to resist genetic adaptation when environmental changes occur. Thus, genetic changes that could impart greater chances for survival of the individual in times of environmental turbulence do not occur. This effect also occurs when groups of genes are linked together (usually by a chromosomal inversion) in such a way as to prevent new gene combinations that might impart the ability to adjust to changed environmental conditions. This phenomenon actually retards the ability of a species to survive and may lead to extinctions.

Genetics may also explain mass extinctions. One biologist has theorized that species which live in environments that change very little over long periods of time probably have low genetic variability (a gene pool in which nonutilitarian genes have disappeared). Conversely, species in

Image Not Available

changeable environments should have much more genetic diversity, allowing them to cope with rapidly altering living conditions. If that is true, then mass extinctions might result from a rapid environmental change after a very long period of stability. When the change came, the theory goes, widespread extinctions of many species resulted. Most geneticists, however, reject this theory of mass extinctions. The species in unstable environments may actually have less genetic variability than those in stable environments. Biologists therefore have not been able to advance a plausible genetic explanation for mass extinctions.

Mass Extinctions

Geologists have identified a number of what they call "mass extinction events." The first such event known to paleontologists occurred 440 million years ago at the end of the Ordovician period, during which more than 22 percent of all families and 57 percent of all genera disappeared. Another mass extinction occurred during the Devonian period, 370 million years ago, during which more than 20 percent of all marine families disappeared. The greatest of all mass extinctions occurred 248 million years ago, at the end of the Permian period. During that event, 52 percent of all marine families, 83 percent of all genera, and a frightening 95 percent of all species became extinct. During this event, land animals and plants vanished, along with marine flora and fauna. Yet another "great dying" took place during the Triassic period, approximately 215 million years ago, when 20 percent of all marine families and 48 percent of all genera disappeared.

The mass extinction known most widely outside the scientific community occurred at the end of the Cretaceous period, about 65 million years ago. During this event, the dinosaurs vanished, along with 50 percent of all marine genera. A number of less-spectacular mass extinctions have taken place in the earth's long history, including a relatively recent one at the end of the Pleistocene epoch, which included among its victims such well-known extinct animals as the woolly mammoth and the so-called saber-toothed tiger.

Some paleobiologists and archaeologists are convinced that many of the Pleistocene extinctions were caused by the activities of human beings. They point out that the extinction of most of the large North American land mammals coincided with one theoretical date for the appearance of humans in the Western Hemisphere, approximately 11,500 years ago. According to these scientists, especially efficient human hunters were responsible for those extinctions; however, this theory seems unlikely as an explanation for all the Pleistocene extinctions. Many species in areas other than North America disappeared at the same time, most of which would have had little or no value as game. In addition, there are huge "boneyards" containing fossils of the extinct species in areas as far separated as Alaska and Florida that apparently died at the same time from causes that seem to be related to some great natural cataclysm.

Asteroids as Agents of Mass Extinctions

The species that disappeared in each of these mass extinctions apparently died at approximately the same time, and scientists were at a loss to explain them until 1980. In that year, a scientific team led by Nobel laureate Luis Alvarez presented what seems to be irrefutable evidence that the extinction of the dinosaurs coincided with the collision of a huge asteroid or comet with the earth. The evidence is based on a layer of clay that separates the rock formations associated with the dinosaurs from the overlying formations, which contain fossils from the era of mammals. The clay contains large amounts of iridium and other elements that are scarce in the crust of the earth but common in asteroids and comets.

Many scientists now contend that the collision between the earth and a large extraterrestrial body would have thrown enormous quantities of dust into the atmosphere, sufficient to block out the sun's radiation for an extended period of time. The resulting subzero weather would have had devastating effects on flora and fauna, including the seemingly invincible dinosaurs. Shortly after the evidence for the collision appeared, other scientists presented evidence for an even more frightening phenomenon—periodicity of extinction events.

A scientist charting the occurrence of mass extinction events showed that they seem to occur at regularly spaced intervals, approximately every 26 to 30 million years. Almost immediately after the presentation of the evidence for periodicity, new scientific studies demonstrated more evidence that several mass extinctions other than the one during which the dinosaurs disappeared are also associated with unusually high concentrations of iridium. Taken together, these data seem to indicate that most, perhaps all, mass extinctions are caused by extraterrestrial agents and recur on a regular basis. If that is indeed the case, the implications for all the sciences, including evolutionary biology, are profound.

An Interdisciplinary Study

Scientists from several different disciplines are currently studying extinctions, including mass extinctions, in a variety of ways. Many biologists believe that the most effective way to understand background extinctions is to examine those that have taken place in historic times. Geologists and paleontologists are subjecting the fossil record to a new and rigorous examination, armed with new, supersensitive techniques for ascertaining the ages of the rocks in which fossils occur in an attempt to understand mass extinctions better. These new techniques are the products of research in nuclear physics. Ecologists are particularly examining currently endangered flora and fauna, which may soon disappear. Even some astronomers are actively engaged in research into mass extinctions, scanning the heavens with powerful telescopes in search of an extraterrestrial agent that might explain the apparent periodicity of mass extinction events.

Biologists studying recent background extinctions conclude that virtually all of them are the results of the activities of humankind. The great auk, the last known specimens of which were killed by Icelandic fishermen in 1844; the Tasmanian tiger cat, the last known specimen of which died in captivity in 1934; and many other species are examples of human-caused extinctions. These studies lend validity to the theory that at least some of the many extinctions during the Pleistocene resulted from the hunting activities of prehistoric peoples. More disturbing are studies which show that such modern phenomena as acid rain and ozone depletion, both results of industrialization, may be doing irreparable damage to the environment, which could result in another mass extinction event in the very near future. Indeed, some biologists and ecologists believe that such an event has already begun.

A number of geologists and paleontologists, using new dating techniques based on the rate of radioactive decay in rocks, are reassessing the ages traditionally assigned to fossils by less sophisticated techniques in the past. These studies should eventually reveal whether the mass extinction events of the remote past occurred in a very short or over a relatively longer period of time. Other geologists are searching for impact craters, to lend further credence to the theory that at least some and perhaps all mass extinctions resulted from periodic collisions between the earth and large celestial bodies.

A team of physicists (including astrophysicists), engaged in an ongoing search for a hypothetical dark companion to our sun, has postulated that the orbit of this presently undiscovered body may periodically disrupt the comet cluster on the outer fringes of the solar system, resulting in many comets being diverted into an intersection with the earth's orbit. If their search is successful, it will provide powerful substantiating evidence for the collision theory, with sobering implications. Some physicists have even proposed ways to prevent future collisions between the earth and large heavenly bodies.

The implications of background and mass extinctions are profound. If, as an overwhelming mass of evidence seems to indicate, the activities of humankind are a major cause of recent background extinctions, then those activities may soon lead to an ecological disaster of gigantic proportions. At present rates of disappearance, as many as two million species currently in existence will disappear by the middle of the twenty-first century. Unless immediate steps are taken, plant extinctions on the scale envisioned by many botanists may also cause massive climatic changes. Some ecologists and geophysicists warn that if the tropical forests disappear, the result will be the greenhouse effect. Of less immediate, but nevertheless great, concern is the theory that mass extinction events in the fossil record have resulted from collisions between the earth and asteroids or comets. The implications of the collision theory for evolutionary biology, however, are far-reaching. If the theory is correct, then the struggle for survival is not the most important feature of evolution. No matter how well adapted to its environment a species may be, survival of a collision would be largely a matter of chance. If the theory proves to be correct, biologists will need to rewrite the textbooks on evolution.

—Paul Madden

See also: Adaptive radiation; Cloning of extinct or endangered species; Ecological niches; Ecology; Ecosystems; Endangered species; Evolution: Historical perspective; Extinctions and evolutionary explosions; Food chains and food webs; Fossils; Habitats and biomes; Hardy-Weinberg law of genetic equilibrium; Natural selection; Neanderthals; Paleoecology; Paleontology; Pollution effects; Population fluctuations; Predation; Punctuated equilibrium and continuous evolution; Reproductive strategies; Veterinary medicine; Zoology; Zoos.

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EXTINCTIONS AND EVOLUTIONARY EXPLOSIONS

Type of animal science: Evolution
Fields of study: Environmental science, evolutionary science, paleontology, zoology

The history of life has been punctuated by episodes of great change, some marked by the loss of large numbers of organisms, others by explosive development. Explanations proposed for these fluctuations have a bearing on current extinction levels and the extent to which they can be controlled.

Principal Terms

ADAPTIVE RADIATION: the rapid production of a new species following invasion of a new geographic region or exploitation of a new ecological opportunity

BOLIDE: an extraterrestrial object (for example, a meteorite) that hits the earth

DIVERSITY: the number of fossil taxa (classification groups) associated with a particular place and time

LAZARUS TAXA: groups that apparently disappear during a mass extinction only to appear again later

MASS EXTINCTION: an event in which a large number of organisms in many different taxa are eliminated

PERIODICITY HYPOTHESIS: the proposal that mass extinctions have occurred approximately every 26 million years over the past 250 million years

PHANEROZOIC: an era of geologic time beginning approximately 544 million years ago at the start of the Cambrian period, when animals with mineralized skeletons became common

REGRESSION: the migration of the shoreline and associated environments toward the sea

Extinction of species is a continuous process, and evidence of its occurrence abounds in the fossil record. It has been estimated that marine species persist for about four million years, which translates into an overall loss of about two or three species each year. This is the "background" extinction rate, and it is balanced by speciation events that result in the development of new species. Mass extinctions are events during which the rate of extinction rises dramatically above this background rate, and a number of these have been recognized in the Phanerozoic era. In each of these events, at least 40 percent of the genera of shallow marine organisms were eliminated. Using statistical methods, it has been estimated that at least 65 percent of species became extinct at each of these events, with 77 percent being eliminated at the event at the end of the Cretaceous period and 95 percent at the event at the end of the Permian period. These mass extinctions were balanced by periods of explosive development that often followed, as organisms moved into vacant adaptive zones during periods of adaptive radiation. The most important of these was at the base of the Cambrian period, 544 million years ago, when all the major groups in existence originated, but other radiations occurred in the Early Triassic period and at the start of the Tertiary period.

Causes of Mass Extinctions

Attempts to explain the causes of mass extinctions have centered on terrestrial phenomena such as sea level changes, climatic changes, or volcanic activity. The sea level has shown regular fluctuations on a global level during the Phanerozoic era, and these appear to be related to the melting or formation of polar ice caps or to major tectonic events such as continental splits or the collision and uplift or subsidence of ocean ridges. Extinction events appear to be correlated mostly with periods of marine regression. During such a regression, the withdrawal of the ocean leaves a much smaller habitat for shallow marine organisms. This leads to increased crowding and competition and ultimately to an increased extinction rate. Reduction of large terrestrial vertebrates during these regressions, as happened during the events at the end of the Permian and Cretaceous periods, may be related to increased seasonality caused by the loss of the ameliorating influence of the shallow epicontinental seas.

It has also been shown that some extinctions are related to transgressive events (the spread of the sea over land areas), possibly resulting from the spread of anoxic (oxygen-poor) waters across epicontinental areas. Climatic changes seem to be correlated with eustatic events (worldwide changes in sea level), and the evidence implicating temperature as the main cause of extinctions seems weak. For example, the most important extinction event at the end of the Permian period occurred at a time of climatic amelioration marked by the disappearance of the Gondwanaland ice sheet. Volcanic activity has been presented as a possible cause of the extinctions that occurred at the end of the Cretaceous period. The Deccan Traps of northern India were erupting at that time and would have produced large quantities of volatile emissions that could have resulted in global cooling, ozone-layer depletion, and changes in ocean chemistry. However, no evidence exists as yet for the involvement of volcanic activity in other extinction events.

Although various extraterrestrial causes for mass extinction events have been suggested in the past, these ideas have gained greater credence since the publication in the early 1980's of work by Luis and Walter Alvarez, who ascribe the end-Cretaceous extinction event to the effects of the impact of a large bolide, or extraterrestrial object, perhaps ten kilometers in diameter. The impact of such a large object would have resulted in some months of darkness because of the global dust clouds generated, and this would have halted photosynthesis and resulted in the collapse of both terrestrial and marine food chains. Although cold would initially have accompanied the darkness, greenhouse effects and global warming would have followed as atmospheric gases and water vapor trapped infrared energy radiating from the earth. Physical evidence for an impact rests on the presence in the period boundary layers of high concentrations of iridium and other elements generally rare at the earth's surface but abundant in asteroids. In addition, these layers often contain shocked quartz grains, otherwise found only in impact craters and at nuclear test sites, and microtectites, glassy droplets formed by impact. Although the evidence for extraterrestrial impacts having caused the other major extinction events is slight, this causal factor has been linked with the apparently regular 26-million-year periodicity exhibited by extinctions. Scientists suggest that the regular passage of an unidentified planetary body by the Oort Cloud of comets and the subsequent perturbation could result in increased asteroid impacts and extinction events on earth.

Historical Mass Extinctions

The first mass extinction event that can be recognized in the fossil record occurred in the Middle Vendian period, about 650 million years ago, when microorganisms underwent a severe decline. This event has been linked to climatic cooling related to glaciation. The extinction in the Late Ordovician period was a major event in which 22 percent of marine families became extinct. As there were two main pulses of extinction and no iridium anomaly was found, an extraterrestrial cause seems unlikely. However, sea level and temperature changes have been cited as likely causes. In addition, biologically toxic bottom waters might have been brought to the surface during periods of climatic change. The event at the end of the

Devonian period had a devastating effect on brachiopods, which lost about 86 percent of genera, and on reef-building organisms such as corals. Shallow-water faunas were most severely affected; only 4 percent of species survived, although 40 percent of deeper-water species did, and cool-water faunas also survived better. This event has been linked to a significant drop in global temperatures of unknown cause.

The mass extinction event at the end of the Permian period was the most severe of the Phanerozoic era and resulted in the extinction of up to 95 percent of all marine invertebrate species. On land, amphibians and mammal-like reptiles were both badly affected, and plant diversity fell by 50 percent. No iridium anomaly was found, and the most likely explanation is climatic instability caused by continental amalgamation and the simultaneous occurrence of marine regressions. These occurrences would have disrupted food webs on a major scale. The event that occurred at the end of the Triassic period was much less severe but still involved extensive reductions in marine invertebrates and reptiles. On land, a major faunal turnover took place. Primitive amphibians, early reptile groups, and mammal-like reptiles died out and were replaced by advanced reptiles and mammals. No evidence of an impact event has been found, and the extinctions are generally correlated with widespread marine regressions.

The extinction that took place at the end of the Cretaceous period has become the most hotly debated, in large part because of the bolide impact hypothesis. Although the broad pattern of extinction among marine organisms is known, the detailed picture only encompasses microorganisms such as planktonic foraminifera and calcareous nannoplankton. Study of the ranges of these microorganisms shows that the extinctions occurred over an extended period, starting well before and finishing well after the boundary. Although much has been made of the extinction of ammonites at the end of the Cretaceous period, there are too few ammonite-bearing sections to show whether it was gradual or abrupt. On land, evidence of an increase in the population of ferns just above the boundary suggests the presence of wildfires, as ferns are usually the first plants to recolonize an area devastated by fire. However, in many sections, a return of the Cretaceous vegetation is seen above the fern increase, indicating little extinction.

Post-Extinction Recoveries

Among the vertebrates, a picture of gradual change is seen for mammals, with drastic reductions occurring only in the marsupials. The boundary also does not seem to have been a barrier for turtles, crocodiles, lizards, and snakes, all of which came through virtually unscathed. The dinosaurs did become extinct, and much argument has centered on whether this was abrupt or occurred after a slow decline. In this context, it must be noted that there is only one area where a dinosaur-bearing sedimentary transition across the boundary can be seen, and that is in Alberta, Canada, and the northwestern United States. Records of dinosaurs in this area during the upper part of the Cretaceous period show a gradual decline in diversity, with a drop from thirty to seven genera over the last eight million years. Although explanations of the extinction of dinosaurs have ranged from mammals eating their eggs to terminal allergies caused by the rise of flowering plants to the current ideas about bolide impacts, the answer may be climate related. A major regression of the oceans occurred at this point, resulting in a drop in mean annual temperatures and an increase in seasonality. The bolide impact may have served as the death blow to taxa (animals in classification groups) that were already declining.

The main period of evolutionary expansion in the Phanerozoic era is at the base of the Cambrian period, 544 million years ago. Termed the “Cambrian explosion,” it marks the development of all the modern phyla of organisms, and as many as one hundred phyla may have existed during the Cambrian period. This period seems to have lasted only about 5 million years, and the subsequent history of animal life consists mainly of variations on the anatomical themes developed during this short period of intense creativity. This period is represented in the fossil record by the remarkably well-preserved Burgess Shale fauna of British Columbia, which has been extensively described, and faunas of similar age from China and Greenland. Why the Cambrian explosion could establish all major anatomical designs so quickly is not clear. Some scientists believe that the lack of complex organisms before the explosion had left large areas of ecological space open, and when experimentation took place, particularly with the advent of hard skeletons, any novelty could find a niche. Also, the earliest multicellular organisms may have maintained a genetic flexibility that became greatly reduced as organisms became locked into stable and successful designs. Why some of the innovations were successful in the long term and others were not is unknown, as no recognized traits unite the successful taxa. It has even been suggested that success may be due to no more than the luck of the draw.

In contrast, the recoveries after the major extinctions at the end of the Permian and Cretaceous periods did not result in the development of new phyla. The earliest Triassic ecosystems were more vacant than at any time since the Cambrian period, yet no new phyla or classes appear in the Triassic period. This suggests that despite the overwhelming nature of the extinctions, the pattern was insufficient to permit major morphological innovations, in part probably because no adaptive zone was entirely vacant. Hence, despite the fact that the mass extinction at the end of the Permian period triggered an explosion in marine diversity described as the Mesozoic marine revolution, persisting species may have limited the success of broad evolutionary jumps.

Reading the Fossil Records

All understanding of extinction events or of evolutionary explosions depends on the fossil record. The study of the diversity of organisms through time—the number of different types of organisms that occur at a particular time and place—is therefore very important. The basic data consist of compilations of extinctions of taxa plotted against similar compilations of originations of taxa. Periods when either extinction or origination was unusually high show as peaks or troughs on a graph. Unfortunately, biases in the preservation, collection, and study of fossils have conspired to obscure patterns of change in diversity.

Geological history of patterns of diversity is obscured by a variety of filters, many of which are sampling biases that cause the observed fossil record to differ from the actual history of the biosphere. The most severe bias is the loss of sedimentary rock volume and area as the age of the record increases because the volume and area correlate strongly with the diversity of organisms described from a stratigraphic interval. The quality of the record also tends to fall with increasing age because the rocks are exposed to changes that may destroy the fossils they contain. The differences in levels of representation among the paleoenvironments in the stratigraphic record also influence the composition of the fossil record; for example, shallow-marine faunas are much better represented than are terrestrial faunas.

Diversity patterns are studied at a variety of levels, from the species upward, that vary in their quality and inclusiveness. A basic problem is that many of the processes that are of interest occur at the species level or even below it, but the biases of the fossil record mean that data are best at higher levels. Diversity of shallow-marine organisms for the Phanerozoic era cannot be read directly at the species level because the record is too fragmentary. The record at the family level is much more complete because the preservation of one species in a family allows the family to be recorded. For this reason, paleodiversity studies are often conducted at the family level. However, higher taxon diversity is a poor predictor of species diversity. For example, an analysis of the mass extinction at the end of the Permian period indicates that the 17 percent reduction in marine orders and 52 percent reduction in marine families probably represent a 95 percent reduction in the number of species. Another problem with the study of fossils is that soft-bodied and poorly skeletonized groups may leave little or no record. It has generally been assumed that the ratio of heavily skeletonized to

Georges Cuvier

Born: August 23, 1769; Montbéliard, France
Died: May 13, 1832; Paris, France
Fields of study: Anatomy, paleontology, zoology
Contribution: Cuvier, the founder of functional anatomy and the father of paleontology, was the first to devise a systematic natural classification of the animal kingdom and to document extinctions of ancient animals.

George Cuvier studied at the Académie Caroline in Stuttgart from 1784 to 1788. In 1795, he was invited to Paris by Étienne Geoffroy Saint-Hilaire, where he was appointed as a professor of animal anatomy at the French National Museum of Natural History.

After dissecting and studying many large animals, Cuvier concluded that organisms are functional wholes, in which the form and function of each part is integrated into the entire body. Each part of an organism bears signs of the entire organism. Thus, any change in an organism's anatomy would render it unable to survive. Consequently, Cuvier did not believe in organic evolution.

Based on rational principles and his knowledge of the comparative anatomy of living organisms, Cuvier reconstructed a number of organisms from fragmentary fossils. His studies led him to believe that any similarities between organisms were due to common functions, not to common ancestry. Paradoxically, some of his findings were later used to help support the theory of evolution.

During Cuvier's lifetime, some scientists interpreted fossils as remains of living species. Others thought that the unusual organisms known as fossils must still survive in unexplored parts of the world. Many could not believe that God would allow any species to become extinct. Cuvier published detailed studies about elephant anatomy showing that the African and Indian elephants were distinct species and that the fossil mammoths of Europe and Siberia were different from any living elephant species. He also published documentation of the past existence of large mammals, including the ground sloth, the Irish elk, and the American mastodon, that resembled no living species. Through these studies, Cuvier established the fact that some animal species had become extinct. The results of his studies, such as his *Discours sur les révolutions de la surface du globe* (1825; discourse on the revolutions of the globe), launched the field of modern vertebrate paleontology.

Georges Cuvier was the first scientist to document the existence of extinctions of animal life. (National Archives)

Cuvier believed that the Earth was very old and that periodic upheavals, rather than the inability of a species to adapt, had annihilated a number of species. He viewed the upheavals as catastrophic events produced by natural causes that were linked to geological conditions, including the periodic rise and fall of sea level. As a result, Cuvier inferred that extinctions of species documented by the fossil record were the result of abrupt changes that caused the strata of the continents to be dislocated and folded.

Eventually, the theory of catastrophism was supplanted in favor of uniformitarianism. However, in addition to the slower natural processes suggested by uniformitarianism, the Earth has also been shaped by occasional catastrophic events, which appear to be the source of major extinctions of animal species.

—Alvin K. Benson

non-skeletonized species has remained approximately constant through the Phanerozoic era; however, there are no data to support this and there is some evidence that skeletons have become more robust through time in response to newly evolving predators. The net result of these biases is severe. Only 10 percent of the skeletonized marine species of the geologic past and far fewer of the soft-bodied species are known.

Despite these problems, it has been possible to show that diversity of organisms has varied in a number of ways during the Phanerozoic era. Tabulations of classes, orders, and families have been used to show that there were significant periods of increased extinction or increased evolutionary rates. One of the most important uses of these data has been the tabulation at the family level that appears to show a regular periodicity of about 26 million years for extinction events and that has been used to support ideas about periodic extraterrestrial events. However, although fluctuations occurred, it has also been possible to show that the number of marine orders increased rapidly to the Late Ordovician period and has remained approximately constant since then.

The Ebb and Flow of Life on Earth

Mass extinctions and evolutionary explosions are the opposite faces of the pattern of diversity of organisms through time. During periods of mass extinction, the diversity of organisms on earth has dropped drastically, and in some cases entire lineages have been wiped out. Evolutionary explosions, on the other hand, resulted in enormous innovation, particularly at the beginning of the Cambrian period, and the development of new variations on established morphotypes (animal and plant forms and structures) later in the geologic record. Understanding the processes that caused these events is of major importance because people have reached the point where they are capable of influencing their environment in drastic ways.

Studies of extinction events have shown that they have a variety of causes, some of which appear to be environmental changes brought about by natural processes while others may be the result of extraterrestrial forces. The most severe of these extinction events occurred at the end of the Permian period, 245 million years ago, and resulted in the loss of up to 95 percent of marine invertebrate species. The cause of this extinction appears to be primarily that continents were amalgamating and oceans were retreating, which resulted in a major reduction in the habitat of shallow-marine organisms. Terrestrial habitats were also affected as the increase in continental area and loss of the ameliorating effect of extensive areas of shallow ocean brought about climatic changes. Although climatic changes are thought to be the main culprit in the majority of extinction events, some scientists believe that large bolides, or extraterrestrial bodies, struck the earth with such force as to create major changes in the environment that significantly reduced diversity. This theory has enjoyed the most popularity as the explanation for the event at the end of the Cretaceous period, during which the dinosaurs became extinct, but evidence for an extraterrestrial body's involvement in any of the other events is slight.

Whatever the cause, environmental change that results in habitat reduction is the main reason for species decline. As humans have risen to dominance over other species, the extinction rate has accelerated, and in the last half-century, this rate has climbed considerably above natural attrition as populations have increased and habitats have been altered. Although the levels of extinction have not yet reached those recorded during major extinction events of the past, some scientists believe people may be facing an ecological disaster. A better understanding of the processes surrounding past extinction events and the rebounds that followed them will help people prepare for and deal with the future.

—David K. Elliott

See also: Adaptations and their mechanisms; Adaptive radiation; Apes to hominids; Biodiversity; Clines, hybrid zones, and introgression; Demographics; Evolution: Animal life; Evolution: Historical perspective; Extinction; Human evolution analysis; Isolating mechanisms in evolution;

Natural selection; Nonrandom mating, genetic drift, and mutation; Paleontology; Population genetics; Punctuated equilibrium and continuous evolution.

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EYES

Type of animal science: Anatomy
Fields of study: Anatomy, biochemistry, cell biology, neurobiology, physiology

The eyes are the sensory organs that allow animals to visualize the world around them. Many different types of eyes have evolved, from very simple light-gathering eye spots to the complex compound eyes of insects. Each type of eye is used to convert a light signal into a useful piece of information for the animal.

Principal Terms

BINOCULAR VISION: the ability to utilize image information from both eyes to form a single image with depth information

CHROMOPHORE: the molecule which interacts with opsin; absorption of light changes the interaction and starts the phototransduction cascade

OMMATIDIUM: individual unit of the multifaceted compound eye

OPSIN: a membrane-bound protein, or pigment, which absorbs light

OPTIC NERVE: the main nerve taking information from the eyes to higher processing areas

PHOTORECEPTOR: cell containing membranes which house light-sensitive pigments

RETINA: the light-sensitive membrane at the back of the eye

There are many different kinds of eyes in the animal kingdom, each type with its own set of benefits for a particular species. The most basic function of the eye is to act as a light-sensitive organ, to detect the presence or absence of light. In addition to this, elaborations are often made, such as the ability to form an actual image on a retina, or the ability to control the amount of light entering the eye; each elaboration is made to provide the visual needs of individual species. The animal kingdom comprises eyes from the very rudimentary to exceptionally complex. The two basic types of eye are the simple eye and the compound eye. The simple eye is made up of a single light-sensitive region, whereas the compound eye comprises several such elements.

Simple Eyes

The most elementary simple eye consists of a photosensitive membrane, or eye spot. Light should enter the membrane from only one direction, and so eyes have a pigmented backing to stop entry of light from the wrong side. In order to give the light entering a sense of directionality, the photosensitive membrane is often shaped like a cup; this basic eye type is called a pigmented cup eye. An example of an animal which possesses a simple eye of this nature is the cephalopod, *Nautilus pompilius*, which is known as a living fossil as it is thought to exemplify the behavior and physiology of ancient organisms. *Nautilus* has a pinhole eye with a pigmented backing; the pinhole aperture is a primitive method to restrict the amount of light entering the eye. This eye has no other formal optics. An elaboration of this type of eye would be to add a spherical lens; this would allow the light entering to be focused and to form an image on the photosensitive membrane. In many animals, the lens can change shape (become thinner or fatter) using surrounding musculature, in order to properly focus the image on the retina; this ability is called accommodation. The lens changes the angle at which light bends, and hence the focal length of the eye. The focal length of the eye is the distance from the eye to the part of the retina on

Optimization of Eyes

In order to adapt to the particular needs of individual species over evolutionary time, simple eyes have had to change and become optimized to deal with unique circumstances. Two major aspects of superior vision are resolution and sensitivity. Resolution, or spatial acuity, refers the ability to tell that two points are separate, and not just one point. Thus, better resolution is beneficial to an animal that needs to resolve images at a distance. To increase resolution, one can build more receptors per retina. However, there is a limit to this; to fit in more photoreceptors, they would have to become smaller (thinner) and at some point they would be too small to trap photons efficiently. This can be counteracted by making the receptors longer to catch more photons of light. Also, with too many receptors the nervous system becomes overloaded; for this reason, throughout most of the retina, many photoreceptors converge onto a single ganglion. Nevertheless, there are regions of high resolution at which each photoreceptor has its own ganglion; this region of the retina is called the fovea and is best described in vertebrate eyes. Increasing the eye size also increases the resolution, since it increases the amount of light getting to each receptor. Some species need to maximize sensitivity of their eyes, for example, animals who are active at night. To do this, the aperture needs to be large. This allows for maximum light entry into the eye. To the same end, the receptors could be made bigger, as could the entire eye. Thus, nocturnal animals, such as the opossum, have much larger eyes and apertures than diurnal animals, such as primates, which use a smaller eye and a smaller lens to give better optics.

which the image is focused. Other animals actually move the entire lens forward or backward in order to accommodate. One drawback that comes along with spherical lenses is that the entire image is rarely totally focused on the retina because, as a result of the spherical shape of the lens, the light rays become focused over several focal lengths (this is called spherical aberration). To correct this, many lenses have a refractive index gradient across their length; basically, the density of the lens is different across its length, which causes the light rays to bend differently and corrects for spherical aberration, allowing proper focusing of the entire image on the retina. In spiders, a different kind of optics is found; instead of a lens, these creatures focus light rays with their corneas. The structure, unlike the lens, is fixed and does not change shape to accommodate.

Compound Eyes

Compound eyes are the most abundant type of eye in the animal kingdom, and can be thought of as being derived from the simple pigmented-cup type of eyes. The simplest compound eye consists of several pigmented-cup-type units, each of which samples a different angle of visual space. Found only in invertebrates, such as certain types of worm, this kind of eye gives very poor quality images, but does give the animal a sense of the direction from which light is coming. A more complicated version of this eye is the apposition compound eye, found in many insects, where each cup has its own optics. Each individual unit is called an ommatidium, comprising the rhabdom (containing the light-sensitive cells), directly contacting a light-focusing apparatus (either a lens or a cornea). In order to fit as many ommatidia into the eye as possible, the facets are hexagonal. Another elaboration is the superposition compound eye; this eye has a space between the cornea (or lens) and the rhabdom of each ommatidia. As such, this allows light from many corneal facets to converge onto each rhabdom. This increases the sensitivity as compared to the apposition eye. Several mechanisms are used to bend the light from each ommatidium; the simplest is the reflecting superposition eye, found in shrimp, which uses a series of mirrors along the edge of each facet to reflect the light onto the rhabdoms.

Photoreceptors

The photoreceptive element common to all eyes differs from species to species, from the cup-shaped retinas of simple eyes to the complex rhabdom structures of compound eyes. In simple eyes, the light-sensitive element is platelike, with projections containing flat layers or discs of membranes. In vertebrates, the two photoreceptor types are the cones (cone-shaped projections), which have layers of photosensitive membrane, and the rods (rod-shaped projections), which contain free-floating discs. Compound eyes have rhabdomeric microvillar photoreceptors; the microvilli are fingerlike structures that project from the rhabdomeres and are light-sensitive. Within each of these structures lies the actual light-sensitive pigment, a membrane-bound protein known as opsin. In the rhabdoms, the orientation of the opsin molecule is parallel to the axis of the microvilli; this fact aids in the perception of polarized light. There are many types of opsin protein, and they can be categorized according to which wavelength of the light spectrum they preferentially absorb. The opsin protein interacts with a Vitamin A-derived molecule called the chromophore. Its chemical name is 11-cis retinal. The absorption of a photon of light changes the chemical interaction between the opsin and the chromophore, and it is this chemical change which initiates the cascade of events that leads to a nerve signal, known as phototransduction.

The actual biochemistry of phototransduction is very complex, but involves the amplification of the signal of reception of light, and its transformation into a nerve impulse. The passage of the information through the nervous system is also very complicated and details are different in different species, but in general, the receptors converge onto axons and the nerve impulse travels through the optic nerve for higher processing. Of the two types of photoreceptor existing in vertebrates, rods are very light-sensitive and are used in situations where light is limited (scotopic conditions). Cones are less sensitive and are used in situations where light is abundant (photopic conditions). The vertebrate retina almost always possesses both rods and cones, although some nocturnal animals or animals living in an environment where light is scarce, for example deep-dwelling fishes, have all-rod retinas. Mammals have rod-dominated retinas, which are probably remnants of the time millions of years ago when mammals were nocturnal. There are several kinds of cones, which are characterized according to which opsins they carry within the membrane layers; this dictates which wavelengths of light the cone preferentially absorbs. Absorption of light by combinations of at least

Other Features of Photoreceptors: Pigments and Oil Droplets

Some vertebrate and invertebrate photoreceptors have been found to possess filtering mechanisms. The classic example of this is oil droplets in the cones of bird eyes. The cone possesses a droplet of oil positioned just behind the outer nuclear layer of the retina, where the photoreceptor layer containing the opsin molecules is located. The droplet is carotenoid in nature and as such can be colored blue, yellow, orange, or red. As light travels through this droplet, it is filtered in intensity and in wavelength. Thus, the droplet acts as a selective spectral filter, only allowing certain wavelengths of light to get through the pigment to be absorbed at the photoreceptor level. It therefore increases the spectral sensitivity of individual receptors, and could enhance the color vision of such animals. Since most of the carotenoid oil droplets block out the shorter wavelengths of light, it is thought that they could also be a mechanism for protecting the receptors from the damage of ultraviolet light. In invertebrates, a similar filtering system has been found, although it is not in the form of an oil droplet but in the form of pigmented vesicle bundles. In the same way, these vesicles filter the incoming light, narrowing the absorbance spectrum of the photoreceptor layer above them.

The placement of the eyes in the head, so that each eye captures a slightly different angle on the same visual field, creates binocular vision and depth perception. (Digital Stock)

two different cone types will allow a species color vision, given the cognitive ability to process such information.

Another important feature of eyes is their position on the head relative to each other. Most vertebrates and some invertebrates have two eyes, allowing them a certain amount of binocular vision depending on the angle between them. In fact, both eyes project a slightly different image onto each retina, but the brain is able to compute this as a single image. This results in a larger field of view and also a sense of depth; these are definite advantages, for example for a hunting animal, which needs to know how far it is from the prey target.

—*Lucy A. Newman*

See also: Anatomy; Beaks and bills; Bone and cartilage; Brain; Claws, nails, and hooves; Digestive tract; Ears; Endoskeletons; Exoskeletons; Eyes; Fins and flippers; Immune system; Kidneys and other excretory structures; Lungs, gills, and tracheas; Muscles in invertebrates; Muscles in vertebrates; Nervous systems of vertebrates; Noses; Physiology; Reproductive system of female mammals; Reproductive system of male mammals; Respiratory system; Sense organs; Skin; Tails; Teeth, fangs, and tusks; Tentacles; Vision; Wings.

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FAUNA: AFRICA

Types of animal science: Ecology, geography
Fields of study: Conservation biology, ecology, environmental science, wildlife ecology, zoology

Africa is renowned for the richness of its wildlife, having a greater variety of large ungulates (some ninety species) and freshwater fish (two thousand species) than any other continent. However, many of these animals are being hunted to near extinction or endangered due to habitat loss.

Principal Terms

ARTIODACTYLS: mammals with an even number of toes

PREDATOR: a carnivorous animal that obtains food by hunting

UNGULATE: a hoofed mammal

Known for the enormous diversity and richness of its wildlife, Africa has a greater variety of large ungulates, or hoofed mammals (some ninety species), and freshwater fish (two thousand species) than any other continent. However, probably no group of animals is more identified with Africa than its flesh-eating carnivore mammals, of which there are more than sixty species. In addition to the better-known big cats, such as lions, leopards, and cheetahs, there are wild dogs, hyenas, servals (long-limbed cats), wildcats, jackals, foxes, weasels, civets, and mongoose.

The African Enigma

There are many theories as to why Africa has such an abundance of wildlife, and large wildlife at that. While early North American human societies drove mammoths, giant beaver, and sabertooth tigers to extinction, early Europeans wiped out lions and rhinos, and Asians domesticated their landscapes, Africans lived in relative accord with creatures that were no less grand or ferocious. Some African folklore places animals on the same footing with people.

Another theory is that the tsetse fly, by spreading the sleeping sickness, made much of tropical Africa uninhabitable by humans and protected the wilderness and wildlife from human depredation. Still another possibility may have been the constancy and small size of the African population in comparison with European and Asian numbers—too few people to either overhunt large mammals or exhaust their habitat. One more possibility is that the savannas of Africa—grassy plains with scattered tree cover—provide good habitat for so many ungulates. Humans cannot hunt ungulates easily under these conditions because the humans can be seen and outrun easily. At the same time, a large population of ungulates supports an appreciable population of predators such as lions and scavengers such as hyenas.

At one time, most African fauna was believed to have originated in the Palearctic regions, that is, Europe, northwest Africa, and much of Asia. There is no doubt that as recently as fifteen thousand years ago, a milder Saharan climate allowed typically Ethiopian forms, such as clariid catfish, to reach the river systems of North Africa. Similarly, northern animal life and vegetation seem to have extended far south into the Sahara. The white rhinoceros evidently coexisted with elklike deer.

The spread of forests during the wetter epochs created separate northern and southern wooded grasslands. This led to the evolution of such closely related northern and southern species of antelope as the kob and puku, the Nile and common lechwe, and the northern and southern forms of white rhinoceros. In earlier periods, the animal life was even more remarkable than in modern times. Fossil deposits have revealed sheep as big as present-day buffalo, huge hippopotamuses, giant baboons, and other types similar to existing species. These "megafauna" probably lived in wetter periods and died out as the climate became drier.

Effects of Human Population Growth

The fine conditions for Africa's fauna in the mid- to late nineteenth century started to come to an end when European settlers arrived in many parts of Africa. Technologies, in the form of Western

Habitats and Selected Vertebrates of Africa and Madagascar

medicine and sanitation, sparked a demographic revolution. In places such as Rhodesia (now Zimbabwe), the human population exploded twenty-fold during the ninety-year reign of white settlers.

Since 1940, the combined pressures of hunting and habitat destruction have cut wildlife numbers greatly. The antelope known as the Zambian black lechwe, believed to have numbered one million in 1900, had been reduced to less than eight thousand by the late twentieth century. The population of African elephants declined from two million in the early 1970's to 600,000 by 1990, largely because of poaching for the ivory trade.

Since the 1960's, poaching has caused a 95 percent decline in the world's black rhino population to fewer than 2,600 in 1997. The African white rhinoceros reached the verge of extinction in 1980. In West Africa, the continual southward advance of the Sahara desert has amplified the twin pressures of habitat destruction and human population. The larger fauna that lived there, caught between the desert and the burgeoning population, are largely gone now.

In Kenya, farmers have long since cleared most of the central part of the country that was once a densely forested region inhabited by wild animals. Some people have invaded national parks for commercial purposes such as logging and cattle grazing, thus forcing wildlife out of their preserved habitats. Some animals have had no alternative but to fight with humans for food and water. Along the Kenyan coast, many people have been attacked and killed by charging hippopotamuses and crocodiles in search of food and space. Similar cases have been common in the highlands, where Kenyans have lost their lives to charging elephants or to leopards and buffalo.

In recent years, human-elephant conflicts in Cameroon have become a major issue. Such conflicts are more acute in the savanna ecosystem, due to the loss of the elephant's range and habitat following the conversion of natural vegetation to farmland and the logging of large tracts of forests. Cameroon still has a relatively large herd of elephants, estimated at about twenty thousand in 1997. Approximately 75 percent of these elephants live in the dense equatorial forest.

Another issue in Cameroon in 1999 was a 652-mile (1,050-kilometer) pipeline proposed to traverse tropical rain forests and link oil fields in landlocked Chad to an export facility in Kribi, Cameroon. The original route of the pipeline was changed to go through two less-fragile ecosystems, but the new route was still designed to cut through tropical areas and provide easier human access to endangered species such as gorillas, chimpanzees, and elephants.

African Mammals

The main group of herbivores is the African antelope, which belong to four subfamilies of the ox family. The first subfamily is further subdivided into the African buffalo and the twist-horned antelope, including the eland (the largest of all antelope), kudu, nyala, and bushbuck. The second subfamily is the duiker, a small primitive antelope that lives in the thickets, bush, and forests. Other well-known large African herbivores include the

Endangered Chimpanzees Source of HIV

A type of chimpanzee that is feared to be headed for extinction by the year 2010 carries a unique genetic blend of human immunodeficiency virus (HIV) and simian immunodeficiency virus (SIV). Scientists have stated that, in the genetic family tree of all known HIVs and SIVs, this virus appears to be the strain that could be the source of all HIVs. Once the strain known as SIVcpz made its way into the human species, probably in the 1950's, it mutated into the existing human strain, adapting naturally to its new host.

The chimpanzees are being driven from their homes by loggers in the rain forests of the Congo River basin. They also are being slaughtered for their meat. However, scientists consider it is crucial that this species of chimpanzee remain in existence so they may study them for critical HIV research.

zebra, giraffe, hippopotamus, rhinoceros, and African elephant.

Africa's large number of endemic or native mammal species is second only to that of South America. These include several families of the ungulate order Artiodactyla (mammals with an even number of toes), such as the giraffe and hippopotamus. Some carnivores—such as civets, their smaller relations, the genets, and hyenas—are chiefly African. The rodent family of jumping hares is endemic, and one order, the aardvark, is exclusively African. The Malagasy Republic (Madagascar) has a remarkable insect-eating family. These are the tenrecs, animals with long, pointed snouts. Some tenrecs are spiny and tailless.

The primates include about forty-five species of Old World monkeys and two of the world's great apes: the chimpanzee and the world's largest ape, the gorilla. The gorilla is present in two subspecies: the lowland gorilla of Central and West Africa and the mountain gorilla of East Africa. The rare mountain gorillas live only in the upland forest on the borders of Uganda, Rwanda, and Congo-Kinshasa (Zaire). There are two populations of roughly equal size. One is in Uganda's Bwindi Impenetrable Forest National Park, where a 1998 census counted 292 gorillas. The second is in the Virunga Mountains, on the borders of the three countries. The last census there, completed in 1989, estimated 324 gorillas in the Virungas, but war has prevented a recount.

Presimian primates include pottos or African lemurs and galagos, bush babies, or small arboreal lemurs. These and other African lemurs tend to be small and nocturnal. In the Malagasy Republic, where there are no true monkeys, the lemurs have occupied all ecological niches, both diurnal and nocturnal, that the monkeys would have taken. Accordingly, the world's most diverse collection of presimian lemurs survives in Madagascar.

African Reptiles, Birds, and Insects

Most African reptiles have their origins elsewhere—mainly in Asia. These include lizards of the agamid family, skinks, crocodiles, and tortoises. Endemic reptiles include girdle-tailed and plated lizards. Large vipers are common and diverse. Certain species have extremely toxic venom, but they are rarely encountered. One of the most noted is the black mamba. Amphibians also belong mainly to Old World groups. Salamanders and toothed tree frogs are confined to the Palearctic northwest Africa. Abundant and more common frogs and toads include such oddities as the so-called hairy frog of Cameroon, whose hairs are auxiliary respiratory organs.

The birdlife south of the Sahara includes almost fifteen hundred resident species. An additional 275 species either reside in northwestern Africa or are winter migrants from Europe. Once there may have been as many as two billion individual migrants, but their numbers have been reduced considerably by severe droughts and by human land use and predation. The few endemic bird species include the ostrich, shoebill, hammerkop, and secretary bird. The many predators of land mammals include eagles, hawks, and owls. Many more, such as storks, waders, and a few species of kingfishers, prey on fish. Even more feed on insects.

Insects include large butterflies, stick insects, mantises, grasshoppers, safari ants, termites, and dung beetles. Spiders abound throughout the continent, and scorpions and locusts can be plentiful locally. Huge swarms of locusts periodically spread over wide areas, causing enormous destruction to vegetation. Mosquitoes that carry malaria are present wherever there is a body of water. Female blackflies transmit the nematode *Onchocera volvulus*, a parasitic filarial or threadlike worm. This organism eventually collects in many parts of the body, including the head near the eye. Nematode clusters around the eyes cause a blindness known as "river blindness." This disease has prevented any significant human habitation in many of Africa's river valleys.

Tsetse flies carry the parasite that causes African sleeping sickness in humans and nagana in livestock. These flies are found in all tropical portions of sub-Saharan Africa. The controversial chemical pesticide, dichloro-diphenyl-trichloro-

Tsetse Fly: Winged Guardian of Wilderness

The tsetse fly acts as a carrier for trypanosomiasis, a parasite that causes sleeping sickness, which is a wasting disease. When sleeping sickness is acute, the symptoms are high temperature, anemia, fitful appetite, and swollen limbs. The victim eventually sinks into an irritable haze, then slips into a coma and dies.

Sleeping sickness has had a long history in Africa. One subspecies of the trypanosomiasis parasite lives amicably in the bloodstream of wild animals such as antelope. However, when it gets into a cow, it makes the animal waste away and die. As a consequence, raising livestock has been difficult or impossible in much of sub-Saharan Africa. More than three million square miles (eight million square kilometers) of that region are off-limits to cattle, and in places where they are raised, three million cows die of the disease each year. The tsetse fly is cheered by conservationists because it makes so much of Africa largely uninhabitable for humans and cattle, thus preserving wildlife. However, it is estimated that the sleeping sickness spread by the tsetse fly threatens fifty million Africans.

ethane (DDT), which is banned in the West, is being used in Zimbabwe and other countries to eliminate the tsetse fly. DDT has adversely affected birds and fish there and has even been found in nursing mothers' breast milk.

Changing Human Attitudes Toward Conservation

If people can benefit from wildlife, their attitudes and actions toward wildlife will improve. Starting in Namibia in 1967 and extending to Zimbabwe in 1975, lawmakers put the idea into action. Large landowners were allotted ownership rights to wildlife, an idea totally alien to the European and the United States' tradition of exclusive state ownership. Landowners, for the first time since the imposition of colonial rule, were free to make economically informed—and, as it turned out, ecologically desirable—market decisions on how best to use their land. By 1990, 75 percent of Zimbabwean ranchers in areas too dry to support crop production had shifted partly or entirely to wildlife ranching. That change was due to the nearly quadruple net profit per acre advantage held by wildlife over cattle.

Rinderpest, a highly contagious bovine plague that has killed millions of Africa's cattle, buffalo, and wildlife in the past century, is finally being brought under control. The disease has been eradicated in West and Central Africa, and is contained in most of East Africa. Rinderpest, caused by morbillivirus, attacks ungulates such as cows, sheep, buffalo, and giraffe and is almost always fatal. It is easily transmitted through direct contact and by drinking water contaminated with the dung of sick animals. It is believed to persist in the Sudan and possibly Somalia, and about four other places in the world.

In Swaziland, pastoralists known as Shewula are breaking with tradition by giving more than 7,400 acres (3,000 hectares) of land used for grazing cattle to a large new game reserve. It will be part of a new transnational reserve with neighboring South Africa and Mozambique. In return, donors have provided funds to build tourism facilities on the land and to train the community in conservation, management, and marketing skills. The goal is to develop the reserve's tourism potential to benefit the rural villagers who have chosen wildlife over cattle.

Similar arrangements have been made between an international hotel chain and a village community outside Tanzania's Serengeti National Park. The agreement involved more than 25,000 acres (10,000 hectares) of land in the Loliondo buffer zone between the Serengeti and the Masai Mara of neighboring Kenya. The Loliondo corridor is used by thousands of stampeding wildebeest during their famed migrations between the Serengeti and the Mara.

Progress has been made in efforts to increase the elephant population. In East Africa, the numbers of elephants are slowly increasing after the poaching rampages of the 1980's. The areas around Tsavo National Park in Kenya and in neighboring Tanzania have reported a count of eighty-one hundred elephants, as opposed to about six thousand elephants in the late 1980's. In 1972, however, there were about twenty-five thousand elephants in the greater Tsavo area. The elephant conservation record of Namibia, Botswana, and Zimbabwe has been impressive. As of the summer of 1999, they had an estimated 200,000 elephants.

—Dana P. McDermott

See also: Aardvarks; Antelope; Baboons; Birds; Camels; Cats; Cattle, buffalo, and bison; Chaparral; Cheetahs; Chimpanzees; Cranes; Crocodiles; Deserts; Dogs, wolves, and coyotes; Ecosystems; Elephants; Endangered species; Fauna: Madagascar; Fish; Flamingos; Flies; Foxes; Giraffes; Gorillas; Grasslands and prairies; Habitats and biomes; Hippopotamuses; Horses and zebras; Hyenas; Hyraxes; Insects; Lakes and rivers; Lemurs; Leopards; Lions; Lizards; Mammals; Manatees; Meerkats; Monkeys; Mosquitoes; Mountains; Ostriches and related birds; Parrots; Primates; Rain forests; Rhinoceroses; Savannas; Ungulates; Vultures; Weasels and related mammals; Wildlife management.

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FAUNA: ANTARCTICA

Types of animal science: Ecology, geography
Fields of study: Conservation biology, ecology, environmental science, evolutionary science, wildlife ecology, zoology

Antarctica, the name meaning "opposite to the Arctic," is the coldest and windiest continent on earth. It is also one of the driest, despite being covered in ice sheets up to four kilometers thick. The faunas of the Antarctic display indistinguishable diversity. Many species of fauna are rare and/or endemic, particularly the invertebrates.

Principal Terms

Antarctica: the continent surrounding the South Pole, almost entirely covered by an ice sheet
collembola: primitive, wingless insects
higher insects: generally larger insects with increasing levels of morphological complexity
pack ice: floating islands of ice that form flows measuring from a few feet wide to ice islands miles across
sub-Antarctic: Antarctic landmasses of lesser southern latitude exhibiting more moderate climatic conditions

The history of life in the Antarctic is a fascinating one, largely because, in geologic terms, Antarctica has been very different from the way it is today. For much of Antarctic history, the continent was fully vegetated and carried all the animal life that depends on plants for a living. This is very different from today. Antarctica's gradual glaciations and long isolation from other continental landmasses has impeded the establishment and development of land-based flora and fauna. Other significant factors that have hampered terrestrial biotic evolution on Antarctica include the harsh climate, the ice cover, and the limited number of ice-free land areas. Consequently, the terrestrial flora and fauna of Antarctica are few.

The Antarctic is an extreme environment for any organism to survive in, yet both marine and terrestrial habitats of the Antarctic contain fauna that have adapted to the extreme conditions in order to effectively utilize available resources. Generally speaking, Antarctic regions are devoid of a wide array of faunal diversity due to lack of habitat. The sub-Antarctic and cool temperate islands have much greater diversity, including shrubs and trees. With this higher plant life comes a correspondingly complex array of animal life. The sub-Antarctic and cool temperate islands also possess high levels of endemism as a consequence of their long-standing geographical and ecological isolation from each other and the surrounding continental landmasses.

Antarctic Fauna

The terrestrial fauna consists of a few invertebrate species of protozoans, rotifers, nematodes, tardigrades, collembola, and a species of mite. These life forms are restricted mainly to moist beds of moss. The diversity of marine mammals and birds in the coastal areas and associated pack ice is dependent on marine food chains in the adjacent seas. Because of the vast ice, the continent supports only a primitive indigenous population of cold-adapted land plants and animals. The surrounding sea is as rich in life as the land is barren.

The resource of Antarctic and sub-Antarctic waters supports vast numbers of a variety of seabirds, which play an important role in the marine ecosystem. Nesting grounds are limited, being confined to the scattered sub-Antarctic islands and ice-free localities during the summer on the Antarctic continent and Antarctic Peninsula.

Few terrestrial vertebrates are resident in Antarctica, and those that do occur are limited to sub-Antarctic islands. There are no naturally occurring mammals, reptiles, or amphibians, although humans have deliberately or accidentally introduced a range of animals such as rats, mice, fish, chickens, rabbits, cats, pigs, sheep, cattle, and reindeer to the sub-Antarctic, many impacting native species. Terrestrial animals of the sub- and maritime Antarctic include arthropods, earthworms, and mollusks. Higher insects include spiders, beetles, and flies, most of which are confined to the less severe areas. Microinvertebrate groups such as nematodes, tardigrades, and rotifers are also numerically well represented. The terrestrial fauna of the severe areas of the Antarctic continent are even more simplified. No higher insects are present; the smallest arthropods are restricted to limited areas of vegetation. Instead, groups such as nematodes become dominant. In the most extreme continental cold deserts, simple food webs consist of as few as one to three nematode species, only one of which may be predatory.

Threats to the Antarctic

Much of the Antarctic bears the distinctive imprint of human modification, particularly through the deliberate introduction of animal pests and predators. Of particular concern are the introduced mammals, notably rodents, cats, rabbits, sheep, cattle, and reindeer. In recent years, there have been several cases of successful eradication of alien mammals from islands, and such efforts are continuing. This is important, since islands are vital breeding and resting grounds for seabirds.

—*Jason A. Hubbart*

See also: Birds; Ecosystems; Fauna: South America; Fish; Habitats and biomes; Marine animals; Penguins; Seals and walruses; Tundra.

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FAUNA: ARCTIC

Types of animal science: Ecology, geography
Fields of study: Conservation biology, ecology, environmental science, evolutionary science, wildlife ecology, zoology

The Arctic, the name derived from the Greek arktos, *meaning, "bear," may appear to be desolate and lifeless, but it is far from these things. Plants exhibit surprising richness even though generally limited to a few inches in height and sparse distribution. The shallow, often sterile soil, abrasively high winds, low soil temperatures, and frequent freezing and thawing fluctuations have forced the development of a wide variety of fauna that have adapted to these harsh conditions.*

Principal Terms

ADAPTATION: the processes of change in a living organism that enable it to adjust to the conditions of the environment in which it lives

ARCTIC: the surface of earth lying above 66.5 degrees North latitude, including the Arctic Ocean between North America and Russia

PERMAFROST: any soil in the arctic regions in which temperatures below freezing have existed continuously for a long time

TUNDRA: a treeless, level or gently rolling plain of the arctic region; characterized by a marshy surface from which mosses, lichens, and low shrubs grow

The Arctic is the northernmost region of the earth, centered on the North Pole. The arctic landscape is mainly tundra. This frozen ground lies above tree line and is covered with hearty plants such as moss and lichen, from which caribou and musk ox feed. Arctic temperatures average 10 degrees to 20 degrees Fahrenheit on an annual basis. Due to its extreme northern latitude, the Arctic gets varying amounts of sunlight at different times of year. Precipitation is very low, with average annual rainfall of only seven inches.

Besides extreme fluctuations between summer and winter temperatures, the arctic landscape contains permanent snow and ice in the high country; grasses, sedges, and low shrubs in the lowlands; and permafrost in almost all locations. The permafrost limits drainage and retains moisture for plant growth within the active layer. This can result in wetland formation, as occurs in level areas of the coastal plains of the Arctic. Here, extensive wetlands are home to aquatic vegetation, invertebrate fauna, waterfowl, and shorebirds. The plant growth season is usually less than one hundred days. However, plants do take advantage of constant sunlight in summer months, which enables them to optimize photosynthesis without the usual nighttime cost of respiration.

Arctic Fauna

Arctic ecosystems lack the diversity and richness of species that characterize temperate or tropical ecosystems. Animal as well as plant species decline in number with increasing latitude. Vertebrate species of the Arctic are limited to approximately twenty species of mammals and more than one hundred species of birds. Most are closely related species, such as the caribou of North America and the reindeer of Eurasia. This similarity in arctic mammalian fauna is a result of the lower sea levels of the Pleistocene glaciations, when a broad land connection, known as the Bering Land Bridge, connected present-day Alaska and Siberia. Some arctic mammalian fauna, primarily herbivores and carnivores, rarely occur outside the Arctic and have adapted to life in this environment. Other fauna, such as species of ground squirrels, voles, shrews, red fox, ermine, wolverine, wolf, and brown bear, are common to other ecosystems but are distributed widely throughout the Arctic.

Wet sedge meadows often associated with lake margins, estuaries, and seacoasts are favored nesting habitats for millions of migrating waterfowl and shore birds during the summer months in arctic regions. In addition to shorebirds and waterfowl, finches, buntings, and sparrows are the most abundant species nesting in the Arctic. Terrestrial avian fauna of the Arctic include only a few resident species, among them the ptarmigan, snowy owl, gyrfalcon, and raven. Nonresident species include raptorial birds that commonly nest in the Arctic, such as the peregrine falcon, rough-legged hawk, short-eared owl, the golden eagle, and the white-tailed eagle. These remaining species are present in the Arctic only in summer to breed and rear young, migrating to southern latitudes during winter.

A wide range of marine mammals and fish live in the severe conditions of the Arctic Ocean. Whales, dolphins, walruses, and seven species of seals all make their home in this northern polar region, which is covered by ice most of the year.

Threats to the Arctic

Human activity has exercised a strong influence on the wildlife of arctic regions. Polar bear, walrus, musk ox, and caribou all have been greatly reduced in numbers through hunting alone. This danger was recognized in 1973 when protective legislation was approved for the polar bear. Still, species diversity continues to decrease at an alarming rate, and measures to protect the wildlife of the Arctic must be taken.

—*Jason A. Hubbart*

See also: Bears; Birds; Dogs, wolves, and coyotes; Dolphins, porpoises, and toothed whales; Ecosystems; Elk; Fauna: Asia; Fauna: Europe; Fauna: North America; Fish; Foxes; Geese; Habitats and biomes; Mammals; Marine animals; Moose; Owls; Polar bears; Reindeer; Seals and walruses; Shrews; Tundra; Weasels and related mammals; Wildlife management.

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FAUNA: ASIA

Types of animal science: Ecology, geography
Fields of study: Conservation biology, ecology, environmental science, wildlife ecology, zoology

Asia is a huge continent with widely varying climate and geography. As might be expected, its animal life is equally diverse. Since Asia has areas of some of the most dense human population on earth, pressure on animal species from habitat loss is particularly dangerous.

Principal Terms

GRAZER: an animal that eats grass; some are wild, but many grazers have also been domesticated

HERBIVORE: an animal that only eats plants

NOCTURNAL: active at night and dormant or asleep during the day

PREDATOR: an animal that obtains food by hunting other animals

TAIGA: a moist, subarctic forest, primarily coniferous

TUNDRA: a rolling arctic or subarctic plain, located too far north for trees to grow

Asia is a vast and diverse continent with many different types of climate, temperature extremes, and large and small human populations. Many portions of Asia, such as Siberia, are almost empty of people. Some areas are quite densely populated, such as Java in Indonesia, Japan, India, and much of China. Unfortunately for the fauna of Asia, in those areas where the human population is thin, the extremes of climate do not allow for an abundance of wildlife. Many species are near extinction, endangered, or at risk because those areas of Asia that have a climate good for fauna are also densely populated. Some species, however, may have become too specialized for survival. The giant panda eats only bamboo and has an inefficient digestive system. This requires a giant panda to eat large quantities of bamboo. The panda also reproduces slowly. This characteristic may have evolved because the panda has few or no natural enemies—except humans. This type of adaptation can prove to be fatal for a species when factors such as climate, habitat, and predators change.

Much of Asian fauna is under pressure as a result of loss of habitat and overhunting. Most primates worldwide live only in tropical rain forests. The tropical rain forest is being rapidly cleared for timber, firewood, and land for agriculture. Species such as the rhinoceros are disappearing because they are hunted down just for their horns, which have been used for dagger handles in Yemen and for medicinal purposes. Many animals of all species are slaughtered because they are considered to be pests or just in the way of the ever-growing human population.

The Tundra, Taiga, and Steppes

Northern Siberia can be characterized as tundra. Because the tundra is partly free from snow only during the short summer, conditions for life are poor. The principal animals of the tundra are the reindeer, arctic hare, arctic fox, wolf, and lemming. With the exception of the lemming, they live in the tundra in the summer only and migrate in autumn. Birds can be found in the tundra, but with the exceptions of the willow grouse and ptarmigan, they also desert the tundra in winter. Many species of waders, the gray plover, and several kinds of sandpipers migrate to the tundra and breed there in the summer. The snow bunting and the Lapland bunting are also found there. Gyrfalcons (a type of large arctic falcon), buzzards, and skuas feed on these smaller birds and lemmings.

The taiga takes in much of the rest of Siberia and is forested mostly by pine trees. Fauna are richer and more diverse in the taiga than in the tundra, because the greater degree of vegetation provides more food and cover. Mammals found there include the brown bear, wolf, glutton (a kind of wolverine), otter, ermine, sable, lynx, elk, and forest reindeer. The rivers of northern Asia have many species of freshwater fish and several types of sturgeon.

The steppes are the southern edges of Siberia, portions of Kazakhstan, western China, and northern Tibet. Those areas are relatively treeless and similar to the northern Plains states of the United States. The steppes were the place of origin of the northern cattle, the horse, and the Bactrian (two-humped) camel. The animal life of the steppes includes burrowing rodents, jerboas, marmots, and piping hares, and larger animals such as diverse types of antelope. Wild sheep and goats live in the mountains and the plateau areas north of the Himalayas. Tibet is the home of the wild yak, which is an endangered species.

East and Southwest Asia

Northeastern and eastern China, Korea, and Japan have several native species of deer. The giant

Habitats and Selected Vertebrates of Asia

panda lives in the lower mountain area of China near Tibet. The lesser panda, a member of the raccoon family or perhaps its own distinct family, is native to the Himalayas. A rare animal in East Asia is the Siberian tiger, which feeds on elk and inhabits a corner of the Russian Far East and possibly small portions of China and North Korea.

As of 1997, there were estimated to be 360 to 406 wild Siberian tigers. Their numbers are declining, evidently due to overhunting of their main food source, the elk. Another endangered animal is China's true dragon, the Chinese alligator. The remaining populations of these timid reptiles, fewer than 150 in the wild, are limited to just a few village ponds in heavily populated southeastern Anhui Province. One of just two alligator species in the world, Chinese alligators are believed to have diverged from their American counterparts at least twenty million years ago. They reach lengths of about six feet (two meters), which is only half the size of American alligators.

The great rivers of China have a rich variety of fish. In the Yangtze and Huang Ho Rivers, the paddlefish is found. Its only close relative is the paddlefish of North America. The giant salamander, which can grow to a length of 4 feet (1.2 meters) or more, is found in Japanese waters. Most members of the carp family are in Southeast Asia and southern China.

Japan's fauna include the bear, wild boar, fox, deer, and antelope. Some of these species are very different from those on the Asian mainland. The Japanese macaque inhabits many areas. Those at the northern tip of Honshu form the northern limit of monkey habitat in the world. There are eagles, hawks, falcons, pheasant, and more than 150 species of songbirds. Waterbirds include gulls, auks, grebes, and albatrosses. Reptiles include sea turtles, freshwater tortoises, sea snakes, and two species of poisonous snakes.

The Philippines has about 220 species of mammals, including as many as fifty-six species of bats. There are more than five hundred species of birds, including jungle fowl (related to the chicken). The rare and endangered monkey-eating eagle is found in a few locales on Mindanao and Luzon. Fossils show that elephants once existed in the Philippines. It is possible that the climate of the Philippines was much drier in the somewhat distant past. If so, there may have been savanna-like grassland that would have favored elephants. As the climate subsequently became wetter, tropical rain forest grew, which would have reduced the elephants' habitat and thus their population.

Fashion Victim: The Tibetan Antelope

Known by its elegant, lyrate horns and the striking black markings on its face and legs, the male Tibetan antelope, or chiru, is considered one of the world's most beautiful mammals. It inhabits the windswept Tibetan steppe. At the end of the twentieth century, the population of the chiru was down to perhaps seventy-five thousand animals, from an estimated several million earlier in the century. The chiru's wool, called shatoosh, is considered to be the finest in the world and a growing status symbol in Western fashion. Tibetan antelope must be slaughtered to harvest the wool, and it takes an average of three to four antelope to make a single scarf. Ironically, sale of shatoosh has been illegal under the Convention on International Trade in Endangered Species since 1975. Nonetheless, despite the CITES ban, as late as 1998 fashion magazines touted the virtues of shatoosh scarves, priced in the thousands of dollars.

West Asia

Fauna in Iran include the leopard, bear, hyena, wild boar, ibex, and gazelle that inhabit the forested mountains. Seagulls, ducks, and geese line the shores of the Caspian Sea and the Persian Gulf. Buzzards nest in the desert. Deer, hedgehogs, foxes, and more than twenty species of rodents live in the semidesert high-altitude regions. Palm squirrels, Asiatic black bears, and perhaps a few lions inhabit Baluchistan in the southeast. Amphibians and reptiles include frogs, salamanders, boas, racers, rat snakes, cat snakes, and vipers. More than two hundred varieties of fish are found in the Persian Gulf, along with shrimp, lobsters, and turtles. Sturgeon is one of thirty species found in the Caspian Sea.

Arabia has camels, both wild and domesticated, sheep, goats, and Arabian horses (now rare there). Gazelles, oryx, and ibex are becoming rare. Other wild animals are the hyena, wolf, and jackal. The baboon, fox, ratel, rabbit, hedgehog, and jerboa are among the smaller animals. Reptiles include the horned viper, a species of cobra; striped sea snakes; and the large desert monitor. Common birds include eagles, vultures, owls, and the lesser bustard. Flamingos, pelicans, and egrets live on the coasts.

Common insects include locusts, which can descend on fields like a biblical plague. Turkey has the wolf, fox, boar, wildcat, beaver, marten, jackal, hyena, bear, deer, gazelle, and mountain goat. Game birds are the partridge, wild goose, quail, and bustard. The rest of Southwest Asia—Israel, Syria, Lebanon, Jordan, and Iraq—have fauna that are a mix of those found in Arabia and Turkey.

The Oriental Region

The oriental region includes India and extends eastward from India over the mainland and much of insular Southeast Asia. A major portion of the oriental region is tropical. That climate supports malaria-bearing mosquitoes and water-borne flukes carrying the schistosomiasis-causing parasite. These two problems are present in much of tropical Asia as well as in Africa.

In tropical rain forest areas, monkeys are common. Larger primates are found only in tropical rain forests because the kind of cover and food supply that they seem to need exists only there. Gibbons are found in Assam in northeast India; Myanmar (formerly Burma); the Indochinese peninsula—Thailand, Laos, Cambodia, and Vietnam; and the Greater Sunda Islands—Java, Sumatra, and Borneo. The orangutan is found only in Sumatra and Borneo. Indonesia is home to the world's two most endangered rhinoceros species, the Javan and Sumatran. The largest group of Javan rhinoceros is in Ujung Kulon National Park in West Java, but the number of rhinoceros there was fewer than seventy in the late 1990's. The only known wild population of Javan rhinos outside Indonesia, a small group of fewer than fifteen animals, is found in Cat Loc Nature Reserve in Vietnam.

India is an important part of the Oriental zoogeographic region. Almost all orders of mammals are found in India. The primates there include diverse types of monkeys, including the rhesus monkey and the Hanuman langur. Wild herds of Indian elephants can be found in several areas such as the Periyar Lake National Park in Kerala and Bandipur National Park in Karnataka. The Indian rhinoceros is protected at Kaziranga National Park and Manas Wildlife Sanctuary in Assam. There are also four species of large cats: the leopard, snow leopard, Bengal tiger, and lion. The Asian lion, once ranging into West Asia including the Levant, is now found only in the Gir Forest Lion Sanctuary in the Kathiawar Peninsula of Gujarat. Tigers are found in the forests of the Tarai region of Uttar Pradesh, Bihar, and Assam; the Ganges delta in West Bengal; the Eastern Ghats; Madhya Pradesh; and, eastern Rajasthan. The snow leopard is found only in the Himalayan regions.

More than twelve hundred species and perhaps two thousand subspecies of birds are found in India. Herons, storks, ibises, and flamingos are well represented, and many of these are found in the Keoladeo Ghana National Park in Rajasthan. The Rann of Kach forms the nesting ground for one of the world's largest breeding colonies of flamingos.

Crocodiles are found in India's rivers, swamps, and lakes. The estuarine crocodile, which can grow as large as thirty feet (nine meters), feeds on the fish, birds, and crabs of muddy delta areas. The long-snouted gavial or gharial, which is similar to the crocodile, is found in several large rivers, including the Ganges and Brahmaputra. There are almost four hundred species of snakes. One-fifth of these are poisonous, including kraits and cobras. The Indian python inhabits marshy areas and grasslands. More than two thousand species of fish are found in India, 20 percent of which are freshwater species. Commercially valuable insects include the silkworm, bees, and the lac insect. The lac insect secretes a sticky, resinous material called "lac," from which shellac and a red dye are made.

Southeast Asia is located where two important divisions of the world's fauna come together. It constitutes the eastern half of the Oriental zoogeographic region. Bordering on the south and east is the Australian zoogeographic region. The eastern part of the Southeast Asian islands—Sulawesi (Celebes), the Moluccas, and the Lesser Sunda Islands (Bali, Sumba, Flores, and Timor)—forms an area of transition between these two faunal regions. Southeast Asia thus has a considerable diversity of wildlife throughout the region. The region has placental mammals as opposed to the marsupials of Australia, but has hybrid species such as the bandicoot of eastern Indonesia. Small mammals such as monkeys and shrews are the most common. Larger mammals have been pushed into remote areas and national preserves.

Indonesia is located in the transitional zone between the Oriental and Australian faunal regions. The so-called boundary between these two zones is known as Wallace's Line. The line runs between Borneo and Sulawesi in the north and Bali and Lombok in the south. A unique species of proboscis monkey lives only in Kalimantan (southern Borneo). The babirusa (a hoglike animal with curved tusks) and anoa (a small, wild ox with straight horns) are found only in Sulawesi. A giant lizard, the Komodo dragon, occurs only on two small islands, Rinca and Komodo. Insect life in Indonesia includes giant walkingsticks that attain 8 inches (3.2 centimeters) in length, walkingsticks, large atlas beetles, luna moths, and bird-wing swallowtails.

Mammals in Vietnam include elephants, tapirs, tigers, leopards, rhinoceros, wild oxen such as gaurs and koupreys, black bears, sun bears, and several species of deer such as the small musk deer and barking deer. In Cambodia, small populations of elephants, wild oxen, rhinoceros, and several deer species can still be found, along with tigers, leopards, and bears. Snakes abound, with the four most dangerous species being the Indian cobra, the king cobra, the banded krait, and Russell's viper. The fauna of Myanmar and Thailand is similar to that found in Cambodia.

—Dana P. McDermott

See also: Antelope; Baboons; Bears; Birds; Camels; Cattle, buffalo, and bison; Chameleons; Cranes; Crocodiles; Deer; Deserts; Dogs, wolves, and coyotes; Ecosystems; Elephants; Elk; Endangered species; Fauna: Arctic; Fauna: Europe; Fauna: Pacific Islands; Fish; Flamingos; Forests, coniferous; Forests, deciduous; Foxes; Goats; Grasslands and prairies; Habitats and biomes; Hyenas; Insects; Lakes and rivers; Leopards; Lions; Lizards; Mammals; Marine animals; Monkeys; Mosquitoes; Mountains; Orangutans; Pandas; Parrots; Rain forests; Reindeer; Rhinoceroses; Salmon and trout; Snakes; Tidepools and beaches; Tigers; Tundra; Vultures; Weasels and related mammals; Wildlife management.

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FAUNA: AUSTRALIA

Types of animal science: Anatomy, classification, ecology, reproduction
Fields of study: Anatomy, ecology, evolutionary science, wildlife ecology, zoology

The animals of the island continent of Australia are diverse and in a number of instances bizarre and strange in appearance and behavior. A large number of mammals are marsupials; native placental mammals are rare.

Principal Terms

ABORIGINE: European name for the Native Australians

MARSUPIAL: a type of mammal where the females possess an external abdominal pouch in which the young are suckled and protected

MONOTREME: a primitive mammal that lays eggs, such as the duck-bill platypus

PLACENTAL: a mammal in which the developing young are nurtured via a blood-rich tissue (the placenta) within the mother's body.

The European exploration of Australia and discovery of its rich but strange animal life was late in coming. The British naval officer, Captain James Cook, sailed around Australia and charted the east coast of Australia, named it New South Wales, and claimed it for England between 1768 and 1771. In 1788, the first Europeans were transported to what is now Sydney. They were prisoners who had been sentenced by the British courts and incarcerated in prisons in Australia.

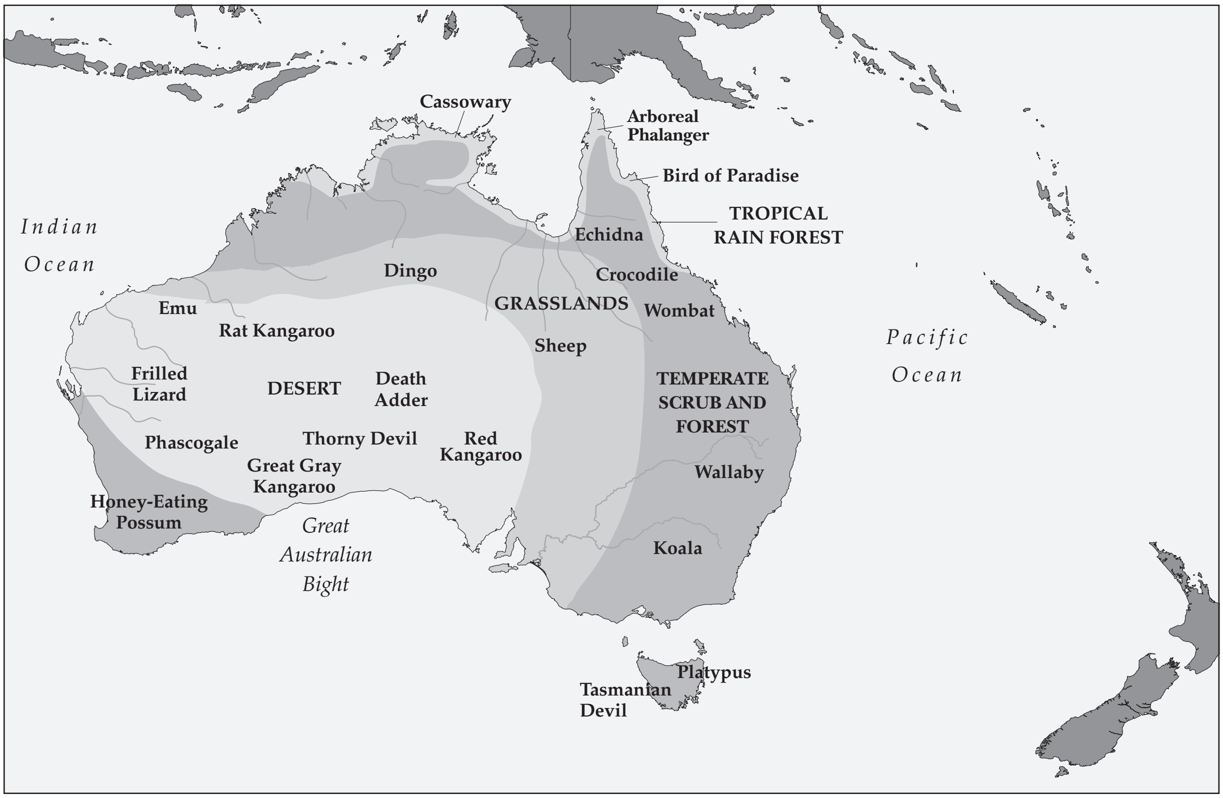
Mammals

The groups of large hopping animals that the aborigines called kangaroo became a favorite source of meat to the prisoners. Like all the other native mammals, the kangaroos are marsupials. Several other marsupials are also hopping animals. They range from the slightly smaller wallaby (which resembles the great gray kangaroo) to the tiny, flat-headed marsupial mouse, which weighs a mere sixth of an ounce. The koala is a well-recognized marsupial, although it is commonly called a bear because of its resemblance to a child's teddy bear. Mainly a tree dweller, its favorite food is the highly fragrant leaves of eucalyptus trees.

In addition to the diverse marsupial mammals, the fauna of Australia includes several species of placental mammals, the majority brought to the island continent by humans. The aborigines, who came to Australia about forty thousand years before the present, were foragers or hunter-gatherers. They brought no animals with them. About eight to ten thousand years ago, fishermen from the islands of Indonesia regularly plied the waters off the north coast of Australia in search of sea cucumbers, a large, marine, wormlike animal. These were dried on board the ship and returned to the home islands as food. These ships apparently also carried the companion of humans through the centuries, the rat. The rats, inadvertently, were among the first placental mammals other than humans to find a foothold in Australia, and quickly established themselves wherever there was food and water. These fishermen also were responsible for taking dogs with them, probably as food. Some of the dogs escaped, becoming the dingoes or wild dogs of Australia.

Other placental mammals were introduced by Europeans for hunting, such as the rabbit and the red fox. Both soon escaped into the wild and became serious pests, especially the rabbit. With no predators to attack them, the rabbits reproduced prodigiously, overwhelming control efforts. The fox had been introduced to serve as quarry for hunters riding to hounds, but it never reached the pest status of the rabbit. Visitors to Australia also

Habitats and Selected Vertebrates of Australia



are often startled to see camels, apparently wild, striding over the sandy wastes of the Outback and other desert areas. These animals, now wild, are the descendants of domestic dromedary camels that had been used to carry freight across the deserts. A few domestic animals, principally dogs and cats, have escaped and established a feral existence. No doubt some cats were easily and swiftly caught and eaten by dingoes, crocodiles, and feral dogs. The dogs formed packs and preyed on a variety of small marsupials. They are a particular predator of the koala. Some feral dogs were preyed on by dingoes but also joined dingo packs, interbred with them, and quickly became part of the predatory fauna of Australia.

The Life Cycle of Marsupials

Marsupials, as mammals, have milk-producing glands and suckle their young. They reproduce similarly to nearly all other mammals: One or more eggs, produced internally by the female, are fertilized internally by the male and develop within the female's body. After a period of developmental stages lasting weeks or months, the fertilized egg becomes an embryo, then a fetus, and finally is ready to be born. Marsupials differ because after only a short development period, the young fetus leaves the female's uterus and painstakingly crawls over her abdomen to enter the brood pouch (marsupium). Here the fetus continues its development until it is a fully formed and viable organism ready to take up an external existence.

The female has prepared the way for the fetal animal to move over her abdomen by vigorously licking the surface hairs from birth canal to pouch. Observers had long believed the licking laid down a scent trail of saliva for the fetus to follow to the entrance of the marsupium. Recent studies suggest the licking is performed primarily to cleanse the path to be followed by the fetus.

The marsupium is endowed with nipples or teats—the number varies according to the species from one or two to a dozen or more—which the fetus takes into its mouth. This action causes the teat to swell, thus effectively sealing it into the fetus's mouth. The quality of the mother's milk varies during the development of the young; the milk fat increases with time to enhance the nutrition available to the developing young.

Kangaroos, Wallabies, Wombats, and Koalas

The most familiar and readily recognized Australian marsupial are the kangaroos. They range in size from the seven-foot-tall red kangaroo, which weighs up to 200 pounds, to the slightly smaller gray kangaroo, which weighs up to 165 pounds and may be as much as six feet tall. In both species, the heavy, muscular tail is nearly as long as the body. It serves as a prop when the animal is sitting and helps to balance it when it is fleeing. The kangaroo moves forward by a series of powerful hops at speeds of up to thirty miles per hour. The small front legs are used primarily in holding objects.

Wallabies are medium-sized members of the kangaroo family. For the most part, they feed in open grasslands at night. The body size, from nose to root of the tail, is eighteen to forty-one inches. The tail ranges from thirteen to thirty inches long. Because of their smaller size, wallabies are preyed on to a greater extent by dingoes, feral dogs, and, in years past, the Tasmanian tiger.

Before Europeans colonized Australia and introduced sheep and beef cattle, wombats and kangaroos were the major grazers in the grasslands of the island continent. Although it is a marsupial, the wombat looks nothing like any of the other marsupials. It has been described as resembling a fur-covered barrel with four legs. An adult may weigh up to one hundred pounds and measure four feet in length. It is a burrower, tunneling passageways one hundred feet long, six feet under the earth's surface.

The tunnels help the wombat conserve energy and water, and thus reduce its need for food. Its chief foods include grasses, generally of poorer quality than required by sheep. Thus, wombats are able to survive in areas where sheep do not thrive, but if there is better quality forage available, the wombat becomes a competitor with the sheep. As a result, sheep ranchers do not like wombats. They also do not like the cylindrical, muscular animals because they burrow under fences, damaging the fence lines and opening routes for rabbits.

The rotund wombat is not a very swift animal and many fall easy prey to dingoes and large, feral dogs. The most serious threat to the animals, however, is the automobile. Many wombats are killed on the highways as they amble across the pavement at night in search of water or new grazing.

Along with the kangaroo, the most readily recognized Australian animal is the koala, another marsupial. The koala produces one young at a time. When it is able to spend time out of the pouch, it clings to the female's fur and is carried along with the mother on her foraging expeditions. Much of the adult's time is spent high in the treetops, especially eucalyptus, whose leaves are a favorite food of the animal.

The average koala male weighs from fifteen to thirty pounds and is about two feet long. The fur is thick and soft

Comparison of Ecological Functions Between Placental Mammals of North America and Marsupial Mammals of Australia

Ecological Function	*North America*	*Australia*
Large grazer	American bison	gray kangaroo
Small grazer	cottontail	wallaby
Tree dweller	porcupine	koala
Burrowing grazer	woodchuck	wombat
Glider	flying squirrel	sugar glider
Large carnivore	gray wolf	Tasmanian wolf
Small carnivore	wolverine	Tasmanian devil

and the animals were hunted in the fur trade. The last fur season occurred in 1927, when six thousand koalas were slaughtered. They were part of the aborigine diet and undoubtedly had a strong eucalyptus flavor as a result of their diet of eucalyptus leaves.

Although there is no longer an open season on koalas, the mortality rate is high. Loss of habitat in land clearing is a major cause of its decline. In addition, many are killed by automobiles while crossing roadways. Dingoes and domestic dogs kill many of them and a significant number drown in backyard swimming pools. Pool owners often suspend a rope in the water so that koalas that fall in can climb out.

Tasmanian Tigers and Devils

Most of the marsupials in Australia have maintained a somewhat shaky coexistence with the European settlers. Two, however, have not. The Tasmanian tiger (more commonly called the thylacine) was the largest living carnivorous marsupial known. It resembled a large, long dog with a long, stiff tail, and brown fur marked with thirteen to twenty dark brown to black stripes on the rear portion of the body. It was active mostly at night and preyed on small animals and birds. The thylacine also occasionally killed and ate sheep and chickens kept by European settlers. It was a fearsome-looking animal, but it was shy and secretive, avoiding contact with humans.

Thylacine females had a back-opening pouch with three to four young in a litter. Pouch life is presumed to have been about four months. The Europeans feared the thylacine, probably because of its bizarre appearance, its nocturnal habits, and its presumed attacks on domestic animals. A bounty was placed on the animal and it was trapped, poisoned, and shot. The last known thylacine died in an Australian zoo in September, 1936. Occasional sighting of thylacines have been reported, but in 1986 the species was declared extinct.

The Tasmanian devil, although it is a relative of the thylacine, differs in a number of ways. Devils are smaller, about two feet long with a tail about one foot long. They weigh up to twenty-six pounds and are heavily built, with a broad head and a short, thick tail. The devil's powerful jaws and strong teeth help it to completely devour its food, bones, fur, and all. It is mainly a scavenger and will eat whatever is available. Wallabies, small mammals, and birds are included in its diet, either captured alive or scavenged as a carcass. It has been suggested that the Tasmanian devil helps maintain countryside sanitation by cleaning up carcasses.

The female devil has a back-opening pouch with four nipples. Since more than four young are born in a litter, the extra young die. On average, about two or three young survive in the pouch.

It is the coloration and behavior of the devil that have given it a fearsome reputation. The fur is black, sometimes marked with white patches, and it makes eerie screeches as it ambles about at night in search of food. At one time the Tasmanian devil was widely distributed on mainland Australia, but in modern times it is restricted to the island of Tasmania, off the southeast coast of the mainland. It is believed that the dingo ousted the devil from the mainland. The Tasmanian devil's population, under government management, appears to be stable.

Reptiles

Australian reptiles consist of a number of species of snakes—some poisonous—several monitor lizards (related to the Komodo dragon), and the most feared reptile, the crocodile. The largest monitor lizard, the giant goanna, reaches a length of 8.5 feet. It lives in rock crevices in desert regions, feeding on any animals that come within reach.

The estuarine or saltwater crocodile is the largest and probably most dangerous Australian reptile. Specimens thirty feet long have been captured, and there may be a few larger than that in some isolated coastal marshes. It can live in freshwater billabongs, brackish coastal estuaries, and has been observed swimming 150 miles out at sea. Its diet consists of any animals that come to waterways to bathe or drink, and it will attack and eat humans. Indeed, many Australian rivers, especially those in the Northern Territory, are marked with signs that warn visitors to beware of crocodiles in the water. The animals once were actively hunted for their hides, to be made into expensive shoes and bags. Prehunting populations were estimated at more than 150,000 crocodiles from Western Australia to Queensland. Hunting pressure reduced their numbers to about seven thousand individuals, but it rebounded to more than seventy thousand after hunting was banned. Today, the crocodile population is closely monitored and a limited number can be taken for their hides and meat.

Birds

The best known of Australian birds are the parrots. Many species of parrots are collected for the pet trade, the most popular being the small budgerigar, or parakeet. They are aptly called "love birds" because of the apparent kissing that goes on between pairs of the "budgies." Some of them can be taught to mimic human speech. Some Australian birds are not as well known as the diminutive (6.5 inch) budgerigar. Bowerbirds build elaborate structures of branches, grasses, and bits of bone or shell to attract females for mating. The kookaburra, though not often seen, is aptly named the "laughing jackass bird" because of its loud and very distinctive call.

Australia's birds also include two large, flightless species—the cassowary and the emu. Cassowaries are about fifty-two to sixty-five inches tall and weigh up to 140 pounds. The skin of the head and neck, in both males and females, is bare of feathers, with bright red, yellow, blue, and purple skin. The top of the head bears a bony structure called a casque. Cassowaries inhabit the tropical rain forests of the Australian northeast coastal region. They are well-muscled and dangerous; they can kill a human by leaping feet first and raking the intruder with sharp claws.

Like the cassowary, the emu is a large, flightless bird. At five to six feet in height, it is topped only by the African ostrich. Emus are found throughout Australia feeding on fruits, seeds, roots, and occasionally insects. They are pests in farming country because of their liking for cereal grains. They are eaten by aborigines and Europeans in the Outback. Attempts to farm them for the American market as a novelty food have not proved to be very successful.

Placental Mammals

Prior to the arrival of humans, especially Europeans, the Australian mammalian fauna consisted almost entirely of marsupials. One major exception was the flying fox, the large fruit bat. Undoubtedly the earliest bats flew, or were blown by storm winds, from the Asian mainland. With few natural enemies, the bats thrived in the tropical and subtropical forests. They continue to be abundant today. Almost all other placental mammals, such as the dingo, were introduced to Australia with the arrival of humans.

Fossil remains indicate the dingo has been a feature of the outback for about four thousand years. Contrary to earlier beliefs, it probably did not arrive with the aborigines forty thousand years ago but is a relative newcomer. Research by Dr. Laurie Corbett, a scientist with the Australian Commonwealth Scientific and Industrial Research Organization (CSIRO) in Darwin, suggests the dingo ancestors were transported, perhaps as food, aboard Malaysian fishing boats. Once in the wild, they soon found a good supply of game in the populations of ground-dwelling marsupials. When Europeans began to raise sheep and beef cattle, the dingo quickly found them a ready source of food. Research on dingo behavior revealed the animals often simply scatter the flocks or, at worse, ravage the animals without eating the carcasses.

To control the dingo, the Australian government has erected a wire mesh fence six feet high, extending nearly four thousand miles across the country. Many ranchers attempt to control the dingo by any means, including poison, traps, and guns. Dr. Corbett reports that the animal, as a separate species, may be naturally sliding toward extinction by being absorbed into the domestic dog population through interbreeding.

The interior sections of Australia, well away from the moist climate of the coastal regions, resemble what most people think of as desert. Vast wastelands of sand and gravel are interspersed with billabongs and other water courses. To complete the desert picture, groups of wild camels troop across as they seek favorable grazing and water. The camels are not native, but were introduced in the nineteenth century to serve as beasts of burden. The trails they followed served as lifelines for most of inland Australia. The animals brought food and other supplies to the settlements, mines, and sheep stations.

The settlers chose the one-humped dromedary, or Arabian camel, rather than the two-humped Bactrian camel. The Bactrian is an animal of the cold Eurasian steppes, whereas the dromedary is common in the hot deserts of Africa and thus better able to survive in the conditions of Australia. Their cloven hooves have cushioned pads underneath that spread with each step and provide good traction in the loose sand and gravel. The hump stores energy-rich fat and the animals conserve water by minimizing perspiration and recycling moisture exhaled through the nostrils.

At their peak there were between ten thousand and twenty thousand dromedaries on the desert trails of Australia. However, when road improvements and motor trucks came along, the camels were no longer needed. The camel owners slaughtered some for food and their hides, the rest were driven into the Outback and set free. Here they thrived and multiplied. Modern estimates of their numbers place the population of feral camels as high as four hundred thousand animals.

The now-wild camels are a nuisance to sheep and cattle station owners. The camels, ambling along, knock down fences, releasing the livestock and also providing entry ways for predatory dingoes. The resourceful Australians are turning a nuisance to a profit. Many of the feral camels are being harvested for food, wool, and leather. In visitor centers, such as Alice Springs, Uluru (Ayer's Rock) National Park, and Ratatjuta, camels are available for rides, either as "picture opportunities" or for guided tours through the Outback.

While the camel and dingo may be considered nuisances, the European rabbit turned out to be an obnoxious pest. In 1859, a homesick Australian stock grazer imported two dozen European rabbits from England and released them on his land. The rabbits bred prodigiously, and six years later he killed twenty thousand on the ranch. In 1895, twenty million rabbits were killed, and still they increased. Five rabbits eat as much grass as one sheep. The rabbits spread over the countryside like a plague. Rabbit-proof fences were erected, but usually the rabbits had already gotten through. By 1953, over a billion rabbits were inhabiting 1.2 million square miles of Australian grassland.

After years of fruitless efforts to control the rabbits, scientists introduced a disease organism, myxoma, a virus, and within one year, 95 percent of the rabbits were dead. However, in the long run, the control agent was not completely successful. A few rabbits were naturally immune to the disease, and others developed immunity and continued to reproduce. Unfortunately, the virus has evolved to an avirulent form. Thus, the biological control of the rabbit is no longer as effective as it once was.

—*Albert C. Jensen*

See also: Bats; Birds; Camels; Chaparral; Coral; Cranes; Crocodiles; Deserts; Dogs, wolves, and coyotes; Ecosystems; Endangered species; Fauna: Antarctica; Fauna: Pacific Islands; Fish; Forests, coniferous; Forests, deciduous; Grasslands and prairies; Habitats and biomes; Insects; Jellyfish; Kangaroos; Koalas; Lizards; Mammals; Marine animals; Marsupials; Mollusks; Ostriches and related birds; Parrots; Penguins; Platypuses; Reefs; Reptiles; Sheep; Snakes; Spiders; Tasmanian devils; Tidepools and beaches; Wildlife management.

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FAUNA: CARIBBEAN

Types of animal science: Ecology, evolution, geography
Fields of study: Conservation biology, ecology, evolutionary science

Biologists have exploited the tremendous diversity and phenomenally high population densities of some West Indian animals to better understand evolutionary, ecological, and biogeographic principles.

Principal Terms

ECOLOGICAL NICHE: the sum of environmental conditions necessary for the survival of a population of any species, including food, shelter, habitat, and all other essential resources

ECOMORPH: species of different phyletic origins (at most distantly related) with similar structural and behavioral adaptations to similar niches

ENDEMISM: the condition of a species that has evolved in a given area, adapted to local conditions, and is found nowhere else in the world

SPECIATION: an increase in the number of species, usually resulting from descendants of a common ancestor adapting to different environmental conditions in different geographic areas

WEST INDIES: a body of islands including the Greater Antilles (Cuba, Jamaica, Hispaniola, Puerto Rico), the Lesser Antilles (an island arc extending from east of the Virgin Islands to the north of Trinidad and Tobago), associated smaller island banks, the Bahamas, and sometimes the islands of the western Caribbean east of Nicaragua, but not the continental islands of Central and South America

The Caribbean Sea is bordered to the west and south by Central and South America, respectively, to the east by the Lesser Antillean island arc, and to the north by the Greater Antilles. When used in a biogeographic context, however, the Caribbean Region is usually defined as the islands that have been called the West Indies since the days of Christopher Columbus. These islands vary greatly in size and age. The oldest islands sit on the Caribbean Plate, which first emerged in what is now the eastern Pacific Ocean, drifted between ancient North and South America before the Isthmus of Panama had formed, and eventually collided with the Bahama Platform and the Atlantic Plate. Throughout this passage, rising and falling sea levels repeatedly inundated entire low-lying islands and at least the lower elevations of the higher ones. In addition, to the east, a subduction zone creates a band of intense and often explosive volcanic activity, which has been responsible for the creation of many Lesser Antillean islands that constitute the newest additions to the archipelago. Islands vary in size from barely emergent rocks to Cuba (over 110,000 square kilometers) and Hispaniola (over 75,000 square kilometers), but sizes have varied as rising sea levels during interglacial periods have fragmented island banks and inundated smaller landmasses.

The island fauna has, like that of any region, been defined by a combination of historical events and current realities. Although transient contact with Central America may have occurred at one time, the vast majority of these islands have never been connected to a continent. Because seas are generally effective barriers to dispersal, relatively few terrestrial animals successfully reached the islands, and even fewer became established. Another factor limiting the number of species is the small number of ecological niches available on relatively small islands. Generally speaking, larger islands with greater elevations are more ecologically complex and contain more niches than smaller islands with less topographical relief, but even the largest islands pale in comparison with the ecological diversity of continents. However, when the region is considered as a whole, the fragmentation and isolation of the islands results in a phenomenally high species richness (of at least some animals) and a very high degree of endemism.

A Fauna Dominated by Reptiles and Amphibians

Studies of West Indian invertebrates are largely limited to those of specific sites or groups, and an overview would be cursory at best. As for terrestrial vertebrates, the quantity of mammalian fauna is relatively impoverished and most birds are migratory; consequently, amphibians and reptiles dominate the fauna in terms of both diversity and numbers. On islands with limited resources, the greater energetic needs of birds and mammals limit population sizes. In contrast, amphibians and reptiles do not require large amounts of energy to sustain stable body temperatures and, as a result, phenomenally high population densities are possible.

Over fifty species of bats and over one hundred species of other nonmarine mammals are known from the region. However, the vast majority of the ninety-four species of nonflying species, all endemic, are extinct, victims of habitat destruction, competition with introduced exotics, or exploitation by humans. Consequently, the mammalian fauna is currently dominated by bats and introduced species. Most of the over 550 West Indian species of birds are migrants, and another large number are sea birds with broad distributions throughout the world. Of the endemic groups, as many as a dozen appear to be relicts of genera that were formerly widespread on adjacent continents. Consequently, the avifauna merely mirrors the greater mainland diversity.

In contrast, almost seven hundred frogs (but no salamanders or caecilians), turtles, crocodilians, and squamate reptiles (lizards and snakes) are known from the region. The vast majority is endemic. Population densities include the highest reported for any vertebrate anywhere in the world (approaching 70,000 per hectare for at least two species of dwarf geckos).

Evolutionary and Ecological Studies

The diversity and population densities of amphibians and reptiles have provided biologists with many opportunities to investigate evolutionary, ecological, and biogeographic questions. In particular, the most diverse groups have demonstrated repeatedly the remarkable abilities of animals to speciate by adapting to varying local conditions on isolated islands or disjunct habitats created by topographic relief on larger islands. West Indian lizards in the genus *Anolis* have provided the best insights into the principle of ecomorphology. Structurally and behaviorally similar species on different islands are more closely related to very different species on the same islands than to their ecological counterparts elsewhere. This phenomenon provided evidence for evolutionary adaptations to local conditions and divergence from relatives that adapted to other available habitats. Many fundamental biogeographic principles have also been developed or supported by studies on West Indian animals. Over-water dispersal of large terrestrial vertebrates, long a staple of biogeographic hypotheses, was first demonstrated in 1995 when green iguanas were transported over hundreds of kilometers of open ocean from Guadeloupe to Anguilla on a floating mass of debris. Other important biogeographic concepts emerging from West Indian studies include positive relationships between biodiversity and area, habitat heterogeneity, and proximity to the nearest large body of land—and between habitat fragmentation and extirpation or extinction.

Conservation Concerns

Studies of habitat fragmentation, unfortunately, also provide many examples of the negative impact humans have had on the survival of the other species on the planet. Although Amerindians began the process, and may have been responsible for the extinction of the few large land mammals known to have lived in the islands, the most harm has resulted from humans of European and African descent, to whom the islands have been subjected longer than any other area in the Western Hemisphere. In addition, human population growth is rapid and island areas are limited. Finally, economic development, often related to tourism, is accelerating to accommodate the growing needs of humans living in a region with few natural resources.

Many West Indian animals have small ranges and are extremely vulnerable to habitat alteration and the impact of introduced exotics. A large percentage of frogs and some lizards are restricted to forests that are disappearing rapidly. Other species, notably the critically endangered iguanas of the genus *Cyclura*, the most endangered reptiles in the world, and hutias, large endemic rodents, have suffered from exploitation by humans for food. Many species in both groups are extinct, and all populations are threatened or endangered. Introduced predators, notably feral cats and the mongoose, which was introduced to control rats in sugar cane fields, have eliminated populations of ground-dwelling snakes and lizards on many islands. Goats denude vegetation on which native species depend. The outlook is grim for many species, but hard lessons learned in the West Indies might lead to more enlightened policies elsewhere.

—Robert Powell

See also: Amphibians; Bats; Birds; Coral; Crocodiles; Ecosystems; Endangered species; Fauna: Central America; Fauna: North America; Fauna: South America; Fish; Flamingos; Frogs and toads; Habitats and biomes; Lizards; Mammals; Manatees; Marine animals; Mollusks; Rain forests; Reefs; Snakes; Sponges; Tidepools and beaches; Turtles and tortoises; Wildlife management.

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FAUNA: CENTRAL AMERICA

Type of animal science: Geography
Fields of study: Ecology, environmental science, zoology

Central America is host to a tremendous diversity of animal life, a fauna quite different from other parts of the world. Central America is a land bridge that connects North America and South America, and it has fauna with similarities to both of these continents, as well as endemic species that have evolved within its own borders.

Principal Terms

ENDEMIC: confined and indigenous to a particular region or locality

HABITAT: the physical and chemical factors of the environment

MARSUPIAL: a pouched mammal that gives birth to embryonic young that complete development in a pouch, attached to the mother's nipples

NEOTROPICAL FAUNA: the geographic faunal region that includes Central and South America

OMNIVOROUS: a diet that consists of both plants and animals

PLACENTAL: a mammal whose young develop in the uterus and are nourished through the mother's blood vessels in the placenta

Central America, according to geographers, is the region that commences at the narrow Isthmus of Tehuantepec, in southern Mexico, and extends all the way down to the Atrato River valley, just east of the Panama border in Colombia, South America. Situated in the Western Hemisphere, it is a tapering isthmus, often called the land bridge that joins the two continents of North and South America. By definition, Central America is part of North America, and it includes the countries of Costa Rica, Panama, Belize, Honduras, Guatemala, Nicaragua, and El Salvador.

The world has been divided into six biogeographic regions based on the characteristics of the different types of animals that reside there. The Neotropical area begins at the southern border of the Mexican desert, and continues through Central America to the sub-Antarctic zone of South America to the south, and the West Indies to the east. There is significant mixing and influence from the northern continent, as well as endemic species that evolved in western Panama, eastern Costa Rica, and the highlands of Guatemala, Honduras, and northern Nicaragua.

The marsupials are the older indigenous mammals. After the land bridge was created, there was an influx of North American mammals into the once isolated ecosystem of Central and South America. This explains why many creatures of the Central American regions seem to have close ties to North American animals. The more recent arrivals (about three million years ago) are the rodents, including guinea pigs, and porcupines, tapirs, bats, deer, and guanaco, as well as carnivores such as the margay and jaguarundi. These are the more efficient placental mammals that have adapted and survived in the evolutionary and predatory struggle.

Warm-Blooded Vertebrates

The forests of Central America have a relatively meager population of mammals compared to reptiles, and it hosts widely varying species of birds and insects. The isthmus is the natural habitat of the jaguarundi, margay, jaguar, and ocelot. These species are excellent examples of the adaptation process of North American mammals that migrated south, eventually evolving into unique and well-situated species. The jaguarundi is a small, unspotted cat found only in the New World. It is also called the otter-cat because of its otterlike countenance and swimming ability. It lives in the forested and brushy regions near water and is very rare north of Mexico. Similarly, the coati or coatimundi is an animal like a raccoon (family Procyonidae), with a body that is slimmer, has a longer tail, and an elongated flexible snout. Like an anteater, this animal uses its snout to find insects in the ground, yet it can also climb trees to acquire birds and eggs, with a preference for fruits and berries. The Central American species is classified as *Nasua narica*. Other animals that have migrated to the central region but have not changed much from their North American counterparts are the coyote, gray fox, and puma.

Habitats and Selected Vertebrates of Central America

Howler Monkeys: Voices to Be Heard

Howler monkeys (primates of the family Cebidae) are among the most fascinating animals of Central America. These heavy-bodied monkeys are the largest primates of the New World tropical rain forests, with a combined head and body length of over 550 millimeters and a prehensile tail that may be even longer. They spend virtually their entire lives in the treetops, where they find food and water and may come down to drink only during the dry season. The fur is long, soft, and luxurious, and the animal almost looks as though it is wearing a cape. Both sexes have a beard, but it is much more developed in males. Color of the fur may range from a dark, glossy black to a dark reddish brown to a light ochre.

As impressive as howler monkeys look, it is not their appearance that makes them so distinctive. Males produce vocalizations which are so strong and loud that the reverberations can be heard up to several miles. If the source of the sound were not known, one would think that a much larger animal, such as a jaguar, was producing it. When making this extraordinary sound, the howler monkey's tongue is dilated and forms a gobletlike chamber. The chorus may begin with an old male, perhaps the leader of the band. The sound builds up, and there does not appear to be any pause. Other males may join in to create a loud cacophony.

Unfortunately, as is true of many animals in the tropical rain forests of Central America, loss of habitat is threatening the species.

On the other hand, some South American animals used the isthmus as a conduit to the northern continent. Some examples of these northbound animals are the armadillo, marley, opossum, anteater, and kinkajou. This north-south migration is why the Central American region has a mixture of Neartic (northern) and Neotropical (southern) animals. Armadillos are mammals that are related to the sloth and anteater, and inhabit open areas as well as forests. These animals have an armor plating on their bodies as a shield against predators. Although most anteaters are arboreal, with a prehensile tail, the giant anteater is not a climber. The opossum is an arboreal marsupial with an ability to swim. The kinkajou is a relative of the raccoon but behaves like a primate. In fact, for a long time scientists mistakenly grouped them with lemurs. Kinkajous are carnivores with a prehensile tail and are both arboreal and good swimmers. The giant tree sloth, a slow-moving arboreal mammal, makes Panama its home.

Primates of Central America are another group of interesting mammals. The New World monkeys are typified by their prehensile tails. They reside in forested areas. Honduras is home to the howler, spider, and capuchin monkeys. The red-backed squirrel money is found in Panama and Costa Rica. This monkey is valued by the biomedical industry.

Other unusual mammals found in this region are the manatee and the river otter. The spectacled bear is found in Panama. Bats are diverse and plentiful. The bloodsucking vampire bat is an endemic species of this area.

South America is called the bird continent. It is no surprise that the avian population of Central America harbors an enormous number of bird species. They are a unique mixture of birds found in both the northern and southern continents, as the isthmus serves as a migratory path between the two. Hummingbirds and parrots are perfect examples of this mixing.

The resplendent quetzal is a type of trogon with iridescent feathers. It is the national emblem of Guatemala, where the monetary unit is also called a quetzal. Brilliantly colored toucans and macaws are also characteristic of this region. Among the predatory birds, the giant harpy is the most powerful of all eagles. It hunts macaws, sloths, and monkeys. The crested eagle of El Salvador is becoming more rare due to extensive logging and the loss of its natural habitat.

Cold-Blooded Vertebrates

The fish life is prolific in Central America. The majority of fish belong to the following groups: catfish, characins, the pacus, the air-breathing eel, and the cichlids. Catfish make up about half of the total fish fauna, the characins are noted for containing the flesh-eating piranha, eel stun their prey with electric shocks, and the cichlids are similar to North American sunfish. One of the more interesting freshwater fish is the landlocked shark, found in Lake Nicaragua. The lowlands of Belize, with their mangroves and swamps, are the prime environment for the lungfish, which breathe through their lungs instead of gills.

Central America flourishes with a multitude of reptiles and amphibians. The effects of solitary evolution and divergent speciation are very noticeable among these animals. In Costa Rica alone, there are about 130 species of frogs. The golden tree frog is native to Panama. From voracious mammal-eating frogs to beautiful but deadly venomous ones, Central America is host to all. Some of the largest snakes in the world, such as the boas and the anacondas, make the tropical forest their home. Some of these constrictors can devour caimans and mammals. There are also colubrids or coral snakes, green snakes that have adapted to living in trees, the ground, the water, and in burrows. Crocodiles, caimans, lizards, iguanas, salamanders, geckos, turtles, and tortoises are all part of this ecosystem. The crested basilisk lizard, a type of iguana, lives on stream banks. This lizard is known in Spanish as Jesus Cristo, because it appears to have the ability to walk on water, which it does by skimming over the surface very fast.

Indiscriminate hunting and logging have caused many of these animals to become rare or endangered. Many Central American nations have passed or are in the process of passing legislation that will prohibit hunting and protect forested areas. It will take concentrated, unified, and consistent effort by these national governments and others to save the unique species of Central America.

—Donald J. Nash

See also: Armadillos, anteaters, and sloths; Bats; Birds; Cats; Chaparral; Cranes; Crocodiles; Deer; Dogs, wolves, and coyotes; Ecosystems; Endangered species; Fauna: Caribbean; Fauna: North America; Fauna: South America; Fish; Forests, deciduous; Frogs and toads; Habitats and biomes; Jaguars; Lakes and rivers; Lizards; Mammals; Manatees; Marine animals; Marsupials; Monkeys; Mountains; Opossums; Otters; Parrots; Porcupines; Raccoons and related mammals; Rain forests; Reptiles; Skunks; Snakes; Tidepools and beaches; Wildlife management.

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FAUNA: EUROPE

Types of animal science: Ecology, geography
Fields of study: Conservation biology, ecology, environmental science, wildlife ecology, zoology

Millennia of urban life and intensive agriculture have made European wildlife especially endangered. Large mammals are at the greatest risk, with many historical species already extinct. Since the 1990's, increasing efforts have been made to restore endangered populations through breeding programs and advanced reproductive technologies.

Principal Terms

ENDANGERED SPECIES: a species of animal or plant that is threatened with extinction

STEPPE: arid, loess-rich land, usually experiencing extremes of temperature

TUNDRA: a rolling arctic or subarctic plain, located too far north for trees to grow

UPPER PALEOLITHIC: the era from 30,000 B.C.E. to 3500 B.C.E., when humans first began to affect European wildlife populations

The number of wildlife species in decline across Europe increased during the second half of the 1990's. Eleven of Europe's twelve most urgent environmental problems, including waste, climate change, and stratospheric ozone depletion, remained static or worsened over the latter half of the 1990's. The threat to Europe's wildlife continues to be severe, with more than a third of bird species in decline, most severely in northwestern and central Europe. Up to half the known vertebrate species were under threat in many countries.

In the countries of the European Union (EU), intensive and subsidized agriculture has devastated the wildlife. Italy is a good example. The extent of animal life in Italy has been reduced greatly by the long presence of human beings. The primary locales in Italy where wildlife survive are the Italian Alps, the Abruzzi (east central Italy on the Adriatic Sea), and Sardinia. Only in those areas can one find the Alpine ibex, brown bear, wolves, foxes, fallow deer, mouflon (wild sheep), and wild boar.

Portugal and Spain are somewhat different from the rest of Europe in that their wildlife is a mixture of European and North African species. In Portugal, about two-thirds of the wildlife overall is Mediterranean, but the farther south one is in Portugal, the more North African the fauna becomes. Birdlife is rich in both countries of Iberia because the peninsula lies on the winter migration route of western and central European species. Nevertheless, major species in Portugal and Spain are endangered.

Despite its reputation for pollution, the eastern portion of Europe is the stronghold of Europe's wildlife. Agriculture in Eastern Europe is starting to intensify, however. One notable exception to the situation of Europe's fauna is Latvia. Although a small country, Latvia contains a number of species and ecosystems rare in other European nations. As many as four thousand Eurasian otters can still be found in Latvian rivers.

Less fortunate European countries struggle to re-establish their beavers, but Latvia has a population of forty-five to fifty thousand beavers, which were reintroduced in 1952 from Russia. There are two hundred to four hundred wolves, as well as three hundred to four hundred lynx. Latvia has more than two hundred breeding species of birds, some of which are rare elsewhere. These include the white-backed woodpecker, lesser-spotted eagle, and black stork. Estonia, which borders on

Habitats of Selected Vertebrates of Europe

Latvia, is similar in some respects. The moose is the largest animal, along with roe deer and red deer. In the forests of northeast Estonia, bears and lynx are found. Along the riverbanks, mink and nutria are common.

The Effects of Humans

Wild animals have been in retreat since Upper Paleolithic times (30,000 B.C.E. to 3500 B.C.E.), when small human groups held their own against such big game as aurochs, a type of bison, and mammoths, now extinct. In more recent centuries, settlers won the land for crops and domesticated animals. As the population increased in industrializing Europe, humans inevitably destroyed, or changed drastically, the wild vegetation cover and the animal life. With difficulty, and largely due to human tolerance, animals have nevertheless survived.

In January, 2000, a dike holding millions of gallons of cyanide-laced wastewater gave way at a gold-extraction operation in northwestern Romania. The collapse of the dike sent a deadly waterborne plume across the Hungarian border and down the nation's second-largest river. Two hundred tons of dead fish floated to the surface of the blighted waters or washed up on the Tisza River's banks. The toxic brew also killed legions of microbes and threatened endangered otters and eagles that ate the tainted fish.

Wildlife Preserves

Even when there are parks and preserves, human activities endanger the fauna and environment. Doñana National Park, an area of wetlands and sand dunes on the Guadalquivir River delta in southern Spain, is one of the most important wildlife sanctuaries in Western Europe. More than 250 bird species, over half of Europe's total, are found there. It is also home to the rare Iberian lynx. The park covers 190,830 acres (77,260 hectares) and is a World Heritage Site. In the 1990's, the park was threatened by falling water levels caused by thirty dams along the Guadalquivir River.

In 1998, the park was further threatened by a flood of toxic waste from a breached dam that was holding back a reservoir used for dumping mining waste. The waste was successfully diverted, but not before wetlands surrounding the park were contaminated by heavy metals. Those heavy metals may yet poison many of the birds that fly there to feed. The aquifer that supplies the park was contaminated, and thousands of fish and amphibians died. These had to be removed to prevent carrion-eating birds from being poisoned.

Mammals

Larger mammals are mostly gone from Western Europe, with the possible exceptions of Spain and Portugal. In the tundra of European Russia and of Lapland in Finland, Norway, and Sweden, caribou or reindeer thrive. In the short summer of the tundra, arctic fox, bear, ermine, and the wolverine

Efforts to Save Europe's Large Carnivores

Habitat destruction and the loss of prey species have contributed to the decline of large carnivores in Europe. In the year 2000, large carnivores occupied fragmented landscapes dominated by humans. The Iberian lynx population is confined to about ten isolated pockets of Spain and Portugal and numbers less than eight hundred. Elsewhere, relic brown bear populations are dangerously small and highly fragmented in southern, central, and western Europe. Like wolves, brown bears face a hostile reception whenever they move into new areas. Wolverines have been reduced to a few hundred in remote areas of Scandinavia. The Eurasian lynx has disappeared from much of its original habitat; where populations are starting to recover, conflict with humans remains a major stumbling block.

The World Wildlife Fund's (WWF) Campaign for Europe's Carnivores aims to challenge ancient prejudices and to help fund projects supporting peaceful coexistence between people and predators. Wolves are beginning to return to old haunts in France, Switzerland, and even Germany. This fact, along with continuing human conflicts with the wolverine, lynx, and brown bear in other areas, emphasizes the need to secure public support for carnivores. WWF's strong European network is working across international boundaries to help secure pan-European cooperation for carnivore populations and to gain public acceptance of their important place in Europe's natural heritage.

may appear. In the deep forests of Poland, Belarus, and European Russia, one still finds the moose, reindeer, roebuck, and brown bear. The brown bear no longer inhabits Scandinavian forests, but the moose is common in Norway, Sweden, and Finland.

Finland is the home of the only species of freshwater seal in the world—an animal depicted on one of the country's coins. The lynx is mostly gone, but wolves, fox, marten, badgers, polecats, and white weasels survive. The sable, which is much hunted for its valuable fur, only just survives in the northeastern forests of European Russia. In Romania, there can still be found bears, wolves, wild goats, and even the European bison.

In much of the rest of Europe, wild fauna are limited to foxes, squirrels, marmots, and other rodents. In higher elevations in France, Italy, and Austria, one can still find the chamois and ibex. Italy's renowned Gran Paradiso National Park in the Valle d'Aosta saved the alpine ibex from extinction. Alpine marmots and chamois can be seen in the Bavarian Alps near Berchtesgaden, Germany. In the steppes of the Ukraine and European Russia, large wildlife is gone except in the semidesert areas north and northwest of the Caspian Sea. There one can still find two types of antelope, the saiga and the jaran, along with rodent sand marmots, desert jerboas, and the sand badger.

Wildlife Drowning Under the High Seas

Some of Great Britain's best-known nature reserves are expected to be covered by the sea before the middle of the twenty-first century. The British government forecast that the sea level around southeast England would rise by two feet (sixty centimeters) by mid-century. A wildlife-rich chain of low-lying grazing marshes, reedbeds, and lagoons behind the shingle beaches of Suffolk and Norfolk in southeast England are at risk. In February, 1996, a combination of storms and exceptionally high tides flooded the freshwater Cley and Salthouse Marshes in Norfolk with saltwater to a depth of six feet (two meters) along a two-mile (three-kilometer) stretch of coast. The marshes there are one of the few British haunts of the bittern, a large heronlike bird that is one of the most critically endangered species in Britain. No bitterns bred there in 1996 because the salt stunted the reeds that give the bitterns cover and killed the freshwater fish they eat.

Reptiles, Amphibians, and Fish

Europe's reptiles are most common in Mediterranean and semidesert areas. In the coastal Mediterranean, vipers and similar snakes, lizards, and turtles are found frequently. In the semidesert areas north and northwest of the Caspian, cobras and steppe boas are found, along with lizards and tortoises.

In Italian waters, freshwater fish are the brown trout, sturgeon, and the eel. Off the coast of Italy, one finds the white shark, bluefin tuna, and swordfish. There is an abundance of red coral and commercial sponge on the rocks of the warm southern seas. Spanish waters contain a diversity of fish and shellfish, especially in the southeast where Atlantic and Mediterranean waters mix. Species include red mullet, mackerel, tuna, octopus, swordfish, pilchard, and anchovy. Bottom-dwelling species include hake and whiting. The striped dolphin and the long-finned whale are found off southeastern Spain, and the bottlenosed dolphin off the delta of the Ebro River. In Scandinavian waters, salmon trout, and the much-esteemed *siika* (whitefish) are relatively abundant in the northern rivers. Baltic herring and cod are the most common sea fish.

Birds

In the short summer of the tundra, seabirds and immigrant birds such as swans, ducks, and snipes can be found. In the great forests of Eastern Europe, black grouse, snipe, hazel hen, white partridge, owls, and blackbirds are common. The steppes have a more abundant selection of fowl. There are eagles, falcons, hawks, and kites and water and marsh birds such as the crane, bittern, and heron.

Insects

Different kinds of locusts and beetles are common in the steppes of the Ukraine and European Russia. In the summer months of 2000, much of the Eurasian steppes was hit by a plague of locusts, devastating Russia's vital grain crops. In Mediterranean and semidesert areas, scorpions, the karakurt spiders, and the palangid are insects dangerous to humans.

Conservation Efforts

In a remote part of northwestern Greece, the lakes of Mikri Prespa and Megali Prespa combine to form rich wetlands. The area has more than fifteen hundred plant species, forty mammals, including the brown bear, otter, and wolf, eleven species of amphibians, twenty-two species of reptiles, and seventeen fish species. Since 1974, Prespa has been a national park, but there was no management plan. In 1991, the World Wildlife Fund (WWF) helped to establish the Society for the Protection of Prespa (SPP) to intervene at a local level and develop the necessary strategies to maintain the area.

Scientists trying to save the Iberian lynx, the most endangered cat in the world, from extinction are using the latest deoxyribonucleic acid (DNA) technology to track the cat by its droppings. The scientists want to put several healthy cats in a captive-breeding center in the Doñana National Park. Once the population is located, DNA testing will reveal whether inbreeding is further endangering the dwindling species by producing unhealthy offspring. The idea is to capture several cats from different regions and bring them to the breeding grounds. In 2000, there was no stock to breed. There are no more than six hundred lynx in Spain and fifty in Portugal. If the rate of decline continues at the current trend, the animal could be extinct by 2010.

The Mediterranean monk seal is one of the ten most endangered species in the world. At the beginning of the twentieth century, it was prevalent throughout the Mediterranean. It is now a rare sight, although still spotted, particularly in the eastern Mediterranean and out in the Atlantic off the Madeira Islands of Portugal. The monk seal is a shy animal with low reproduction rates. It is thus highly sensitive to changes in its habitat and external disturbances. Increasing pollution from industrial waste, plastics, insecticides, and heavy metals have also affected its habitat, food, and most probably its mating ability. More important, since the seals are perceived by commercial fishermen to be in competition for limited fish stocks, they have been deliberately killed.

The WWF began a project in 1993 in the eastern Mediterranean to monitor the presence of the seal and to determine its interaction with the local population. The WWF has mounted information campaigns and government lobbying in Greece, Turkey, and Cyprus in order to pass protective measures to achieve a balance between increasing human use of decreasing marine resources and the basic survival needs of the monk seal.

—Dana P. McDermott

See also: Bears; Birds; Chameleons; Chaparral; Chickens, turkeys, pheasant, and quail; Cranes; Deer; Dogs, wolves, and coyotes; Ecosystems; Elk; Endangered species; Fauna: Arctic; Fauna: Asia; Fish; Forests, coniferous; Forests, deciduous; Foxes; Geese; Goats; Habitats and biomes; Lakes and rivers; Mammals; Moose; Mountains; Otters; Owls; Pigs and hogs; Reindeer; Seals and walruses; Sheep; Shrews; Storks; Tundra; Weasels and related mammals; Wildlife management; Woodpeckers.

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FAUNA: GALÁPAGOS ISLANDS

Types of animal science: Classification, ecology, evolution, geography
Fields of study: Ecology, evolutionary science, herpetology, ornithology, wildlife ecology, zoology

The Galápagos Islands, clustered around the equator six hundred miles west of the coast of Ecuador, are renowned for their remarkable fauna, including the giant Galápagos tortoise, the world's only marine iguana, and Darwin's finches, whose variety and ecological diversity inspired Charles Darwin's revolutionary theory of evolution.

Principal Terms

CARAPACE: hard case covering the back of an animal

DISHARMONIC: ecologically unbalanced

ENDEMIC: belonging to or native to a particular place

NOCTURNAL: active at night and dormant or asleep during the day

VESTIGIAL: less developed or degenerated from an original useful form

The Galápagos are oceanic islands, created by submarine volcanoes that emerged from the ocean devoid of life. Because of the great distance between an oceanic island and the nearest continent, only animals and plants that can disperse easily through the air or water are likely to reach such an island. Even fewer will survive its particular environmental conditions and thrive. For this reason, oceanic islands tend to be disharmonic.

For animals to reach the Galápagos before humans arrived, there were only three options: by sea, whether by swimming, floating, or drifting on natural rafts of logs or other vegetation; by air, either by flying or drifting in wind currents; or by hitching a ride on or in the body of another animal. As a result of such limited, haphazard possibilities, freshwater fishes and amphibians are totally absent from the islands, and endemic mammals are few. Only birds and reptiles well represent the vertebrates, and only beetles and butterflies the invertebrates.

Reptiles

Reptiles dominate the Galápagos. Seventeen out of twenty-seven species are endemic. They include geckos, snakes, lava lizards, iguanas, and giant tortoises. Geckos are small, mostly nocturnal lizards. The one endemic snake is a small constrictor. Lava lizards are so named for their habit of basking on lava rocks, and range in size up to twenty-five centimeters (almost ten inches).

The islands have both land and marine species of iguanas. Land iguanas grow up to 1.2 meters (almost four feet) long, have a large dorsal crest, and can live up to seventy years. They prefer fruits, flowers, cactus pads, and other vegetarian fare but also consume insects and carrion. The marine iguana is the only sea-going iguana in the world and can drink seawater, utilizing special salt glands to excrete the excess salt. It spends most of the day basking but dives to depths of twenty meters (over sixty feet) to feed almost exclusively on marine algae. It can reach a length of 1.5 meters (five feet) and live up to thirty years.

The most famous reptile on the islands is the Galápagos tortoise, *Geochelone elephantopus*. Males can weigh up to 250 kilograms (550 pounds); females are considerably smaller. They drink from pools at any opportunity and browse on plants, but they can survive a year or more without eating or drinking and can live 170 years or more. There are two distinct types of tortoise with one intermediate type. One type has a dome-shaped carapace and lives in moist, lush areas where vegetation is abundant and easy to reach. The other inhabits more arid regions and has a saddle-shaped carapace, allowing extension of its long neck to reach leaves and cactus pads high overhead. It is this tortoise's distinctive shell that gave the islands their name: "Galápago" refers to a light saddle or sidesaddle in Spanish.

Birds

Although sea birds are abundant on the islands, most are nonnative migrants. Only a quarter of sea birds species are endemic: the lava and swallowtail gulls, the waved albatross, the flightless cormorant, and the Galápagos penguin. The Galápagos penguin is the northernmost penguin species and one of the smallest, standing forty centimeters (sixteen inches) tall. The flightless cormorant has a strong, hooked beak and vestigial wings. Like the penguin, it swims underwater to catch fish, propelled by its webbed feet.

Twenty-two out of twenty-nine land birds are endemic. There are four species of mockingbird, one dove, one flycatcher, one hawk, one martin, one rail, and thirteen species of Darwin's finches. Darwin's finches all originated from a species native to the Caribbean, *Melanospiza richardsonii*, evolving over time into thirteen species, with different bill sizes and shapes and varying habits.

Mammals

Not including the sea lions that gather in colonies on the beaches, only eight species of mammals are endemic to the Galápagos, six species of omnivorous rice rats and two species of bats. Unfortunately, many nonnative mammals, feral and domestic, have moved in and decimated many native populations of both flora and fauna. Lush vegetation has been converted to grazing land for goats, cattle, and horses. Donkeys trample tortoise nests while pigs root up and devour the eggs of giant tortoises, sea turtles, and birds. Dogs, cats, and nonnative rats prey on any reptile or bird they can catch.

Arthropods

About one thousand insect species inhabit the Galápagos. Because of the arid environment, most are nocturnal. Although there are relatively few species, insects are plentiful, particularly during the rainy season.

Of the arachnids, two endemic species of scorpions are found on the islands. Although there are over fifty spider species, only a few are endemic. The least popular animal on the island is an endemic centipede that can grow as long as thirty centimeters (approximately one foot) and administers a very painful bite.

—Sue Tarjan

See also: Birds; Ecosystems; Endangered species; Fish; Habitats and biomes; Lizards; Marine animals; Mollusks; Penguins; Reptiles; Sparrows and finches; Tidepools and beaches; Turtles and tortoises; Wildlife management.

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FAUNA: MADAGASCAR

Types of animal science: Classification, evolution
Fields of study: Conservation biology, population biology, wildlife ecology, zoology

Madagascar is home to a rich variety of unique and remarkable animal species, most of which are found nowhere else in the world. These animals have evolved in isolation after the island split off from mainland Africa over 120 million years ago.

Principal Terms

ARBOREAL: living in or among trees
CAMOUFLAGE: to blend in with one's surroundings
ENDANGERED: at risk of becoming extinct
ENDEMIC: existing only in a particular locality
NOCTURNAL: active at night
OMNIVOROUS: feeds on both plants and animals
PROSIMIANS: a group of primates that retain some primitive characteristics absent in higher primates

Madagascar is a large island located in the Indian Ocean about 250 miles east of the African continent. Its varied geography and the resulting differences in temperature and rainfall have led to the identification of five distinct climatic regions, each having its own specialized floras and faunas. Because of the island's isolation, up to 90 percent of its estimated 200,000 evolved animal species so far identified are endemic. Biologists are discovering additional species every year. This unique biodiversity makes it a source of fascination for amateur and professional naturalists alike, as well as a hotspot for bioconservation efforts.

Mammals

There are relatively few mammal species on Madagascar. The ancestors of these unusual, diminutive creatures first arrived on the island by floating across the water on mats of vegetation or by hopping on temporary landmasses. Large mammals are thus conspicuously absent. Excluding bats, Madagascar's native mammals are 100 percent endemic.

Lemurs (order Primates, infraorder Lemuriformes) are Madagascar's trademark animals. These curious prosimians occupy a singular place in primate evolution. Lacking some of the characteristics of the higher primates, such as monkeys and apes, they are nevertheless intelligent and display social organization. Lemurs have excellent night vision, an acute sense of smell, distinctive bright eyes, pointed snouts, long tails, and are about the size of a cat. Most are arboreal and have the ability to jump great distances from tree to tree. They are primarily vegetarians, although some species also eat insects. There are thirty-three living species in five families. Of the true lemurs (family Lemuridae), the ringtail lemur is best known, the most sociable, and the only species that spends most of its time on the ground. Others species include the bamboo, mongoose, brown, black, and ruffed lemurs. The indri (family Indriidae) is the largest lemur, growing up to three feet tall and weighing up to fifteen pounds. It is famous for its loud, wailing, territorial call that can be heard at great distances. Woolly and sifaka lemurs are also in this family. The nocturnal mouse and dwarf lemurs (family Cheirogaleidae) are the smallest primates in the world, travel on all fours, and are the most numerous group on Madagascar. The aye-aye (family Daubentoniidae) is a single species that is quite different from all others. This solitary lemur has scruffy black fur, huge ears, rodentlike teeth, a thick tail, and a long, skeletal middle finger. It hunts for insects by listening for sounds underneath bark, then gnaws a hole and inserts its long finger into the hole to scoop out its prey. Lepilemurs (family Megaladapidae) are medium-sized, nocturnal lemurs.

Madagascan carnivores consist of civets (family Viverridae) and mongooses (family Herpestidae). The fossa is the largest civet and predator on the island, with a body length of about 2.5 feet. It is a catlike creature, with powerful legs and a long tail, and is an agile tree climber. It preys on reptiles, birds, and mammals, including lemurs. Other civets are smaller and more foxlike. The five species of mongoose are even smaller.

Tenrecs (order Insectivora, family Tenrecidae) are among the most primitive of all living mammals and were probably the first to arrive on the island. These small creatures resemble hedgehogs or shrews. Tenrecs feed primarily on insects, but many are omnivorous.

There are twenty-nine species of bats. Only 60 percent are endemic, due to their ability to migrate off the island. The flying fox, a fruit bat, is the largest.

Only eleven species of rodents exist on Madagascar. The giant jumping rat is the largest, about the size of a rabbit and weighing about 2.5 pounds.

Reptiles and Amphibians

Madagascar's amphibian population consists of about 150 species of frogs. The true frogs (family Ranidae) are most abundant, followed by the narrow-mouthed frogs (family Microphyidae) and just a few species of the Hyperoliidae and Rhacophoridae families. Most are arboreal forest dwellers.

The reptiles are better represented, with approximately 260 species identified. The lizards (subclass Lepidosauria, order Squamata, suborder Sauria) comprise the largest diversity, and include Madagascar's famous chameleons, whose color-changing ability, multidirectional vision, sharpshooting tongues, and V-shaped feet make them fascinating subjects. Madagascar is home to the majority of the world's chameleon species. Fifty-four species inhabit the island. The parsonii are the world's largest chameleons, and the pardalis is the most common. They eat insects as well as small birds and lizards. The sixty-three species of geckos include those with perfect camouflage as well as brightly colored ones. Iguanas inhabit only the dry regions. Skinks and girdle-tailed lizards are widespread.

There are no venomous snakes on Madagascar. The largest group are harmless snakes from the family Colubridae, the giant hog-nosed snake being the most common. The rest are blind snakes (family Typhlopidae) and boas (family Boidae). Madagascar is also home to a few species of sea turtles and tortoises. The endangered radiated tortoise is one of the rarest animals on earth. The Nile crocodile is also rare on Madagascar.

Birds

Madagascar has a relative paucity of bird species. Only 250 species have been recorded, and they are generally less colorful than those in other tropical areas. Of these, 106 species are endemic, and in fact there are five endemic families: the mesites, ground-rollers, cuckoo-rollers, asities, and vangas. The couas, a subfamily of the cuckoo, are among the most attractive, as are the kingfishers, flycatchers, sunbirds, weavers, lovebirds, and red fody. Of the sixteen species of birds of prey, eleven are endemic, and include kestrels, fish-eagles, and owls. There are nine species of partridges, quails, and grouse. Most of Madagascar's seabirds and wading birds are also found elsewhere in the world.

Invertebrates

A huge variety of invertebrates exist on Madagascar, due to the abundance of different ecological niches. The largest group is the insects, and most are endemic, many even to a particular locality. These include dragonflies and damselflies, grasshoppers, termites, flies, ants, fifty-two species of praying mantis, and over one hundred species of hissing cockroach. The more than eighty species of stick insects are amazing masters of camouflage. There are over one thousand species of true bugs, many strikingly colored. These include stinkbugs, water bugs, cotton-stainer bugs, and assassin bugs. At least twenty thousand species of beetles exist. These are colorful and varied in appearance, with descriptive names such as jewel-beetles, longhorn beetles, tiger beetles, darkling beetles, scarabs, and the bizarre giraffe-necked weevils. Madagascar has hundreds of moth and butterfly species, including many varieties of swallowtails and the attractive pansy butterflies. Hundreds of species of wasps and bees live in Madagascar, and several have bright metallic green coloring. Of the remaining invertebrates, there are many worms, leeches, and flatworms, and a huge variety of endemic land snails. There are about 430 species of spiders, 12 species of scorpions (only two have a painful sting), 64 species of centipedes, and also many millipedes, some reaching giant sizes of six inches or more.

Conservation

Humans arrived on Madagascar about two thousand years ago, and since then wildlife populations have been steadily decreasing due to hunting and habitat destruction. Several large species have already become extinct. The elephant bird, which stood about ten feet tall and weighed about one thousand pounds, died out about five hundred years ago, and its huge eggs are still found. Several species of the lemur, one the size of a gorilla, have also become extinct, as well as the giant tortoise and pigmy hippopotamus. The Malagasy people of Madagascar use the tavy method of slash and burn rice farming, which destroys the forests and erodes the soil. Only about 10 percent of the original forest cover remains. Cattle grazing, the production of charcoal, and the growing human population add to the problem. Many of Madagascar's unique animal species are severely threatened.

There are now a number of national parks and special reserves throughout the island, created to protect ecosystems and their endangered plant and animal species. A program of education to teach the Malagasy about the importance of their environment and wildlife is also under way.

—Barbara C. Beattie

See also: Amphibians; Bats; Bees; Beetles; Butterflies and moths; Centipedes and millipedes; Chameleons; Ecosystems; Endangered species; Fauna: Africa; Fish; Frogs and toads; Habitats and biomes; Insects; Lemurs; Lizards; Mammals; Marine animals; Mollusks; Parrots; Primates; Rain forests; Reptiles; Scorpions; Snails; Snakes; Spiders; Tidepools and beaches; Wasps and hornets; Wildlife management.

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FAUNA: NORTH AMERICA

Types of animal science: Ecology, geography
Fields of study: Conservation biology, ecology, environmental science, wildlife ecology, zoology

North America, stretching from the Arctic Circle in Canada to the tropics of southern Mexico, encompasses every type of climate and habitat, and as a result has a correspondingly diverse animal population.

Principal Terms

GRAZING SPECIES: animals that eat grass; some are wild, but many grazers have also been domesticated
HERBIVORE: an animal that only eats plants
MIGRATORY SPECIES: a species of animal that lives part of the year in one habitat and then moves to another habitat for another part of the year
PREDATOR: an animal that obtains food by hunting other animals

The wildlife of North America can be grouped within two large regions: the Nearctic realm, which covers most of North America from the Arctic to northern Mexico; and the Neotropical realm, which covers southern Mexico and all of Central America. Species in the Nearctic region are similar to those of Eurasia and North Africa, and originally reached North America from Eurasia by passing over the Bering Strait land bridge that once connected Siberia and Alaska, about 60 million years ago. Species in the Neotropical zone are distinctly different from Nearctic wildlife, and reached Central America and Mexico by gradual movement up the isthmus of Panama from South America.

North America's fauna also can be grouped by regions that reflect such climatic influences as latitude, the position of mountain ranges and oceans, and the plants and trees that grow in that area (grasslands, desert, forest, or tundra). Generally, arctic animals are found to the far north, and on the highest slopes of mountains. As one goes farther south, or farther down the sides of mountains, the animals to be found will be those of the forest, grasslands, or desert environments.

Arctic Tundra

Animals of the far north are similar to those found in Eurasia and are well adapted to their cold, treeless environment. Many of these animals evolved from Ice Age species as the glaciers that once covered North America slowly retreated northward. They are large in size and thickly furred, allowing them to maximize conservation of body heat. Large herbivores such as musk oxen and caribou graze on grasses, lichens, and mosses and are, in turn, a food source for polar bears and arctic wolves. Smaller predators such as the arctic white fox feed on arctic hares and small rodents such as voles, lemmings, or the arctic ground squirrels that subsist upon the small shrubs, berries, and grass seeds of the tundra.

Seals and whales proliferate in the Arctic seas. Birdlife in the Arctic tundra is nearly absent in the winter months, with the exception of willow ptarmigans and snowy owls. In the three to four months of summer, several bird species use the region as a breeding ground where young can be hatched and fed with the abundant insect life that emerges during the long and warmer days of summer. Among these migratory species are many varieties of waterfowl, including Canada geese, snow geese, whooping swans, trumpeter swans, phalaropes, plovers, and arctic terns.

Forests

Farther south, below the tree line, coniferous northern forests of fir, spruce, cedar, hemlock, and pine provide shelter and food for the moose, mule

Habitats and Selected Vertebrates of North America

deer, and snowshoe hares that browse on the needles of these trees. Squirrels, chipmunks, and porcupines also thrive in the forests of the far north. Predators of this region include martens, fishers, lynx, wolves, weasels, red foxes, and wolverines. Ponds, rivers, marshes, and swamps are common in this habitat, and provide homes for beavers, muskrats, river otters, mink, and such common fish species as whitefish, perch, pickerel, and pike.

Bird species native to the boreal forest include jays (Canada, blue, and gray), thrushes, finches, nuthatches, loons, osprey, ravens, and crows. A wide variety of songbirds (warblers) and some hummingbirds nest in the boreal woods in the summer months.

The eastern half of North America, from southern Canada to Florida, was once thickly covered by deciduous forests of maple, oak, beech, ash, sycamore, hickory, and other trees that shed their leaves in the winter. Where this forest remains, it provides food for a wide variety of mammals, including black bears, red foxes, raccoons, red and gray squirrels, mink, muskrats, jackrabbits, cottontail rabbits, groundhogs, chipmunks, mice, moles, bobcats, skunks, ermine, opossums, and porcupines. Fish species common to the rivers of eastern and southeastern North America include catfish, suckers, and gar. Several species of salamanders and turtles live in the marshes, streams, and rivers of the deciduous forests, especially in the Appalachians. Waterfowl such as kingfishers, herons, ducks, and grebes also live along the waterways of the hardwood forest region.

Adapting to Extremes

The extremes of climate in North America have caused many animals to adapt in interesting ways. In the far north, animals such as polar bears, musk oxen, and caribou tend to be large in size, so that their external skin area is minimized in relation to their internal portions, allowing the least possible heat loss to the cold air. Many arctic animals have both inner and outer layers of fur, trapping their body heat in the insulating layer. The feet of arctic animals are thickly furred and quite broad, allowing the animals to move over snow without sinking into it.

Animals of the southern deserts have equally effective ways of adapting to the extreme dryness and heat of their environment. They collect and store food when it is abundant after a rare rainfall and then survive long periods of drought on the surplus. They obtain water from the vegetation they eat, rather than from lakes or streams. Many desert animals are pale in color, reflecting back the heat of the sun and blending in with the surrounding landscape. Desert animals are largely nocturnal, moving about only in the cool of the night, after the moist dew falls.

Grasslands

The prairies in the center of North America provide abundant grasses and other herbaceous plants for many small mammals and grazing animals. Jackrabbits, badgers, prairie chickens, and small rodents such as pocket gophers, prairie dogs, and Richardson's ground squirrels, feed on grass and roots, as do such larger herbivores as pronghorn antelope and the American bison. The numerous small rodents and the openness of the grasslands provides optimal habitat conditions for such raptors as owls, hawks, and falcons. Waterfowl nest in the many seasonal watering holes (sloughs) that dot the prairies, although farm drainage and extended periods of drought have greatly reduced this habitat. Seeds and insects are plentiful in the grasslands, supporting such bird species as grouse, quail, partridge, and finches.

Rocky Mountains

The high mountains that run along the western side of North America are inhabited by a number of unique species. Bighorn sheep, Rocky mountain goats, mule deer, and elk graze on the grasses of the foothills and slopes of the mountains. Kodiak bears, grizzly bears, and mountain lions prey upon the grazing animals, and bald and golden eagles subsist upon the ground squirrels, marmots, voles, shrews, and pikas that live in the grasses and scattered forests of the lower mountain slopes. Dipper birds feed from the fast-running mountain streams and are found nowhere else on the continent.

Southwestern Deserts

A large number of animals have adapted to the lack of vegetation and water that exists in much of the southwestern United States and Mexico. Kangaroo rats, pocket mice, jackrabbits, armadillos, peccaries, ring-tailed cats, and ground squirrels all survive in that hostile environment. Predators include bobcats, desert foxes, badgers, and coyotes.

The most prolific forms of wildlife in the arid deserts of southernmost North America are the reptiles, including many different species of lizards, rattlesnakes, toads, and iguanas. Because they can only be active when the outside air temperature provides warmth for basic body functions, reptiles and amphibians are quite rare in the most northern parts of the continent but thrive in the arid and hot southern parts of North America. Roadrunners are a major bird predator of these reptiles, along with eagles and hawks.

Neotropical Forests

The tropical rain forests of Central America and southern Mexico have an astonishing variety of wildlife. The forest canopy has abundant bird life in the form of macaws, parrots, turkey vultures, and flycatchers. Monkeys of many varieties (spider, howler, squirrel, and capuchin) as well as sloths and tamarinds also live in the canopy, feeding on the many fruiting trees. On the floor of the forest, many varieties of ants, spiders, beetles, and chiggers provide food for smaller predators such as anteaters and various species of bats. A number of animals indigenous to South America have adapted to and thrive in Central America, including tapirs, capybaras, pacas, jaguars, ocelots, and agoutis.

Coastal Regions

The beaches, shores, lagoons, and marshes that line the North American continent are home to many kinds of animals that feed upon the ocean life or the intertidal plants and animals that live in the midzone between fresh and salt water. Many different kinds of migratory waterfowl exploit the small crustaceans and mollusks that live at the water's edge, including sandpipers, stilts, curlews, and flamingos. Seals, sea otters, and walruses are found on both coasts in the north of the continent, while Steller's sea lions and California sea lions are found only on the Pacific coast. The lagoons of the southern Atlantic coast and the Gulf of Mexico are home to alligators, pelicans, egrets, and spoonbills.

—Helen Salmon

See also: American pronghorns; Antelope; Armadillos, anteaters, and sloths; Bears; Beavers; Birds; Cats; Cattle, buffalo, and bison; Chaparral; Chickens, turkeys, pheasant, and quail; Cranes; Crocodiles; Deer; Deserts; Dogs, wolves, and coyotes; Donkeys and mules; Ducks; Eagles; Ecosystems; Elephant seals; Elk; Endangered species; Fauna: Arctic; Fauna: Caribbean; Fauna: Central America; Fish; Forests, coniferous; Forests, deciduous; Foxes; Frogs and toads; Geese; Goats; Gophers; Grasslands and prairies; Grizzly bears; Habitats and biomes; Horses and zebras; Lakes and rivers; Lizards; Mammals; Manatees; Marine animals; Moles; Moose; Mountain lions; Mountains; Opossums; Otters; Owls; Parrots; Porcupines; Rabbits, hares, and pikas; Raccoons and related mammals; Rain forests; Reptiles; Salmon and trout; Scorpions; Seals and walruses; Sheep; Shrews; Skunks; Snakes; Squirrels; Swamps and marshes; Tidepools and beaches; Tundra; Turtles and tortoises; Vultures; Weasels and related mammals; Wildlife management; Woodpeckers.

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FAUNA: PACIFIC ISLANDS

Types of animal science: Ecology, geography
Fields of study: Conservation biology, ecology, environmental science, wildlife ecology, zoology

The thousands of islands that dot the Pacific Ocean contain a wide variety of animal species. The restricted conditions of island life result in interesting examples of fauna that have developed in relative isolation, but also increased threat to species that have nowhere to go to escape human encroachment on their habitats.

Principal Terms

ENDEMIC: native to a specific environment and found nowhere else on earth

EXOTICS: nonnative species introduced into an ecosystem

FERAL: an animal, formerly domesticated, which is now living wild

MARSUPIAL: animal with a pouch in which immature young complete their fetal development

The vast region of the Pacific, collectively called Oceania, comprises thousands of islands. Oceania spreads across the Pacific Ocean from 20 degrees north latitude to 50 degrees south latitude and from longitude 125 degrees east to 130 degrees west. The major groupings are Melanesia, Micronesia, Polynesia, and New Zealand. Melanesia ("black islands") is a group of large islands immediately north and east of Australia, from New Guinea to New Caledonia. Micronesia ("little islands") is made up of hundreds of tiny atolls in the western Pacific. Polynesia ("many islands") covers a huge region in the central Pacific. New Zealand lies east and south of Australia. Climates range from tropical to sub-Antarctic, dry to very rainy. Types include volcanic (Fiji, Guam, and Hawaii), tectonic (New Zealand and New Guinea), and low coral atolls (nearly all of Micronesia's islands).

Organisms have a hard time reaching the islands across the broad expanses of the Pacific Ocean. This isolation leads to trends in the number of species found on any given island: Bigger islands have more species; those farthest from continents have fewer species. To reach the islands, animals must fly (birds and bats), float on logs, or be carried in by humans. Birds are usually the first visitors, bringing with them hitchhiking insects. Bats are the only mammals to reach many islands without human help.

Island plants and animals evolve together, affected by difficult conditions; soil is often poor and food limited. Harsh environments and isolation contribute to the formation of new and unique species; some of the strangest creatures on earth are endemic to particular islands. Most of the world's flightless birds developed on islands, where there originally were no large land predators. Island ecosystems are sensitive to disturbances, whether from natural causes such as severe storms, or human activities such as construction, agriculture, logging, and introduced species.

Introduced species (exotics), both accidental and deliberate, are a serious problem. Rats and feral animals can devastate island ecologies. Pigs, cats, rats, and goats are particularly devastating—goats devour vegetation, cats eat birds and small animals, and rats and pigs eat anything.

Exotics also bring diseases to which native animals have no resistance. Humans have tried to deal with exotics, with mixed results. For example, the mongoose was intentionally brought to Fiji to control accidentally introduced rats. No one considered that rats are active at night and mongooses during the day. The mongoose did not control the rats, but they did eat seven native Fijian bird species to extinction.

Another strange example occurred in Hawaii. A Hawaiian bee crawls headfirst into native, barrel-shaped flowers, gathers the nectar, and then backs out. A plant that was introduced by landscapers attracted bees, but the flowers were smaller than the native plants. Once a bee crawled in, it became stuck like a cork in a bottle. There are thousands of these plants, each with hundreds of flowers stoppered with dead bees.

Many tropical and temperate islands have coastal wetlands and mangrove swamps growing at the edge of the sea. Mangroves are low-growing, salt-tolerant trees that form dense tangles that are virtually impenetrable to humans. Wetlands and mangrove swamps are important breeding grounds for many types of fish and crabs, and also trap sediment, stabilize shorelines, and protect coastlines from storms. Humans often fill in the wetlands and cut down the mangroves, causing coastal erosion and the loss of food fish.

Easter Island

Easter Island (Rapa Nui) lies in the South Pacific 2,400 miles (3,862 kilometers) from Chile, South America. It is best known for its huge, mysterious stone statues. Archaeological evidence proves that Easter Island once was densely forested and supported many animal and bird species. The inhabitants burned or cut down the forests before Europeans discovered the island in the eighteenth century. The only plants now living on the island are sparse grasses, a few shrubs, and two species of trees. There are almost no land animals larger than insects. The few thousand people who still live on the island must import nearly all of their food. The devastation of Easter Island is an extreme example of what can happen to island ecologies when human development exceeds natural capacity.

Fiji

The Fiji Islands are mostly volcanic in origin and lie in the South Pacific Ocean about 1,300 miles (2,100 km.) north of Auckland, New Zealand. Some parts of the islands receive up to 13 feet (4 meters) of rain per year, while other parts remain dry. A range of volcanic peaks divides the islands; the highest, Mount Tomanivi (formerly Mount Victoria), is 1,322 meters (4,341 feet). These differences in weather and elevation create a variety of habitats—dense rain forests, grassy savanna, and mangrove swamps—and a large diversity of species.

Human disruption on Fiji has been moderate. About half the total area is still forested, and less than 25 percent of the land is suitable for agriculture. Endemic animals include birds such as lorikeets (parrots that eat flowers or nectar), the Fiji goshawk, spectacularly colored pigeons and parrots, and a pigeon that barks like a dog. The Vanikoro broadbill, which holds its mossy nest together with spider webs, is one of the few native birds that has adapted to forest clearing. It is commonly seen in town gardens and suburbs.

Other creatures native to Fiji are snakes, including a rare, tiny cobra, two species of frog, and several species of geckos and skinks (small lizards). The crested iguana was not discovered until 1978 and lives only on the island of Yaduataba. Yaduataba is now a preserve, and the crested iguana is more likely to survive since feral goats were removed from the island.

There are twelve reserve areas in the Fijian islands, but several are being logged and provide little sanctuary to native plants and animals. The University of the South Pacific is located in Fiji and is a source of serious research into South Pacific species. Tourism is important to Fiji's economy and, with management, could be a source of income to Fijians while still preserving native wildlife.

New Guinea

The world's largest tropical island, New Guinea is located north of Australia and just south of the equator. It is tectonic in origin, with large changes in elevation and many different habitats. Because of its size and varied terrain, New Guinea has a greater variety of habitats than any similar-sized land area in the world. In fact, New Guinea is so rugged that it is one of the least explored or developed places on earth. It provides the best remaining example of the types of organisms that can develop in island isolation.

New Guinea habitats include cold tundra, tropical rain forests, grassy savannas, coastal zones, montane rain forests, cloud forests, and bogs. There are at least twenty thousand species of flowering plants, including more than twenty-five hundred species of orchids, and hundreds of birds and animals. Many New Guinea species are unusual.

Native birds range from the beautiful to the bizarre. There are several species of birds of paradise, some of the most beautiful birds in the world. They have brilliant colors or long, wiry feathers with metallic-looking feather disks that they wave and tremble to attract mates. The bower bird builds large, complicated structures and decorates them with colorful flowers, feathers, or trash, and even uses berry juice as paint. The megapode tunnels into the earth near volcanic hot springs with huge, powerful feet. It lays its eggs in the warm tunnel so that it does not have to sit on them.

New Guinea has several parrots, including the endangered Pesquet's parrot, whose face is completely bald so it can stick its head into fruit without getting sticky feathers. Lorikeets are colorful, nectar-eating parrots. New Guinea is also home to the flightless cassowary, a large bird up to 6.6 feet (2 meters) tall and weighing up to 130 pounds (60 kilograms). Other bird species include feathery crowned pigeons, kingfishers (twenty-two species), ducks, herons, hawks, and egrets.

As in Australia, primates and large mammals never arrived in New Guinea. Marsupials took their ecological places. There are several species of tree-living kangaroos. The basic kangaroo shape is modified in the tree species; they have larger forearms and smaller hind legs. Other marsupials include striped and feather-tailed possums, ringtails, and land wallabies that look like small, dainty kangaroos.

Other odd New Guinea animals are the echidnas, perhaps the most primitive mammal in the world. Echidnas lay eggs and are related to the duck-billed platypus. There are several echidna species; the largest is the giant spiny anteater, which has long spines, dense fur, thick claws, and a long, slender snout. Despite its name, it eats mostly earthworms, which it reels into its mouth using spines on its tongue.

New Guinea has many types of fruit bat. One large species, the flying fox, roosts in colonies. The largest roost is in a tree directly in front of the main police station in the town of Madang. Thousands of bats roosting overhead cause significant problems in street cleaning and for pedestrians without hats.

Reptiles and amphibians on New Guinea consist of snakes, lizards, frogs, and toads. The Salvadori monitor lizard is the longest in the world, growing up to sixteen feet (five meters) long, most of which is tail. Crocodiles live in many rivers and are endangered from hunting and demand for their hides. Some locals have begun crocodile ranches, where they breed and raise the crocodiles for meat and hides without damaging

Biological Mass Murder

The brown tree snake vividly illustrates the dangers of introducing an exotic species to an island ecosystem. The brown tree snake, a native of Australia, was accidentally introduced to Guam after World War II. It reproduced in incredible numbers and reached the highest density of any snake population on Earth, with up to sixteen to twenty thousand snakes per square mile. In the late 1970's, biologists noticed that birds were disappearing from Guam. Of the fourteen bird species endemic to the island, at least nine had become extinct by the 1990's. Many small animal species, as well as chickens raised by the island's inhabitants, also disappeared. The snakes harm humans as well; they bite viciously and cause frequent power outages by climbing on power lines. Millions of dollars have been spent on unsuccessful attempts to control the brown tree snake.

wild populations. Snakes include adders and pythons (eight species), and the deadly taipan and Papuan black snakes. There are many species of frogs, including several odd rain forest species that no longer have a tadpole stage.

New Guinea's insects include the largest moth in the world and the largest butterfly, the Queen Alexandra's birdwing. This species is endangered due to collecting and loss of habitat, but some New Guineans run butterfly ranches. They raise the insects, sell them to collectors and museums, and still preserve the species. There are also giant millipedes, stick insects twelve inches (thirty centimeters) long, and a fly with its eyes on stalks. Several species of flies have antlers on their heads, which they use to fight in defense of egg-laying territory.

Many forests host "ant-plants," warty looking epiphytes that have hollow mazes inside their tissues. Ants live in the maze, safe from predators. The ants provide nutrition for the plant in the form of droppings, scraps of food, and dead ants.

Even though New Guinea is rugged and isolated, human impact is increasing. It has proven difficult to develop New Guinea economically without destroying the unique life of the island. It is hoped that lessons learned on other islands, such as Guam and New Zealand, may be applied to New Guinea. The government has tried incentives to keep wild areas wild, such as encouraging ecologically friendly businesses like crocodile and butterfly farms and ecotourism. The National Park reserve that includes Mount Jaya is the only place in the world where it is possible to visit a glacier and a coral reef in the same park.

New Zealand

Located off the eastern edge of Australia, New Zealand has a fairly moderate climate that comes from conflicting warm, humid Pacific and colder Antarctic weather. It is similar to New Guinea, with rugged terrain, high mountains, and habitats from grassy open plains to dense forests, wet areas to near-deserts. Unlike New Guinea, however, New Zealand has been occupied and developed by humans for hundreds of years. Before large-scale agriculture, about half of New Zealand was covered with forests and one-third with grassland communities. Now, half is pasture for grazing and a quarter is forest, mostly introduced species. Much of the remaining native forest is maintained as national parks and reserves. Pasture land usually consists of a single species of grass and does not support the wide variety of bird and animal life of the original grassland communities.

It is sometimes said that the dominant mammal in New Zealand is the sheep. Sheep are vital to the economy but have caused problems for native animals; more than six hundred native species are threatened and several are extinct, including 43 percent of New Zealand's frogs and more than 40 percent of its native birds.

Like New Guinea and Australia, New Zealand did not originally have any large mammals or carnivores. Fourteen flightless or weak-flying birds developed there. The native Maori people hunted the large, flightless moa to extinction before the Europeans arrived, one of the rare instances in recent history when humans not from a Western culture were responsible for a species' extinction.

Flightless birds that still survive in New Zealand are the kiwi and the kakapo parrot. The introduction of cats, dogs, rats, and pigs has severely endangered both species, and at the end of the twentieth century, there were fewer than seventy kakapo left. All had been moved to predator-free, offshore islands. The kiwi is New Zealand's state bird, and efforts are being made to save it as well. Two species of another flightless bird, the penguin, breed on the south and east coasts. There are more than two hundred species of flying birds, at least forty of them introduced, including tropic birds, gulls, hawks, harriers, skuas, spoonbills, and pheasant.

The only original endemic mammals were two species of bats. In the last two hundred years, many exotic marsupials and mammals have appeared, including rabbits, rats, mice, weasels, otters, cats, pigs, cattle, deer, goats, and sheep. Domestic cattle, sheep, and pigs are economically important.

Amphibians and reptiles are interesting but not numerous. Among them is a frog that retains its tail as an adult and one that bypasses the tadpole stage. Some frog species have been introduced but have had little impact. Reptiles include geckos, skinks, and the extremely primitive, lizardlike tuatara.

Invertebrate species include such oddities as a giant carnivorous land snail. There are more than four thousand species of beetles, two thousand species of flies, and fifteen hundred species of butterflies and moths. In a reversal of the usual ecological concerns, some native insects are destroying introduced pasture grasses.

Micronesia

The Federated States of Micronesia consists mainly of small atolls. Coral atolls are found only in tropical latitudes because coral (small, colonial animals) grows only in warm water. Coral reefs support a tremendous variety of fish, crabs, and mollusks. Atolls tend to have porous, infertile soil and to be very low in elevation; the inhabited state of Tokelau, comprising three small islands, has a maximum elevation of sixteen feet (five meters). Fauna usually consists of lizards, rodents, crabs, and other small creatures. Pigs, ducks, and chickens are raised for food, and dogs and cats are kept as pets.

Human disturbances on coral atolls often have been particularly violent; several nuclear test bombs were exploded on Bikini Atoll and other islands in the 1940's and 1950's. Kwajalein, the largest atoll in the world, is used by the U.S. military for intercontinental ballistic missile target practice. Johnston Atoll, about 820 miles (1,320 km.) southwest of Honolulu, Hawaii, is a U.S. military base and storage facility for radioactive and toxic substances. It is also designated as a protected area and bird-breeding ground.

The Prospect for Island Ecologies

Island ecologies are unique and fragile. Some, like those in Guam and New Zealand, can never be returned to their original state, but with extensive wildlife management, many native species can be saved from extinction. Ironically, people in the developed world who visit zoos see more native Pacific island species than those who live on those islands. Some endemic species have been wiped out or had their habitat destroyed, so zoos are the last refuge for many creatures.

New Guinea, Fiji, and many smaller islands are in earlier stages of modern development and wildlife destruction can still be controlled. Conservationists sometimes do not realize that islands are not small, geographical zoos; people live there and want to improve their lives. Development cannot be stopped, but it can be managed so that the humans can improve their standard of living as they wish, and the original, amazing island dwellers can still survive.

—*Kelly Howard*

See also: Amphibians; Bats; Birds; Butterflies and moths; Centipedes and millipedes; Coral; Crocodiles; Ecosystems; Endangered species; Fauna: Asia; Fauna: Australia; Fish; Flies; Frogs and toads; Grasslands and prairies; Habitats and biomes; Insects; Lizards; Marine animals; Marsupials; Mollusks; Mountains; Ostriches and related birds; Parrots; Penguins; Rain forests; Reefs; Snails; Snakes; Swamps and marshes; Tidepools and beaches; Wildlife management.

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FAUNA: SOUTH AMERICA

Types of animal science: Ecology, geography
Fields of study: Conservation biology, ecology, environmental science, wildlife ecology, zoology

South America, stretching from the tropics of southern Mexico and Central America to the Antarctic, encompasses every type of climate and habitat, and as a result has a correspondingly diverse animal population.

Principal Terms

GRAZER: an animal that eats grass; some are wild, but many grazers have also been domesticated

HERBIVORE: an animal that only eats plants

NOCTURNAL: active at night and dormant or asleep during the day

PREDATOR: an animal that obtains food by hunting other animals

A wide range of animals, both ordinary and exotic, inhabit the continent of South America. The types of animals found in any geographical area are determined by the climate and the terrain. In the Andes, animals such as the llama have adapted to the terrain and climate of the high, steep mountains. North of Antarctica, in the archipelago known as Tierra del Fuego, there are many penguins, whose layers of feathers help them to survive the frigid sea waters in that area.

Camelids of the Andes

Four members of the camel family live in the Andes Mountains of Peru, Bolivia, Ecuador, and Chile: alpacas, vicuñas, guanacos, and llamas. These camelids all have commercial value in the Andes, as pack animals and for their meat and fur. Many people of the Andes also raise sheep on the mountains for both wool and meat.

More than four thousand years ago, alpacas, which are raised for meat and for their fine cashmere fur, were reserved for the exclusive use of the Incas, who prized their coats. Alpacas live from fifteen to twenty-five years. The average adult is about three feet (one meter) high at the shoulder and weighs up to 180 pounds. In 1999, there were approximately three million alpacas in South America, mostly in Bolivia, Chile, and Peru.

Closely related to the alpaca is the llama, domesticated as a work animal more than three thousand years ago. Llamas, used primarily in Peru and Bolivia, have historically been the beasts of burden in the Andes Mountains. A single animal can carry about two hundred pounds (ninety kilograms) for twelve hours a day. However, they cannot be ridden, and when they tire, they often simply lie down and refuse to move. They even spit at their drivers when they no longer want to work. Reaching heights of nearly 4.5 feet (1.5 meters) llamas are generally larger than alpacas. A llama's fur is usually white with black and brown, but some are pure white and others pure black. Although llamas are used for work, they are also kept as pets in many homes of South America.

Vicuña fur has historical importance in South America. It was used by Incas to make cloth, and only members of Inca royalty could wear clothing made from this cloth. Anyone else found with such clothing was executed. By 1979, only four thousand vicuñas were left in South America. They had been hunted for their fleeces by poachers who killed the animals. Representatives of the governments of Bolivia, Chile, Ecuador, and Peru signed a treaty for protection of the vicuña. Twenty years later, there had been a resurgence of vicuñas in Peru, Chile, and Argentina: in 1999, there were 103,000 in Peru, 30,000 in Argentina, 16,000 in Chile, and a small transplanted herd in Ecuador. Even though *el chacu*, the communal hunting of vicuña, continued after 1979, laws lim-

Habitats and Selected Vertebrates of South America

ited these hunts to local people. Those local hunters sold the fiber from the animals as an important source of income for their families.

Vicuñas weigh ninety pounds and are a little less than three feet (one meter) in height at the shoulder. They have long necks, slender legs, padded cloven feet, large round eyes, and a fine, dense, tawny coat. Aside from their economic value, the vicuña is valuable for scientific study. They are highly communicative animals, signaling each other with body postures and ear and tail positions. They emit soft humming sounds as symbols of bonding and greeting.

The fourth member of the camel family found in South America is the guanaco. The guanaco is more adaptable than the other three camelids. It is found throughout the Andes, in the dry Atacama Desert of Chile, and in Tierra del Fuego, where it rains year-round. This animal, from which the llama was domesticated, began life in the semiarid desert and has developed physiological mechanisms for coping with both heat and dehydration. It is similar in structure to the other camelids, but is the largest member of the camel family living in South America.

Other Andean Mammals

Throughout the Andes, from Argentina to Colombia, and on into Central America, pumas roam. This reddish brown feline can reach lengths of about 6.5 feet (2 meters), not including its long tail. In some areas of South America, the puma is endangered. It is a carnivore whose natural prey are elk, deer, and small wild animals; however, it also eats sheep and cattle. Thus, ranchers have retaliated by killing the predators. Another member of the cat family is the elusive Andean mountain cat. Rarely sighted by humans, it is the least-known New World cat. The Andean wild cat is considered sacred by the native people of the *altiplano* of Bolivia, the Aymara.

In the forests of the Andes lives the spectacled bear. Its range extends as far north as Ecuador. This bear, which is endangered because of overhunting and destruction of its environment, has a shaggy brown coat with yellow facial markings and a cream-colored muzzle, throat, and chest.

Several rodents are native to the Andes. Chinchillas were found living in crevices in the mountains when early Spanish explorers first arrived there. Living off berries and fruits in Peru, Chile, and Argentina, these rodents belonged to Inca royalty, who used their fur to make chinchilla stoles. In the latter part of the twentieth century, they were nearly extinct in the wild but existed in captivity. Related to the chinchilla is the viscacha, which is prey for such animals as the Andean mountain cat. Mountain viscachas have long, rabbitlike ears, and long, squirrel-like tails. East of the mountains lives the plains viscacha, which has shorter ears and a blunter head. The cavy, the South American guinea pig, lives in the crevices of the Andes.

Andean Birds

Various exotic birds also live in the Andes, many of which also are found in the Amazon Basin to the east. Among these birds are the Andean cock-of-the-rock, the scarlet macaw, the quetzal, the Andean condor, and the James flamingo. The cock-of-the-rock is a huge dancing bird found in the mountain forests. The scarlet macaw, a brilliantly plumed member of the parrot family, is an endangered species. The quetzal had religious significance to early Andeans; even at the beginning of the twentieth-first century, it is regarded as a symbol of the Andes Mountains. The Andean condor is found in the high plains area of Bolivia and Chile. With a wingspan of twelve feet (four meters), it is the largest flying bird in the world. It can soar to a distance of 26,000 feet (7,925 meters) above sea level.

In the southern Andes lives the rhea, a flightless bird related to the ostrich, which often is called the South American ostrich. The rhea is much smaller than an ostrich and has three toes on each foot, whereas an ostrich has two toes on each. Rheas live in flocks of twenty to thirty in Brazil's southern plains and in Argentina, Paraguay, and Uruguay.

Animals of the Amazon Basin

Representatives of almost one-fourth of all known varieties of animals live in South America, mostly in the Amazon Basin. The basin includes the rain forests, plateaus, rivers, and swamps southeast of the Andes Mountains.

The tapir, found in the Andes and in the forests east of the Andes, is South America's largest animal. With its short, hairy body, it resembles a pig, but is actually related to the horse and the rhinoceros. The number of tapirs in South America lessened over the twentieth century because they were hunted for their flesh and their thick hides, and also because the cutting of forest has reduced the land available for their habitat.

The tapir's natural enemy, the jaguar, also is found in the eastern Andes and in the forests east of the high mountains. This feline, which was worshiped by pre-Columbian civilizations as a god, lives in the area between the southern United States and northern Argentina and is especially prevalent in Brazil. Strong swimmers, jaguars like to live near rivers and other streams. At the end of the twentieth century, they were on the list of threatened animals in South America. They were threatened because farmers were farming lands that previously were their natural habitat, and also because farmers, claiming that the cats killed their cattle and sheep, were killing the jaguars.

Several types of foxes are indigenous to the Amazon Basin and roam through lower mountain areas to the east and the west of the Amazon. Among them are the gray fox and the crab-eating zorro. The gray fox roams over the plains, the Pampas, the desert, and the low mountains, but its number is decreasing because farmers are cultivating lands that previously were its habitat. In Argentina, where it has been hunted for its skin, the gray fox has been placed on the endangered species list. In Chile it is protected by law, but enforcement of the law has been lax. The crab-eating zorro is found in Colombia, Venezuela, Suriname, eastern Peru, Bolivia, Paraguay, Uruguay, Brazil, and northern Argentina. An omnivore, it eats not only crabs but also insects, rodents, fruit, reptiles, and birds.

Also living within the Amazon Basin are the giant anteater, the sloth, and the peba. The giant anteater has value to the environment and to farmers because it consumes up to thirty thousand insects per day. The peba, a nine-banded armadillo found widely throughout South America, also contributes to agriculture by consuming insects and worms. This nocturnal animal is protected from its predators by a horn and bony plates covering its body. The sloth is the world's slowest-moving large mammal.

Within the Amazon Basin lives one of the world's most interesting rodents, the huge capybara. It generally is as large as a big dog, but can reach 4 feet (1.2 meters) in length and can weigh as much as one hundred pounds (forty-five kilograms). Humans have little to fear from the amphibious capybara, however, since it is a vegetarian.

The coatimundi inhabits areas from Arizona to northern Argentina. A member of the raccoon family, it is brown or rust-colored. It eats snails, fish, berries, insects, spiders, lizards, birds, eggs, and mice, and is often kept as a pet by South Americans.

The rain forest is also inhabited by many bats, squirrels, and parrots, which eat the fruits and nuts of the upper and lower canopies. In the lower canopy live lemurs, flying squirrels, and marmosets, small monkeys found mostly in eastern Brazil. These animals use their sweat glands for communication. Animals of the lower canopy eat the fruits, nuts, and insects that are found there. Within the rain forests also live vampire bats; these fascinating animals have to have two tablespoons of blood per day in order to survive.

Other residents of the Amazon Basin include the yapok, a member of the opossum family that has webbed feet for swamp travel; the sapajou monkey, a small New World primate; and the octodont, an eight-toothed rodent also known as a spiny rat or a spiny hedgehog because of the sharp spines embedded in its fur.

Birds and Reptiles of the Amazon

Many types of birds live in the Amazon Basin, some deep within the rain forest, others closer to the mountains. Among the birds in the basin are hummingbirds, parrots, ospreys, macaws, boat-billed herons, great egrets, white-necked herons, least bitterns, and blue and yellow macaws. Tou-

The Anaconda

Another name for the anaconda is the water boa, an appropriate name for a snake that is almost always found near water. Anacondas live in the Amazon and Orinoco basins of tropical South America, and their habitat extends to Trinidad. Like the crocodile, the anaconda has nostrils high on its snout so that it can swim with its head above water to breathe. The anaconda lies near the shore, waiting for its prey. When a deer, bird, or other prey comes to the water to drink, the anaconda quickly strikes, dragging its victim underwater to drown it. The anaconda then eats the unfortunate animal whole. A good meal can last an anaconda for several weeks, during which it will lie in the water, digesting its food.

cans, which also live at high elevations up to 10,000 feet (3,050 meters), can be found deep within the Amazon rain forest.

Both the land iguana and the lava lizard live in the Amazon Basin. Land iguanas can live up to twenty-five years and weigh up to 15 pounds (6.8 kilograms). They eat low-growing plants, shrubs, fallen fruits, and cactus tree pads. The lava lizard, about 1 foot (30.5 centimeters) long, is smaller than the land iguana. Lava lizards are beneficial to agriculture because they eat beetles, spiders, and ants.

The boa constrictor also lives in the jungles of this basin. This snake, which is usually six to nine feet (two to three meters) in length, but can reach thirteen feet (four meters), kills its prey by squeezing it to death, using its body coils to suffocate its victims. After killing its meal, the boa constrictor stretches its jaws wide apart and pulls the entire victim into its mouth. Using this method of killing, a boa is able to eat animals that are much larger than its head.

Another large snake native to the Amazon Basin is the anaconda. Most anacondas weigh several hundred pounds (100 kilograms) but can reach weights of 550 pounds (250 kilograms) and can reach thirty-six feet (eleven meters) in length. The anaconda is found in the Guyanas and throughout tropical South America, east of the Andes. With eyes high on its head, the anaconda can submerge its body in water and watch for the approach of unsuspecting prey.

River Animals

Many animals spend all or part of their lives within the Amazon. The black caiman, an alligator that is nearly extinct, is one such animal. It can weigh as much as a ton. It will eat all vertebrates, including humans, if that is the only food available.

The semiaquatic brown water lizard also is found in the jungle area around the Amazon. Within the Amazon are manatees as well as Boto River dolphins, also known as an Amazon River dolphin. This endangered animal is the only dolphin to have a neck. Giant otters live in the waters of the Amazon as do many types of fish, including piranhas, which, with their sharp teeth, can quickly strip the flesh from their prey.

Animals of the Eastern Highlands

The Eastern Highlands of South America host many unique animals, including the bush dog, woolly tree porcupine, maned wolf, peccary, bushmaster, and coypu rat, and many birds such as flamingos.

The bush dog is a wild dog, but, with its webbed feet, it resembles an otter more than a dog. Bush dogs live in packs and hunt small deer and rodents. Bush dogs can be found from the rain forests into the grasslands, in Colombia, Venezuela, the Guyanas, Brazil, Paraguay, northeastern Argentina, eastern Bolivia, and eastern Peru.

The maned wolf is one of South America's most beautiful and revered animals. Weighing on average one hundred pounds (forty-five kilograms), it is South America's largest canid. It is found mostly in Argentina and Brazil and has no natural enemies. An omnivore, it will eat nearly anything, including fruits, insects, and small vertebrates. At the end of the twentieth century, the Smithsonian Institution estimated that fewer than ten thousand maned wolves existed in the wild, living mostly in Argentina and Brazil. Because of its beautiful red and gold fur, the maned wolf is a tourist attraction. Many South Americans regard it as an important part of their cultural heritage. The rural people of the Sierra de Canastra of Brazil believe that the maned wolf has medicinal and supernatural powers.

The peccary and the bushmaster are also found in the Eastern Highlands. The peccary resembles the tapir, but is much smaller. It has a big head, sharp teeth, and prickly fur. It eats smaller animals and plants such as cactus flowers. The bushmaster, the largest poisonous snake in the Americas, is a type of pit viper related to the rattlesnake. Like the rattlesnake, it shakes its tail before striking, but it has no rattles. Gray and brown with a diamond pattern, it averages 8 to 12 feet (2.5 to 5.5 meters) in length.

The coypu rat is also known as a swamp beaver. This relative of the muskrat is found in southern Brazil, Bolivia, and Colombia. The agouti, a rodent nearly two feet (sixty centimeters) long,

Baron Alexander von Humboldt

Born: September 14, 1769; Berlin, Germany
Died: May 6, 1859; Berlin, Germany
Fields of study: Environmental science, wildlife ecology, zoology
Contribution: Von Humboldt was a great German naturalist and explorer who founded the field of physical geography. He also studied the relationship between regional geography and its flora and fauna.

Alexander von Humboldt was born in Berlin, Germany, the son of an army officer. After his father's death in 1779, his mother raised him in the family castle at Potsdam. Von Humboldt was privately tutored to prepare him for a life in public service. He began studying economics at the University of Frankfurt, then switched to engineering. At that time, von Humboldt became interested in botany.

Study at the University of Göttingen turned von Humboldt's interest to geology, and he studied at the Frieberg School of Mines for two years. This led to an appointment to the Prussian Department of Mining. In this position, he reorganized numerous mines and supervised mining activities. In 1797, von Humboldt resigned this post to study meteorology and geomagnetism. He obtained permission from Spain to visit its Central and South American colonies.

In 1799, his self-financed expedition set off in a small ship, the *Pizarro*. He was accompanied by botanist Aimé Bonpland. Over the next five years, the expedition thoroughly explored Central and South America. First, it proved that the Casiquiare River connected the Amazon and Orinoco rivers. Next came exploration of the Andes, including von Humboldt's climb to near the top of Mount Chimborazo, a world record that stood for many years.

In 1803, the *Pizarro* sailed to Mexico for a study of that country. Then it returned to France with a huge collection of plants and data on physical geography. From 1804 to 1827, von Humboldt processed the data. In Paris, he published thirty volumes of findings. Meteorological data included weather maps which helped to found comparative climatology, studies of the relationship between regional geography and its flora and fauna, and proof that the earth's surface was not formed by sedimentation from the liquid state.

In 1827, von Humboldt returned to Berlin and the royal court, where he tutored the crown prince, was on the privy council, and was court chamberlain. In 1829, he was invited to Russia to examine gold mines and advise on mining techniques. This experience produced important geographical, geological, and meteorological observations on Central Asia. Von Humboldt, also hugely interested in fluctuations of Earth's geomagnetic field (magnetic storms), saw that a world net of observatories was needed to identify their origin. In 1836, he convinced the British Royal Society to establish such stations. Data obtained proved that the storms were due to sunspot activity.

Amid these other activities, over twenty-five years von Humboldt wrote four volumes of *Kosmos*, a work which gave a clear account of the structure of the known universe. A great success, it was translated into every European language. At age eighty-nine, while working on the fifth volume, von Humboldt died in Berlin.

—Sanford S. Singer

also lives in the Eastern Highlands. Farmers detest the agouti because it eats sugar and banana plants. A cousin of the jaguar, the ocelot, also makes its home in this area. This slender cat is camouflaged in the forests and deserts of the highlands.

Birds that live in the Eastern Highlands include the James flamingo, which lives on Bolivia's frigid salt lakes, and the giant antshrike, more than a foot (30 centimeters) in length.

Animals of Tierra del Fuego

In the islands that make up Tierra del Fuego, many unusual animals are found, including penguins and many other types of birds. Penguins cannot fly; they use their wings for swimming in the icy waters near their home. Penguins are insulated from the frigid ocean waters by three layers of short feathers and an underlying layer of fat. Other birds common to Tierra del Fuego are Magellanic cormorants, imperial cormorants, albatrosses, and various petrels. Sea lions also live on these islands.

—Annita Marie Ward

See also: Armadillos, anteaters, and sloths; Bats; Bears; Birds; Camels; Cats; Crocodiles; Deer; Deserts; Dogs, wolves, and coyotes; Dolphins, porpoises, and toothed whales; Donkeys and mules; Ecosystems; Endangered species; Fauna: Antarctica; Fauna: Caribbean; Fauna: Central America; Fish; Flamingos; Foxes; Frogs and toads; Habitats and biomes; Jaguars; Lakes and rivers; Lizards; Mammals; Manatees; Marine animals; Marsupials; Monkeys; Mountains; Opossums; Ostriches and related birds; Parrots; Penguins; Porcupines; Raccoons and related mammals; Rain forests; Reptiles; Rodents; Shrews; Snakes; Tidepools and beaches; Wildlife management.

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FEATHERS

Types of animal science: Anatomy, evolution
Fields of study: Anatomy, archaeology, ornithology

Feathers are a unique physical characteristic of birds. There are many types of feathers serving a variety of purposes, including flight, insulation, communication, breeding, and camouflage.

Principal Terms

KERATIN: fibrous proteins that are the chemical basis for feathers
MOLT: the process of replacing feathers
PIGMENTS: a variety of colored substances which impart color to feathers
SHAFT: long, central spine of the feather
VANE: flat, broad web emerging from opposing sides of the feather shaft

In 1860, a quarryman from southern Germany discovered a fossil preserved in limestone revealing a single, 2.5-inch-long feather. This feather was asymmetric, with the vane on one side of the quill being twice the width of the vane on the other side, and similar to the flight feathers of modern birds. A year later, a fossil was discovered in a nearby quarry which demonstrated a feathered creature named *Archaeopteryx*, which means "ancient wing." *Archaeopteryx* is generally regarded as the first bird because of its feathers, and it flew 150 million years ago.

Structure and Color of Feathers

Feathers continue to define birds. They are the only animals that have feathers, and all birds have some type of feathers. Feathers result from a modification of the outer layer of the bird's skin, the epidermis, and probably evolved from scales as found on reptiles, such as snakes and lizards. Feathers are composed largely of keratin, an inert substance that is light, strong, and long-lasting. The developing bird inside the egg is covered with bumps called papillae, and the epidermis folds inward around each of the papillae to form follicles. From these structures feathers are grown and regrown. The number of feathers on birds varies greatly, from less than 1,000 on a ruby-throated hummingbird to over 25,000 on a tundra swan.

A typical feather has a central shaft with two vanes arising from opposite sides. On flight feathers, the vane from the leading edge of the feather is narrower and more rigid, thereby maintaining the wing structure and producing the lift necessary for flight. Amazingly, this basic feather structure has remained unchanged since *Archaeopteryx* flew above the dinosaurs of the late Jurassic period. The portion of the feather shaft within the follicle and beneath the skin is called the calamus. The portion of the shaft above the skin is called the rachis, from which extend numerous opposing parallel branches, called barbs, that collectively form the vanes. Hooked structures called barbules join the barbs together, producing a smooth, sheetlike surface.

Color is imparted to feathers by colored substances called pigments and by variations in feather structure, which alter the manner in which light is reflected. There are three types of pigments. The most common pigment is melanin, which produces black, a spectrum of brownish shades, and light yellow. Examples include the black of a crow or yellow of a baby chicken. Birds synthesize melanin from dietary proteins. Carotenoids are produced by plants and are ingested by birds. They produce red, orange, and yellow feathers, such as the red of the northern cardinal. Porphyrins are metabolic breakdown products produced by birds from hemoglobin, the oxygen-carrying component of red blood cells, when red blood cells become old and are broken down by the liver. Porphyrins produce a variety of colors, including red, brown, green, or pink. Porphyrins produce the brown feathers of many owls. Structural properties of the feathers, such as layers, often containing pigments, and microscopic air bubbles, produce iridescent colors, such as the colored throats of hummingbirds, or noniridescent colors, such as the blue of a bluejay. Often the multiple colors of a bird's feathers result from some combination of both pigment and structure.

Image Not Available

Functions of Feathers and Molting

While flight is certainly the most outstanding function of feathers, they serve many important functions, enabling birds to exist and thrive in environments all over the globe. Feathers provide insulation by trapping air and thereby helping to control body temperature. The color and form of feathers help birds communicate and signal breeding, as well as keep them camouflaged from predators. Adults sitting on a nest or fledgling birds often depend greatly on their feather coats to make them less visible against the background of the environment. Feathers also help birds remain waterproof while swimming or diving. Some feathers help birds remain clean, and others help the birds to support themselves, as can be seen when the stiff tail feathers of a woodpecker act as a strut against the trunk of a tree. Specially modified feathers serve as sense organs able to detect feather position and movement essential for the complexities of flying.

A fully developed feather is a dead structure and when it becomes worn or broken it must be replaced, as repair is not possible. Molting is the process of replacing all (complete molt) or a portion (partial molt) of the feather coat. This process varies widely among birds in timing as well as completeness and annual number. However, most adult birds undergo a partial molt prior to breeding season. This partial molt frequently yields bright colorful feathers and is called the alternate plumage. A good example is the bright yellow and black of the American goldfinch, seen in the spring. A complete molt occurs after the breeding season and results in the basic plumage. The basic plumage of the American goldfinch is a drab olive. This complete molt provides some migrating birds with new feathers for the long flights to their home territories. Other birds get new feathers to help insulate them from the winter cold.

The beauty of feathers and the wonder of flight have attracted the attention of humans throughout history. Feathers have adorned priests and warriors as well as the hats of fashionable women. In 1905, Guy Bradley, a warden hired to patrol wading-bird rookeries in southern Florida, was shot and killed by plume hunters. He is buried in Everglades National Park and his death resulted, in 1913, in stricter laws to protect birds in the United States and a change in public opinion that abolished the use of feathers in hats sold in America. It is currently illegal to possess wild bird feathers in the United States.

—H. Bradford Hawley

See also: *Archaeopteryx*; Birds; Evolution: Animal life; Flight; Fur and hair; Insects; Locomotion; Molting and shedding; Scales; Velociraptors; Wings.

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FERTILIZATION

Types of animal science: Development, reproduction
Fields of study: Cell biology, developmental biology, embryology, reproduction science

Fertilization occurs when the genetic information in a haploid sperm combines with the genetic information of the haploid ovum to form the diploid zygote.

Principal Terms

CORONA RADIATA: the layers of follicle cells that still surround the mammalian egg after ovulation
VITELLINE ENVELOPE: the protective layers that form around the egg while it is still in the ovary
ZONA PELLUCIDA: mammalian protective layer analogous to the vitelline envelope

For fertilization to occur, several things must happen: Sperm and eggs must be in close proximity, the gametes need to be compatible, the sperm must be able to penetrate the egg, and the haploid egg nucleus must combine with the haploid sperm nucleus. If any one of these is missing, fertilization will not occur.

Assuring Eggs and Sperm Are in Proximity

Animals have many mechanisms to ensure that sperm and eggs are in close proximity. This can be a major concern for aquatic organisms with external fertilization, and many release gametes in the millions or even billions to assure that at least some sperm reach the appropriate eggs. To increase the chances of a meeting between same-species gametes, animals often have specialized mating behaviors. Corals are among those animals that release their gametes into the water and depend on currents to bring egg and sperm together. This is not, however, as random as it may seem. As the first coral releases its gametes, it also releases hormones that induce nearby corals of the same species to release their gametes. These also release the same chemicals with their gametes, and soon there are clouds of eggs and sperm, and the chances of a proper meeting are increased dramatically. One species of polychaete annelid, *Eunice viridis*, or the palolo worm, has another method of assuring male and female gametes are in the same place. In this species, sexually mature worms called epitokes swarm together at the ocean's surface in response to the lunar cycle. Females then secrete a hormone that induces males to release sperm, and the sperm induce the females to shed eggs. Many fish go through elaborate courtship rituals, during which males and females release gametes at a specific point, thus assuring that egg and sperm are together. Other fish build nests where females lay eggs and males deposit sperm. Frogs and toads usually breed in the water, but the female will only release her eggs when the male is clasped to her back in amplexus. Thus, sperm are deposited on the eggs as they are being laid.

Males of other species place sperm directly in the female's reproductive tract. The male octopus has a special tentacle that is used to place one of his sperm packets in the mantle cavity of the female. Some salamander males deposit their sperm packets on the substrate during a squat dance courtship ritual. Females also do the squat dance and pick up the packet with the lips of their cloacae. In some species of water mites, females mount a special saddle-shaped extension of the males' abdomen. The male squats to deposit a sperm packet, moves ahead slightly and then squats again when the opening of the female's reproductive system is over the packet, forcing the packet into her reproductive system. Another interesting way to assure fertilization is seen in the sea horse. In these animals, a female deposits her eggs into a pouch on the male's abdomen and the male releases sperm into the pouch at the same time. The most common way to introduce sperm into a female's reproductive tract is through copulation, where the male ejaculates sperm directly into the female's reproductive tract. The motile sperm then travel to the egg. For a sperm to gain full motility, it usually must undergo a little-understood process called capacitation.

Penetration

Once eggs and sperm are in close proximity, the sperm must begin to penetrate the egg's protective layers. All eggs have at least one protective layer outside the cell membrane. Called the vitelline envelope in most organisms, it is synthesized in the ovary and composed primarily of polysaccharides and glycoproteins. The oviducts and uterus often secrete other protective layers around the egg. In some instances, the sperm must also penetrate these layers, for example, the jelly layers that surround sea urchin and frog eggs. In other instances, the egg is fertilized before these layers are added, as is the case with the many protective layers that surround bird and reptile eggs. A protective layer made up of cells is seen in most mammals, since the egg is released by the ovary with cells of the cumulus oophorus still attached. For the sperm to penetrate these layers, its acrosome must contain the appropriate enzymes to lyse (disintegrate) the chemicals that block its way. The acrosomal reaction must also take place in order to expose the digestive enzymes of the acrosome. This reaction depends on changes in membrane permeability to ions and subsequent changes in pH.

Once through the protective layers, the sperm makes contact with the egg's plasma membrane. If the sperm and egg are of the same species, sperm receptor molecules on the egg membrane attach to complementary molecules, called bindins, on the sperm membrane and the two membranes fuse. If the bindins on the sperm do not complement the receptors on the egg, there is no fusion and fertilization does not continue, thus preventing most interspecies crosses. However, closely related species often have bindins and receptors sufficiently alike to allow some fertilization to proceed. The products of these interspecific matings are hybrids, such as the mule.

Once the first sperm fuses with the egg, mechanisms to prevent polyspermy, the fertilization of an egg by more than one sperm, are put into place. The first block to polyspermy is common to most animals studied: a very quick and only temporary depolarization of the plasma membrane. In sea urchins, the resting membrane potential of the egg plasma membrane is approximately –70 millivolts, the inside being more negative than the outside. Fusion of the sperm plasma membrane with the egg cell membrane causes a rapid influx of sodium ions. The positive charges neutralize negative charges in the egg until the membrane potential is raised to +10 millivolts. All this happens in less than five seconds, and lasts for about one minute before the egg cell has actively transported enough sodium out of the cell to repolarize it. While the cell is depolarized, no further sperm membranes can fuse with the egg membrane. This is often referred to as the fast or temporary block to polyspermy and seems to occur in all animals thus far studied. The fast block also sets into motion the slow or permanent block to polyspermy. The changed membrane potential of the fast block and the release of nitrous oxide by the sperm allows cells to release calcium ions from storage. The initial calcium ion release causes the egg to release nitrous oxide, which then increases the egg's release of calcium ions. The release of calcium ions induces the cortical reaction by which cortical granules move to the surface of the cell, fuse with the cell membrane, and empty their contents into the space between the cell membrane and the vitelline envelope. In sea urchins, the first acrosomal enzymes released break the bonds between the cell membrane and the vitelline envelope. In the presence of water, other chemicals released by the cortical granules swell, lifting the vitelline envelope away from the cell membrane. Finally, other enzymes released by the cortical granules alter the vitelline envelope, knocking off any attached sperm and causing the release of peroxide ions, which harden the envelope, making it impermeable to sperm. This impermeable barrier is renamed the fertilization membrane. The released peroxide may also provide another benefit. Any sperm that had penetrated the vitelline envelope before it hardened would be killed by the peroxide and would thus not lead to polyspermy. In other animals studied, although cortical granules do empty their contents into the perivitelline space, the permanent block to polyspermy does not seem to involve the same extensive changes to the vitelline envelope (or *zona pellucida* in mammals) that are seen in the sea urchin. In large, yolky eggs, some polyspermy does occur, but the extra sperm remain in the yolk and never reach the egg nucleus for fusion.

Cell Metabolism and Meiosis

Concomitant with the cortical reactions is an increase of metabolism in the egg, which will be necessary for nuclear fusion and cleavage. In species where the egg has not completed meiosis, it does so at this time. Which parts of the sperm enter the egg is dependent on the species. In many mammals, the entire sperm enters, while all but the tail enters in echinoderms. In other organisms, the head with the nucleus and centrioles seem to be the only things that enter. There is no evidence that any parts of the sperm other than the nucleus and centrioles are used by the zygote, and other parts that enter most probably degenerate and their components are recycled.

Studies on the mitochondria of sperm indicate that soon after entering the egg, the sperm's mitochondria are tagged by ubiquitin, the first step in breakdown and recycling. After entry, the sperm nucleus imbibes water and is converted into the male pronucleus. At the same time, the egg nucleus becomes the female pronucleus. In most animals, the male pronucleus and the female pronucleus fuse to form the diploid zygote nucleus. In some nematodes, mollusks, and annelids, however, the pronuclei remain separate until after the first cleavage division. In a few others, like the copepod *Cyclops*, the pronuclei divide separately for several cleavage divisions.

The fusion of the sperm with the egg nucleus affects many other cellular processes. One of the most interesting is the displacement of some cytoplasmic constituents. These constituents of the egg determine the fate of cells derived from the parts of the egg in which they were located and probably determine the plane of bilateral symmetry. Sperm attachment and entry often causes shifts in the position of the viscous cortical and subcortical cytoplasm, where many of the fate-determining chemicals are located.

—Richard W. Cheney, Jr.

In Vitro Fertilization of Endangered Species

Techniques of in vitro fertilization were first developed to aid couples who had not been able to conceive through normal sexual relations. In this technique, eggs were surgically removed from the mother and mixed with the father's sperm in the laboratory. If fertilization took place, one or more embryos were introduced into the mother's uterus in the hope that an embryo would implant and develop into a full-term infant. Almost immediately, these techniques were used in other animals, especially endangered species. It offered many advantages over natural reproduction. In pairs that showed little sexual interest in each other, eggs and sperm could be extracted, mixed in the laboratory, and viable embryos could be introduced into the female's uterus. Also, if there was little genetic diversity in a zoo population, sperm from a donor at another location could be sent and used. By the end of the twentieth century, in vitro fertilization was being coupled with surrogate motherhood. Here, after the embryos are formed, they are introduced into the uteri of females of similar, but not endangered, species. This increases the number of uteri available for the endangered species' reproduction.

See also: Asexual reproduction; Breeding programs; Cleavage, gastrulation, and neurulation; Cloning of extinct or endangered species; Copulation; Courtship; Determination and differentiation; Development: Evolutionary perspective; Estrus; Gametogenesis; Hermaphrodites; Hydrostatic skeletons; Mating; Parthenogenesis; Pregnancy and prenatal development; Reproduction; Reproductive strategies; Reproductive system of female mammals; Reproductive system of male mammals; Sexual development.

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FINS AND FLIPPERS

Type of animal science: Anatomy
Fields of study: Anatomy, behavior

Vertebrate animals first evolved in an aquatic environment. The necessity to move in a stable and directed manner resulted in the evolution of fins, which impart both stability and lift while swimming. As fishes have evolved, fins and their related structures have become more complex and may play a direct role in starting, stopping, and turning. When certain fish groups moved from an aquatic to a terrestrial environment, the paired fins of fishes eventually gave rise to forelimbs and hindlimbs. When, much later, certain mammalian groups (including whales and dolphins) returned to the oceans, their forelimbs evolved into finlike structures called flippers, which retained the internal bone structure of the limbs from which they are derived.

Principal Terms

FIN-FOLD THEORY: theory that fins initially evolved as long folds of tissue extending around the body

FLIPPER: finlike structures of marine mammals that have evolved from the forelimbs of their terrestrial ancestors

FOUR-FIN SYSTEM: the combined activity of paired fins in some bony fishes that makes them highly maneuverable

HETEROCERCAL: a tail in which the spine extends into the upper lobe, giving a distinctly sharklike impression

HOMOCERCAL: a type of tail at which the spine ends at the base of the tail, which consists of two equal lobes

LEPIDOTRICHIA: modified scales that form the supporting rays of the fins of bony fishes

PECTORAL AND PELVIC GIRDLES: skeletal structures that form a structural base for attachment of the paired fins in fishes, connecting them to the rest of the body's skeleton

One of the characteristic features of aquatic vertebrate animals is the presence of single and paired appendages used for locomotion. In fishes these structures are known as fins and in marine mammals they are known as flippers or flukes (on the tail). Although these structures bear superficial resemblances to each other, there are significant differences in their anatomies, attesting their different evolutionary histories. However, at a deeper level, they are related structures, having evolved from the same basic structures found in the earliest vertebrates. This is a classic example of evolutionary parallelism: Finlike structures have evolved independently in both fishes and marine mammals from a common ancestral structure.

The Evolution of Fins

The earliest vertebrates were elongated aquatic animals, and locomotion in these animals was probably accomplished by an eel-like undulation of the body. The efficiency of this form of locomotion is decreased by unwanted motion resulting in an up-and-down (pitch) or side-to-side (yaw) seesawing and rolling around the long axis of the body. Fins first evolved as stabilizers to resist these motions and increase swimming efficiency. Since their appearance, however, they have also evolved other functions.

There are two theories as to how fins first evolved. The fin-fold theory suggests that the early vertebrates had two paired folds of tissue extending along the side of the body. These folds fused just behind the anus to form a single fin which extended around the tail and up onto the midline of the upper body (dorsal) surface. The theory states that several regions of these fin folds have persisted, resulting in the paired and unpaired fins in modern fishes, whereas the rest of the early fin folds have been lost. As evidence for this theory, the sand launce, *Brachiostoma* (amphioxus) is used as an example. Amphioxus is an animal that is closely related to the vertebrates, and the earliest protovertebrates are believed to have resembled it. It has extensive folds that closely resemble the theoretical fin-folds of the earliest vertebrates. A different theory, the body-spine theory, states that the earliest vertebrates possessed two or more pairs of spines extending from both sides of the lower portion of the body. Fins were then formed when membranes extended from the tip of the spine to the side of the body, rather like a sail extending from the mast of a boat. Internal support structures within the fin (the endoskeleton) developed at a later date. At the current time there is no evidence to conclusively support one theory or the other.

The Uses of Fins

Fins in fishes are either paired, meaning there are equivalent fins on either side of the body trunk, or unpaired, meaning that there is a single fin located on the midline of the upper or lower body. The paired fins are the pectoral fins, generally located just behind the gills, and the pelvic fins, which are located behind and below the pectoral fins. The unpaired fins comprise one or more dorsal fins, located on the midline of the back, the anal fin, located on the midline of the bottom (ventral) surface of the body, behind the anus, and the caudal fin, or tail.

Dorsal fins, as on this killer whale, help maintain stability and straightforward movement while swimming through the water. (Digital Stock)

Other Uses of Fins

Although the principal roles of fins are in locomotion, there are numerous other ways in which they are employed. Many fishes possess fins with stout or serrated spines that serve in defense; often such spines are associated with venom glands. In the elasmobranch fishes (sharks and rays) and the related ratfishes, the pelvic fins of males are modified into claspers, the male organs of reproduction. In the common aquarium swordtail (platy), the unpaired anal fin performs a similar role.

The dorsal fin of the deep-sea anglerfishes has an elongated fin ray that possesses a fleshy lobe at its tip. A fish pursuing this "lure" soon finds itself engulfed in the sharp-toothed maw of the anglerfish.

The remoras and sharksuckers are well known for attaching themselves to larger fishes such as sharks and tunas. Despite their name, these fishes do not attach themselves to larger fishes by "sucking" with their mouths, but rather via a modified first dorsal fin. This fin has been modified into a series of flattened plates that can be retracted by the remora, creating a suction that leaves the fish attached to its host.

The deep-sea tripodfishes (family Bathyperidae) have pelvic fins with extremely long fin rays, set well forward on the body, and long fin rays on the lower lobe of the caudal fin. When extended, these form a three-point landing gear, upon which the fish rests above the oozy surface of the ocean floor.

Finally, the first three pectoral fin rays of the sea robin are covered with taste buds and can be moved independently. As this fish "walks" across the bottom, it is actually tasting the substrate, searching for food.

In fishes, the tail, or caudal fin, provides a large portion of the forward thrust required for moving through the water and has evolved as a specialized portion of the rearward end of the body trunk and spine. The spine itself is composed of repeating skeletal structures, the vertebrae, which together form a flexible column extending through the long axis of the animal. Sharks, sturgeon, and paddlefish possess a heterocercal tail, in which the vertebral column extends into the upper portion, or lobe, of the tail, giving it a distinctly asymmetric and sharklike appearance. The majority of bony fishes possess a homocercal tail, in which the spine ends at the base of the tail and in which the tail is composed of equal-sized upper and lower lobes. A few extinct species of fishes possessed hypocercal tails, in which the spine extended into the ventral lobe of the tail. These animals therefore possessed caudal fins in which the lower lobe was larger than the upper, the opposite of what is seen today in sharks.

The paired and unpaired fins of sharks are solid, broad-based, and relatively inflexible. Like all fins they possess an internal skeleton, which provides structural support as well as attachment for muscles that allow the fin to be moved. These consist of a series of cartilages, known as basals and radials, located in the base of the fins. Long rods of cartilage called ceratotrichia extend from the radials out to the edges of the fin, providing support. The principal role of these fins is to resist the yawing, pitching, and rolling motions generated during swimming. Because of the asymmetric heterocercal tail, the thrust generated in forward swimming extends downward from the upper lobe of the tail through the shark's center of gravity, pushing the animal downward. An important function of the large pectoral fins in sharks is to generate lift, in much the same manner as an airplane's wing. The lift generated by the pectoral fins counters the downward thrust and moves the animal forward through the water. The pelvic fins are specialized in male sharks and rays to form claspers, which serve as the male organs of reproduction in internal fertilization.

The fins of bony fishes are distinctly different from those seen in sharks, although the endoskeleton of the fins also consists of basal and radial bones. The fins of the majority of bony fishes, particularly the paired fins, are much narrower at their base, more flexible, and may play a more direct role in locomotion in addition to stabilizing the fish during swimming. The radials of the endoskeleton are reduced to very small structures located within the muscles at the base of the fin. These articulate with modified scales called lepidotrichia, or fin rays, which extend out to form the main structural elements of the fin. Membranous connective tissue extends between the fin rays, giving them their typical weblike appearance. The vast majority of bony fishes possess this type of fin structure, and they are known collectively as the ray-finned fishes, or Actinopterygii.

The Fins of Bony Fishes

A key development in the evolution of bony fishes was the appearance of a swim bladder, a gas-filled sac in the abdominal cavity that counters the fish's tendency to sink in the water and thus provides it with neutral buoyancy. With the evolution of this structure, it was no longer necessary for the pectoral fins to generate lift, and they could then be employed as brakes to stop forward motion. The pectoral fins of most bony fishes have a large surface area and a narrow base that is inserted into the body wall almost vertically, as opposed to horizontally in sharks. They are therefore admirably suited to act as brakes both singly and together, and greatly increase the ability of the fish to stop or change direction rapidly. The pelvic fins act to counterbalance any pitching or rolling motion generated by the pectorals. The combined activity of the paired pectoral and pelvic fins, often called the four fin system, provides enhanced maneuverability and control. This system is best observed in many types of coral reef butterfly fishes (Chaetodontidae), in which the pelvic fins are inserted almost directly below the pectoral fins. These fishes are highly maneuverable, able to move, turn, and stop quickly and accurately within the complex and constrained multidimensional environment of the coral reef.

A relatively small group of bony fishes possesses paired fins of a different sort. This group of fish, which includes the lungfishes and the coelacanth, is characterized by pelvic and pectoral fins that possess fleshy lobes at their base. The lobes contain muscles and skeletal elements; however, only a single basal bone articulates with the rest of the skeleton of the fish. These lobe-finned fishes (the Crossopterygii) are important because they represent descendants of the lineage that moved from the aquatic environment onto land. The pectoral and pelvic fins of these fishes gave rise to the forelimbs and hindlimbs of terrestrial vertebrates, and the single bone articulating with the body skeleton is the forebear of the humerus, the bone of the upper arm.

In all fishes, the paired fins are connected to the rest of the body's support framework, the skeleton, via structures known as the pectoral and pelvic girdles. The pectoral girdle in sharks is relatively simple and consists of a large bar of cartilage that extends across between the two pectoral fins, known as the coracoid bar. Scapular processes extend above the base of the pectoral fin and connect the pectoral girdle to the skeleton. The pelvic girdle of sharks has fused into a single bar of cartilage, the puboischiac bar.

The pectoral girdle of bony fishes contains a large number of small bones including the cleithrum, supracleithrum, and the clavicle. A posttemporal bone attaches the pectoral girdle to the rear of the skull. The pelvic girdle in most bony fishes is composed of a pair of bones that act as extensions of the basal bones of the fins.

Flippers

During the Tertiary period (approximately thirty-five to fifty-seven million years ago) several groups of land-dwelling mammals returned partly or completely to the aquatic environment. The best known of these are the cetaceans (whales and dolphins), but other groups include the Sirenidae (manatees) and the pinnipeds (seals and sea lions). These animals faced the same problems of locomotion in water as did their fish ancestors, and in the course of evolution they have evolved finlike structures called flippers and flukes. These perform the same stabilizing functions as in fishes, and bear a superficial resemblance to fins. However, closer examination of whales and dolphins demonstrates that the pectoral flippers of cetaceans are in fact modified mammalian forelimbs and contain the same bones present in the forelimbs (arms) of terrestrial mammals. Thus, the bones of the pectoral fins, which gave rise to the forelimbs of terrestrial vertebrates, have evolved back into finlike structures in these mammals as an adaptation to an aquatic lifestyle. The hindlimbs, along with their bones and supporting pelvic girdle (the hip bones in land mammals) have been lost in modern dolphins and whales, although they are still present in fossil forms such as the extinct fossil whale *Basilosaurus*. These mammals also possess fleshy dorsal fins to help stabilize them during swimming and large horizontal flukes on the tail, which provide the main forward propulsive thrust to these animals as they move through the water.

—*John G. New*

See also: Anatomy; Bone and cartilage; Convergent and divergent evolution; Dolphins, porpoises, and other toothed whales; Fish; Locomotion; Manatees; Marine animals; Physiology; Seals and walruses; Tails; Whales, baleen.

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FISH

Type of animal science: Systematics (taxonomy)
Fields of study: Anatomy, liminology, marine biology, oceanography, zoology

Bony fishes constitute one of the seven living classes of vertebrates. There are approximately twenty thousand recognized living species, nearly as many as all other vertebrates combined.

Principal Terms

CTENOID SCALES: thin, flat, bony scales with tiny spines on the exposed rear edge, found on sunfish, perch, sea bass, and other advanced teleosts

CYCLOID SCALES: thin, flat bony scales with a smooth surface; rounded in shape, found on herrings, minnows, trout, and other primitive teleosts

GANOID SCALES: thick, diamond-shaped, bony scales that are covered with ganoine, a hard inorganic substance; found on bichirs, gars, and other primitive bony fishes

OSTEICHTHYES: the taxonomic class in which the bony fishes are placed; contains species related to the ancestors of higher vertebrates

PECTORAL FINS: paired fins found near the head end of the fish body; related to the forelimbs of higher vertebrates

PELVIC FINS: paired fins found either near the tail end of the fish body or below the pectoral fins; related to the hindlimbs of higher vertebrates

SWIM BLADDER: the hydrostatic (buoyancy) organ of teleost fishes derived from the lung of more primitive bony fishes

TELEOSTS: members of the infraclass Teleostei, the most advanced of the ray-finned fishes; they compose the vast majority of living bony fish species

The Osteichthyes, or bony fishes, constitute the largest and most diverse of the classes of vertebrates. Like the jawless and cartilaginous fishes, they are characterized by gills, fins, and a dependence on water as a medium in which to live. Unlike those fishes, however, they typically possess a skeleton made of bone. Additional features characteristic of most bony fishes include a lateral line system, scales, osmoregulation (salt balance) by means of salt retention or secretion, and a bony operculum (gill cover) over the gill openings.

The fossil record of bony fishes begins nearly 400 million years ago in the early Devonian geological period, mostly in freshwater deposits. Thus there is reason to believe that bony fishes originated in freshwater habitats. Living bony fish species inhabit both freshwater habitats (58 percent of species) and marine habitats (41 percent), and some (1 percent) move between the two environments on a regular basis. This distribution does not reflect the relative proportions of these environments, since 97 percent of the earth's water is in the oceans and only 0.001 percent is in freshwater lakes, rivers, and streams (the rest is ice, groundwater, and atmospheric water). Rather, the high diversity of freshwater species is a reflection of the ease with which freshwater populations become isolated and evolve into new species.

Fish Subclasses

There are four subclasses of bony fishes: Dipneusti (or Dipnoi), Crossopterygii, Brachiopterygii, and Actinopterygii. The first three of these include a total of only eighteen primitive living species.

Subclass Actinopterygii includes all the rest. The Dipneusti, or lungfish, are named for their possession of lungs, an ancestral characteristic suggesting that the earliest steps of bony fish evolution took place in tropical freshwaters subject to stagnation. Modern lungfishes (six species) are able to cope with such conditions by swallowing air and exchanging respiratory gases (oxygen and carbon dioxide) in the lung. Once considered closely related to terrestrial vertebrates, they are now believed to share certain similarities merely because of convergence (independent evolution of characteristics that appear similar).

The Crossopterygii, or fringe-finned fishes, were the dominant freshwater predators of the Devonian period. One fossil subgroup, the rhipidistians, had many features intermediate between fishes and ancestral amphibians, including tooth structure, lobed fins, and a jaw connected directly to the skull. Therefore, they are believed to represent a link between fishes and higher vertebrates. The other subgroup, the coelacanths, was also believed to be extinct (for 70 million years) until a coelacanth was taken from deep water off South Africa in 1938. This species, *Latimeria chalumnae*, is the only known living crossopterygian fish, and is of great interest as a kind of "living fossil."

The Brachiopterygii, or bichirs, include eleven living species known from swamps and rivers in tropical Africa. Though they share some characteristics with the other bony fish subclasses, they have some distinct features that warrant placing them in a separate subclass. One such feature is a dorsal fin consisting of many separate finlets, each supported by a single spine.

The Actinopterygii, or ray-finned fishes, comprise three major infraclasses: the Chondrostei, Holostei, and Teleostei. Chondrosteans, which have reverted to a largely cartilaginous skeleton, include the sturgeons (twenty-three species) and paddlefishes (two species). One species, the beluga sturgeon (*Huso huso*), source of the famous Russian caviar, may be the largest living Osteichthyes species. It is known to achieve a length of 8.5 meters and a weight of nearly 1,300 kilograms.

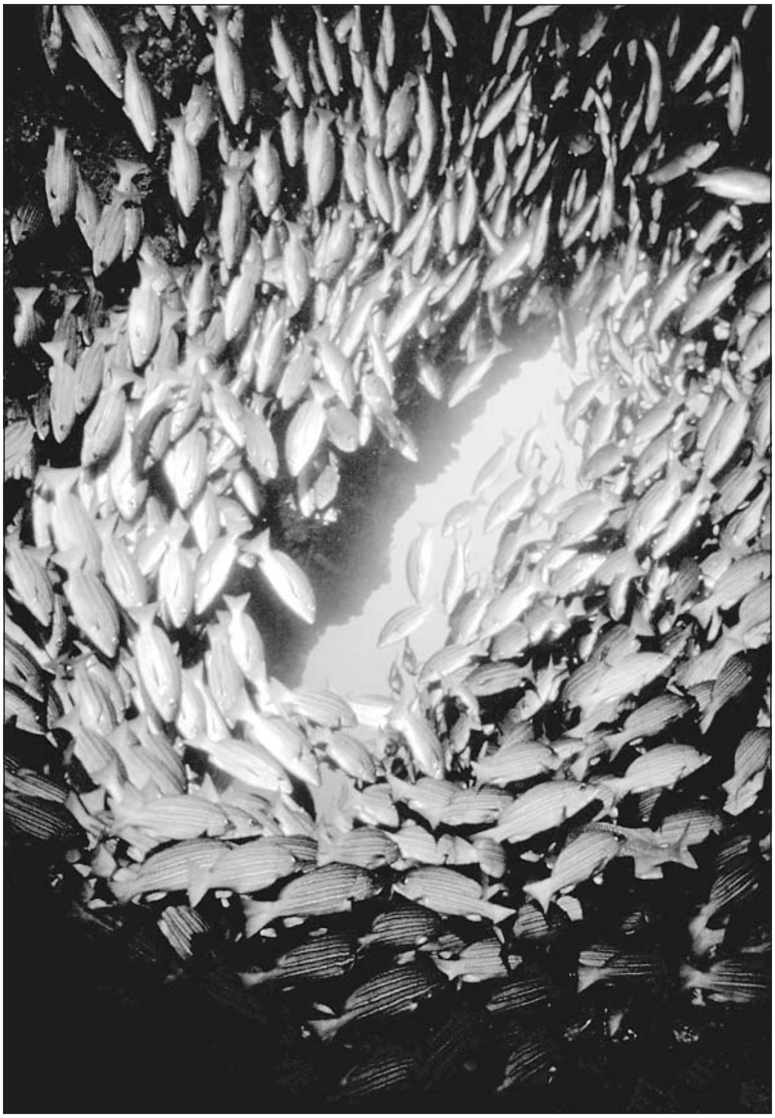
Holosteans include eight species: seven gar and one bowfin species, all known from North America. These freshwater piscivors (fish predators) are characterized by a skeleton made entirely of bone, but they do have certain other features in common with their more primitive ancestors, such as the ability to breathe air (with the swim bladder) and ganoid scales (also found in sturgeons).

The vast majority of ray-finned fishes, hence, of bony fishes—and indeed nearly half of all living vertebrates—belong to the infraclass Teleostei. It includes nineteen to twenty thousand living species. Among the features characteristic of teleosts are cycloid or stenoid scales (though some are scaleless), a swim bladder (lost in many bottom fishes), highly maneuverable fins, and a homocercal tail (meaning that its upper and lower lobes are symmetrical). Teleosts are represented by an amazing range of body sizes and shapes. A large number of species are quite small, enabling them to occupy niches (ways of living) unavailable to other fishes. The smallest known fish, in fact the smallest vertebrate of any kind, is a goby from the Indian Ocean, *Trimmatom nanus*, which matures at 8 to 10 millimeters in length.

Fish Shapes and Habits

There are several common body shape categories among teleosts which relate strongly to the fishes' habits. "Rover-predators" have the fusiform (streamlined) body shape that is perhaps most typically fishlike. Fins are distributed evenly around the body, and the mouth is terminal (at the end of the snout). This category includes minnows, basses, tunas, and others that typically are constantly moving—searching for and pursuing prey. "Lie-in-wait predators" tend to be more elongated, with the unpaired fins far back on the body, favoring a sudden lunge for their prey. The pike, barracuda, and needlefish typify this category.

"Bottom fishes" include a wide variety of shapes. Some are flattened for lying in close contact with the bottom (as are flatfishes such as flounder), some have flattened heads and sensory barbels (filaments with taste buds) near the mouth (as do catfishes), and some have fleshy lips for



Many species of marine fish live in large schools, such as these four-line snappers. (Digital Stock)

sucking food from the bottom sediment (as do suckers). A number of bottom-fish species have structures, usually modified pelvic fins, that enable them to cling to the bottom in areas with strong currents (sculpins and clingfishes have these).

"Surface-oriented fishes" tend to be small, with upward-pointing mouths, heads flattened from top to bottom, and large eyes. The mosquitofish, killifish, and flying fish belong to this category. "Deep-bodied fishes" are laterally flattened and have pectoral fins high on the body, with pelvic fins immediately below. This arrangement favors maneuverability in tight quarters such as coral reefs, thick plant beds, or dense schools of their own species. Examples include angelfishes, surgeonfishes, and freshwater sunfishes. "Eel-like fishes" have highly elongated bodies, tapering or rounded tails, and small, embedded scales (or no scales at all). They are adapted for maneuvering through crevices and holes in reefs and rocks and for burrowing in sediments. Eels, loaches, and gunnels typify this category.

Teleosts occupy habitats ranging from torrential streams high in the Himalayas to the bottom of the deepest oceanic trenches. They are found in the world's highest large lake (Lake Titicaca) and deepest lake (Lake Baikal). Some blind species live in the total darkness of underground caves. One *Tilapia* species lives in hot soda lakes in Africa at 44 degrees Celsius, while the Antarctic icefish *Trematomus* lives at –2 degrees Celsius.

The vast majority of teleost fishes, both marine and freshwater, are tropical. Southeast Asia contains the greatest number of freshwater fish species, but the Amazon and its tributaries contain almost as many (and perhaps many hundreds more, still undiscovered). Marine teleosts are most diverse in the Indo-Pacific region, especially in the area from New Guinea to Queensland, Australia. A single collection made in the Great Barrier Reef off northeastern Australia may contain one hundred or more species. Some marine teleost species have a nearly worldwide distribution, while certain freshwater species have highly restricted ranges. The Devil's Hole pupfish (*Cyprinodon diabolis*), for example, is found only in one small spring in Nevada.

Many teleosts have highly specialized associations, called symbioses, with other organisms. Some live among the stinging tentacles of sea anemones (the clownfish *Amphiprion*), within the gut of sea cucumbers (the pearlfish *Carapus*), within the mantle cavity of giant snails (the conchfish *Astrapogon*), or among the stinging tentacles of the Portuguese man-of-war jellyfish (the man-of-war fish *Nomeus*).

Reproduction

Reproduction among teleosts is incredibly varied. Most species are egg-layers, often producing an enormous number of eggs. The female ocean sunfish *Mola mola* may produce up to 300 million eggs, making it the most fecund vertebrate of all. Some species are livebearers, such as the platyfishes, swordtails, and surfperches. Some species are oral brooders, incubating the eggs in the mouth of the male (as in many cardinal fishes) or of the female (as in many cichlids). In one South American cichlid species, *Symphysodon discus*, the female "nurses" its young with a whitish milklike substance secreted by the skin.

Many teleost species are hermaphroditic. A few of these are synchronous hermaphrodites (functioning as male and female at the same time), such as the hamlet *Hypoplectrus*, but many more are sequential hermaphrodites (first one sex, then the other), such as the sea bass *Serranus*. In some coral reef fishes in the wrasse family, a dominant male mates with a harem of females. If this male is removed, the largest female becomes male and takes over the missing male's behavioral and reproductive function.

In a few species, all individuals are female, as in the Amazon molly *Poecilia formosa*. It has been shown that this species is a "sexual parasite" of two related "host" species. Sperm from host males are required to activate development of Amazon molly eggs, but male and female chromosomes (genetic material) do not join, and the offspring are all genetically uniform females.

Ichthyology

The scientific study of bony fishes dates back to Aristotle, who was the first to note, for example, that the sea bass is hermaphroditic. The "father of ichthyology" in more recent times was Peter Artedi (1705-1735), whose classification system was used by Carolus Linnaeus (1707-1778) in his *Systema Naturae*, which became the basis for all future classification systems.

Bony fish classification depends on the study of taxonomic features, or characters, which vary from one species, or group of species, to another. Useful characters include countable features (meristic characters), such as the number of fin supports (rays) or the number of scales in the lateral line, and measurable features (morphometric characters), such as the relative lengths of body parts. Such studies are typically done on museum specimens that are preserved in alcohol solution after fixation in formaldehyde solution. Dissecting tools, microscopes, and even X-ray machines are used for revealing meristic and morphometric characters. For studying bones, dry skeletons are sometimes prepared, or (especially for small species) specimens are "cleared and stained." This latter technique involves clearing the flesh with potassium hydroxide and staining the bones with Alizarin red stain.

Other techniques use samples of living tissue for finding taxonomic characters. Karyotyping (analysis of the chromosomes) and enzyme electrophoresis (using an electric field to separate similar proteins) are also important sources of taxonomic information.

Specimens for taxonomic studies are collected by means of netting, trapping, catching with hook and line, and spearing. Specialized techniques include electrofishing (use of an electric shocking device) for stream fishes, and ichthyocide (fish poison such as rotenone) for coral reef fishes.

Understanding the evolutionary history and classification of the Osteichthyes also depends on paleontological studies (the study of fossils). Bony fishes are well represented in the fossil record because of the superior fossilizing nature of their bony skeletons. Many fish biologists are concerned with matters other than taxonomy. Because of the economic importance of both marine and freshwater bony fishes, the science of fisheries biology (concerned with the management and exploitation of fish populations) is of great significance. Fish populations are often studied with "age and growth" techniques. Age (determined by scale analysis), length, and weight data can be used to calculate growth and mortality rates, age at maturity, and life span. Other techniques for studying fish populations involve tagging individuals (useful for making estimates of population size) and even using tiny radio transmitters that can be followed by aircraft (useful for studying fish migrations).

Ecologists and ethologists (behavioral biologists) are also active in fish studies, particularly since the invention of scuba diving, which allows direct observation of fishes in their natural habitat. An example of an important discovery made possible by scuba diving is cleaning symbiosis, common in coral reef areas. This symbiosis (an association involving members of two different species) involves a "cleaner" species (often a goby or wrasse), which feeds on the external parasites and diseased tissue of a host ("cleanee") species, which visits the cleaner for this service.

Questions Still to Be Answered

Bony fishes are by far the most numerous of all vertebrates. They are also arguably the most diverse in terms of body form, reproductive habits, symbiotic relationships, and other characteristics. Yet much remains to be learned. Virtually every ichthyological expedition into the Amazon region, for example, returns with specimens of previously unknown species. Some ichthyologists estimate that perhaps five or ten thousand undiscovered teleosts remain in unexplored streams and remote coral reefs.

Many biological mysteries remain about even some of the most familiar species. A good example is the American eel, *Anguilla rostrata*. This predatory species spends most of its life in the rivers, streams, and lakes of eastern North America, where it is often one of the dominant species. After six to twelve years in these habitats, the adult eels swim to the ocean and apparently migrate more than five thousand kilometers to spawn in deep water in the Sargasso Sea (an area in the western Atlantic south of Bermuda).

This general location of eel spawning has been inferred from the appearance there of the tiniest eel larvae (called leptocephali, these were once considered a separate species). The larvae become larger and larger as they drift in the Gulf Stream toward the North American coast. This much has been known since 1922. The adult migration has never actually been followed, however, and no one knows exactly where, at what depth, or how they mate and spawn, nor is it known what then happens to the adults.

Despite many advances in scientific knowledge, much remains to be learned about the interrelationships, ecology, behavior, and fishery potential of the world's bony fish species.

—*George Dale*

See also: Cold-blooded animals; Deep-sea animals; Eels; Fins and flippers; Lakes and rivers; Lampreys and hagfish; Lungfish; Lungs, gills, and tracheas; Marine animals; Marine biology; Reefs; Salmon and trout; Scales; Seahorses; Sharks and rays; Tidepools and beaches; Vertebrates; Whale sharks; White sharks.

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FLAMINGOS

Types of animal science: Anatomy, classification
Fields of study: Anatomy, ornithology, zoology

Eight flamingo types exist, all beautiful red, pink, or white water birds. Hunted to near extinction in the United States, they inhabit Europe, Africa, Asia, South America, and the West Indies. A great threat to flamingos everywhere is pollution and destruction of their habitats

Principal Terms

GASTRONOMIC: pertaining to the art of fine dining
MANDIBLES: the beaks of birds
PLUMAGE: the feathers of birds

Eight kinds of flamingos make up the avian family Phoenicopteridae. Flamingos are beautiful water birds with long legs and luxuriant deep red, light red, pink, or white plumage. They inhabit Europe, Africa, Asia, South America and the West Indies. European flamingos migrate to Africa in the winter.

The birds usually live in tropical and temperate regions along oceans and lakes or in marshes. Flamingos are also found in the Andes mountains. It is thought that flamingos are pink to red because they eat varied amounts of blue-green algae and other organisms, which contain the substances that make carrots orange and tomatoes red. Flamingos also eat diatoms, shrimp, and small mollusks.

There are four flamingo (Phoenicoparrus) species: the American and Caribbean, the Andean, the James', and the lesser flamingos. Several Phoenicoparrus species have subspecies. For example, American and Caribbean flamingos (*Phoenicopterus ruber*) have three subspecies: greater (*P. ruber roseus*), Chilean (*P. ruber chilensis*), Galápagos (*P. ruber ruber*) flamingos. Regrettably, few of these birds are seen in the United States, as feather hunters made them almost extinct. A Chilean flamingo is a bit smaller than a greater flamingo. It is pink, with red streaks on its back, and nests in Andean mountain lakes and southern South American lowlands. Two smaller species, are the Andean (*Phoenicoparrus andinus*) and James' flamingo (*Phoenicoparrus jamesi*). The smallest, most abundant species, numbering in the millions, is the lesser flamingo (*Phoeniconaias minor*) of Africa and India. It has a subspecies (*Phoeniconaias minor jamesi*).

Physical Characteristics of Flamingos

All flamingos have very long legs, webbed feet, and long, flexible necks. The long legs and webbed feet allow them to wade into fairly deep waters and stir up the muddy bottoms of lagoons and lakes, causing food to rise up closer to them. Their bills bend sharply about halfway from their ends. The upper mandible (beak half) is narrow and, when closed, fits tightly into the lower mandible. To feed, flamingos dip their heads into water upside down and scoop backward, taking in food-containing water. Then they press their mandibles together and push their tongues upward. As mandible edges have small ridges, the tongue pressure pushes water out and the strainerlike action retains the small animals and vegetation they feed on.

Different species and subspecies are colored differently and have different sizes. Overall, adult flamingos attain heights and weights of 2.5 to 5.5 feet and weigh four to seven pounds, depending on species. Females are usually shorter and weigh less than males. Flamingo plumage is white, various pinks, or crimson red. Their legs, webbed feet, bills, and faces are red, pink, orange, or yellow.

The Flamingo Life Cycle

Most flamingos live in colonies which number tens to hundreds of thousands. The colonies are usually located in or around lagoons and lakes. A well-known, very populous example is Kenya's Lake Nakuru, where millions of flamingos congregate. During breeding season, a male and female mate. It is believed that once mated, pairs of flamingos are monogamous.

The female lays one 3.5-ounce white egg in a depression atop a nest which is a conical mound of mud, one foot tall, built by the breeding pair. The pair then incubate the egg for about a month, until it hatches. On hatching, the baby flamingo stays in the nest for about three months. At first, it has gray, downy feathers and its legs and bill are pink. Its feathers turn pink and its bill curves into the adult shape as it grows. Both parents feed the young bird. It is given regurgitated food for as long as it remains in the nest, though it can feed itself thirty days after hatching. In the wild, flamingos may live for forty to fifty years.

Flamingo Conservation

Flamingos live in isolated habitats and have few natural predators except for humans. In the distant past, the ancient Romans hunted flamingos for their tasty tongues, thought to be a gastronomic delicacy. Regrettably, the American greater flamingo (*P. ruber roseus*), once common in the South, is now seen only rarely in the United States. They were hunted for their beautiful plumage faster than they could reproduce. This is unfortunate, because few sights are more beautiful than a flock of pink, rose, or scarlet flamingos standing

Flamingos are wading birds, living at the edges of lakes or oceans, or in marshes. (PhotoDisc)

Flamingo Facts

Classification:
Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Class: Aves
Order: Ciconiiformes
Family: Phoenicopteridae (flamingos, three genera, seven species)
Geographical location: Europe, Africa, Asia, South America, the West Indies
Habitat: Lagoons, lakes, and marshes
Gestational period: One month of incubation
Life span: Forty to fifty years in the wild
Special anatomy: Long, storklike legs; bills that strain shellfish and other food out of water

together or flying in the sun of the United States tropics. They are still plentiful in the West Indies and South America.

It might be thought advantageous to restock the wild with zoo-bred flamingos. However, this has not been possible because flamingos captured for zoos often die in transit, and those in zoos rarely breed successfully. It is hoped that with time and with the cessation of feather hunting, flamingos will reestablish themselves in the United States. A great threat to this prospect, and to flamingos elsewhere, is pollution and destruction of their habitats

—Sanford S. Singer

See also: Beaks and bills; Birds; Feathers; Flight; Molting and shedding; Nesting; Respiration in birds; Wildlife management; Wings.

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FLATWORMS

Type of animal science: Classification
Fields of study: Anatomy, invertebrate biology, physiology

Flatworms are wormlike animals with a single major opening to the gut. Many are parasitic for at least part of their life cycle.

Principal Terms

DEFINITIVE HOST: the host in which a symbiont (the organism living within the host) matures and reproduces

ECTOPARASITE: a parasitic organism that attaches to the host on the exterior of the body

ENDOPARASITE: a parasitic organism that attaches to an interior portion of the host's body

FREE-LIVING: an organism that does not have to spend a portion of its life cycle attached to another organism

HERMAPHRODITIC: a situation in which both functional ovaries and testes are present in the same organism

PROGLOTTID: a body segment of a tapeworm that contains a set of reproductive organs, usually both ovaries and testes

SNAILING: the process in which the free-swimming larva (miracidium) of the flukes utilizes the tissue of a snail as an intermediate host

The flatworms or Platyhelminthes are wormlike animals with a single major opening to the gut. This opening functions as both a mouth and an anus. Between the gastrodermis (lining of the gut) and the epidermis, the body is filled with tissues, including layers of muscle, connective tissue, and reproductive organs. Included in the flatworms are free-living forms (class Turbellaria), and two major groups of animal parasites (class Trematoda—flukes—and class Cestoda—tapeworms). Most tubellarians are bottom dwellers in marine water or freshwater or live in moist terrestrial environments, but a few species are symbiotic or parasitic. The majority of the larger species are found on the underside of rocks or other hard objects in freshwater streams or in the littoral zones of the ocean. All of the cestodes and trematodes exist as endoparasites and most exhibit indirect life cycles with more than one host. The initial host is usually an invertebrate, and the final host is most often a vertebrate. A number of species utilize humans as a final host.

General Characteristics of Flatworms

The free-living flatworms generally range in size from five to fifty millimeters. The epidermis is covered with cilia, and locomotion is achieved through a combination of ciliary movements and the contraction and relaxation of layer of circular muscles that go around the body, and a layer of longitudinal muscles that extent down the length of the body. The most commonly studied turbellarians are the planarians. The digestive system consists of a mouth on the ventral surface, a pharynx, and an intestine. Planarians are mostly carnivorous, feeding mainly on nematodes, rotifers, and insects. In contrast to the parasitic species, the turbellarians have simple life cycle. Some can reproduce by asexual fission, but most reproduce sexually. While the turbellarians are hermaphroditic, they generally crossbreed. Planarians demonstrate a remarkable ability to regenerate. If a section is excised from the middle of the worm, it will regenerate both a new tail and a new head.

Flukes primarily differ from the turbellarians in their adaptions for parasitism, including organs

Flatworm Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Platyhelminthes
Classes: Turbellaria (free-living), Monogenea (ectoparasitic flukes with a one-host life cycle), Trematoda (endoparasitic flukes), Cestoda (tapeworms)
Subclasses: Cestoda—Cestodaria (body not segmented), Eucestoda (body segmented into proglottids)
Orders: Turbellaria—Acoela (no gut cavity), Rhabdocoela (simple tubular gut), Alloeocoela (gut with one main branch and small side branches), Tricladia (gut with three branches), Polycladia (gut with many main branches); Trematoda—Aspidogastrea (endoparasitic with a one-host life cycle), Digenea (endoparasitic with at least a two-host life cycle); Eucestoda—Bothriocephaloidea (fish tapeworms), Taenioidea (pig and beef tapeworms)
Geographical location: All over the world
Habitat: Turbellaria—generally found in ponds, lakes, streams, and oceans; Monogenea, Trematoda, and Cestoda—larvae may be found in streams, but adults live within the body of a host
Gestational period: Varies among species, but most species lay eggs within a few days after fertilization; eggs usually hatch within a few days to a few weeks after being deposited
Life span: Varies among species; can be as short as a year in some turbellarians and up to thirty years in some flukes
Special anatomy: Elongated, bilateral invertebrates without appendages, have neither a true body cavity nor a circulatory system; parasitic species have specially adapted mouth parts for attaching to the tissues of the host

for adhesion such as suckers or hooks and an increased reproductive capacity. They are generally leaf-shaped, varying in size from ten to twenty millimeters. Most flukes, such as those in the class Digenea, have complex life cycles. The eggs produced by the mature fluke pass from the definitive host and hatch in water to form free-swimming larvae called miracidia. The miracidium enters the tissue of an intermediate host, snails, and transforms into a sporocyst, which reproduces asexually to form rediae. The rediae reproduce asexually to form cercariae, which leave the snail and penetrate a second intermediate host, such as fish, or encyst on vegetation, where they become metacercariae, juvenile flukes. When the metacercariae are eaten by the definitive host, they develop into mature flukes.

Tapeworms are also keenly adapted for parasitism, but unlike the flukes, they have long, slender bodies that can reach lengths of several meters and lack a digestive system. They obtain digested nutrients directly from the gut of the host. The tapeworm body consists of a linear series of proglottids. The tapeworm grows lengthwise by adding new proglottids. Mature proglottids contain fertilized eggs and break off the end of the tapeworm to be excreted out of the host. Almost all cestodes require at least two hosts, and the adult is a parasite in the digestive tract of vertebrates. One of the intermediate hosts is usually an invertebrate. Almost all species of vertebrates are subject to tapeworm infection.

—D. R. Gossett

See also: Asexual reproduction; Hermaphrodites; Invertebrates; Regeneration; Roundworms; Symbiosis; Worms, segmented.

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FLIES

Types of animal science: Anatomy, classification, reproduction
Fields of study: Anatomy, entomology

Flies are members of the order Diptera, two-winged insects, of which there are 95,000 species. Flies are related to the other dipterans, the mosquitoes.

Principal Terms

IRIDESCENT: showing the colors of the rainbow depending on light reflection
MOLT: shed an insect shell
SYMBIOSIS: beneficial relationship between two organisms

Flies belong to the fourth largest animal order, Diptera, which comprises 95,000 species of two-winged insects. The Diptera evolved from four-winged insects, and their vestigial rear wings are stalks that act as gyroscope balance organs, enabling the forewings to move the fly forward without causing nose dives, and keeps it on a steady course.

Dipterans occur worldwide, including Antarctica, but are most plentiful in moist, warm climates. The main dipteran suborders are Nematocera, Brachycera, and Cyclorrapha. Nematocera are mosquitoes, slender, with long antennae. The other orders have stout bodies and short antennae; among them are houseflies and tsetse flies.

Physical Characteristics of Flies

A fly body has three parts: a head, thorax or middle part that holds six legs, and an abdomen or rear end. Two compound eyes containing up to four thousand facets cover most of the head. The eyes see light changes and sudden movement from many different directions at once. This is why flies are hard to catch

Atop a fly's head, paired antennae provide the senses of touch and smell. Dipterans have a mouth part called a proboscis. It is funnel-shaped, with its wide part at the bottom. The proboscis is like a straw, sucking up fluid via a pump in the head. The proboscis of a housefly is soft, so it cannot bite. Bee flies have a long proboscis that enters flowers for nectar. Biting flies, such as horseflies, have hard, sharp proboscises that pierce the skin of their victim.

Each foot on a fly is tipped by claws that grip rough surfaces. Under the claws are pads called pulvilli. On smooth surfaces, they flatten and grip tightly, allowing a fly to walk upside down on ceilings without falling. Flies breathe through openings called spiracles, located on each side of thorax and abdomen.

Fly Life

The life of a fly begins when a female lays hundreds to thousands of eggs in manure, garbage, vegetable waste, fruit, plant stems, or stagnant water. Houseflies have telescoping ovipositors that place eggs in soft matter. Other species have stiff ovipositors that penetrate plant stems or fruit. Flies, like mosquitoes, also lay eggs on water.

The heat given off in these environments incubates the eggs. In one or two days they hatch as white, legless larvae (maggots), which eat the material surrounding them. Maggots rapidly grow too large for their skins, which split and allow molting. After molting twice, the larvae find sheltered places to form upariums, where they molt a final time and become pupae, and then become winged flies. The process usually takes four to ten days. Adult flies emerge from the pupae full-sized. Most live for thirty days. In winter most die,

Image Not Available

but larvae and pupae live to become adults in the spring. The development of a fly from egg, to larva, to pupa, to adult is called metamorphosis.

Tsetse Flies, Horseflies, and Blowflies

Tsetse flies are twenty species of genus *Glossina*. Five of these species carry sleeping sickness. They live in grasslands, forests, and river and lake shores in Africa, between the Sahara and Kalahari deserts. Tsetse flies suck blood with their sharp proboscises; the blood is digested with the assistance of a membrane that is secreted around the blood meal in the foregut. Tsetse flies mate year round. Females have one offspring per mating. After fertilization, an egg hatches in the mother and is later born as a full-sized maggot, which burrows into the soil, pupates, and becomes adult in a month. The flies carry trypanosomes that can infect people with sleeping sickness. When the tsetse fly bites a victim, the trypanosomes enter, multiply, make them very tired, and quickly kill them.

The 3,500 Brachycera species of horseflies occur worldwide, most in tropical and temperate fields and forest areas near water. They have inch-long, stout bodies, large heads, short antennae, and iridescent compound eyes. Their mouths pierce the surfaces of plants and animals to suck fluids. Males eat nectar and plant juices, while females suck blood. The time of mating varies according to species and climate. Females must eat blood before laying eggs or the eggs do not develop. A female lays one thousand eggs in damp sites such as rotten wood. Larvae hatch in two to three weeks, although some hibernate all winter. Before becoming adults, larvae pupate for about three weeks. Adults live for six weeks before mating and dying. Horsefly bites are painful and may cause anthrax or tularemia.

Fly Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Arthopoda
Subphylum: Uniramia
Class: Insecta
Order: Diptera
Suborder: Brachycera, thirty-five families
Geographical location: Every continent
Habitat: Grasslands, forests, near rivers and lakes
Gestational period: Eggs hatch in two to seven days; adulthood occurs in one to six weeks
Life span: One to six months
Special anatomy: Six legs; compound eyes; one pair of wings, antennae, proboscises; pulvilli

Blowflies are metallic blue-green and are larger than houseflies. Females lay eggs on meat or in the open wounds of animals. Eggs or larvae that are in food swallowed by animals and humans cause pain and sickness when the maggots eat into the wound or tissue where they were laid. When the larvae enter an animal's skin, puss-filled sores form. The screwworm, a blowfly larva, harms livestock. If screwworms are not controlled, animals die.

Flies and Disease

A housefly can carry pathogenic bacteria disease because it lives in manure and garbage. Thousands of related species transmit germs to whatever surface they land on, spreading disease. Often it is best to kill flies and stop their reproduction. Flies destroy crops; parasitize animals; and carry typhoid and cholera.

However, flies are also useful. Some flies, such as hoverflies, pollinate plants. Larvae also eat aphids, which kill crops. Flies speed the decomposition of animal carcasses and manure. In addition, flies consume other harmful insects, controlling their numbers. Finally, flies are the food source for numerous insectivores higher up the food chain.

—Sanford S. Singer

See also: Antennae; Flight; Insects; Metamorphosis; Molting and shedding; Mosquitoes; Wings.

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FLIGHT

Types of animal science: Anatomy, evolution
Fields of study: Anatomy, biophysics, evolutionary science, invertebrate biology, ornithology, paleontology, zoology

Flight has evolved in a number of groups of organisms. Seed pods, insects, pterosaurs, birds, and bats are all familiar examples of organisms that have evolved some flight capability. Depending on the definition of flight, certain organisms inhabiting the oceans and freshwater realms, such as fish, ocean turtles, penguins, sea snakes, and even crocodiles can fly underwater.

Principal Terms

DRAG: a force that acts in the opposite direction of the movement of a body through a fluid medium; sources of drag vary but include friction and pressure suction

FLUID: a substance, either liquid or gas, that flows or conforms to the outline of its container

INERTIA: the property of an object with kinetic energy to move in a straight line unless acted upon by an outside force

LIFT: an aerodynamic force created through differential flow above and below a structure

REYNOLDS NUMBERS: the results of a formula that takes into account the velocity of an object, its characteristic length divided by the dynamic viscosity of the fluid

TURBULENCE: flow that is chaotic and may create stall conditions through the loss of lift

VISCOSITY: the stickiness of a fluid created by internal forces as molecular attractions

There are two types of movement through a fluid environment: rowing and flying. Organisms that row use the viscosity (stickiness) of the fluid to propel themselves along. These organisms generally have limbs used as oars with which to row; these oars push up against the fluid (usually water) and the fluid exerts a force back onto the oars that drives the animal forward. Organisms that fly use the inertial qualities of the fluid (usually air); essentially, they will use differential flow rates over the body surfaces to create thrust and lift. Flying is necessary when animals are large, and the drag on the body becomes too high for rowing to be effective. The choice between rowing and flying has to do with the organism's Reynolds number, which is a ratio between length and inertial viscosity forces. Viscosity dominates at low Reynolds numbers, whereas inertial forces dominate at high Reynolds numbers. Drag can be defined as any force that tends to retard the forward movement of an object in a fluid environment. Drag can be due to friction on the body surface; pressure drag is due to the fluid not adhering to the shape of the object and peeling away as a wake. The size of an organism capable of achieving airborne flight by means of rowing is quite small (hypothesized for insects such as mymarid wasps, which are smaller than fruit flies). In aquatic environments, larger forms can row due to the greater viscosity of water.

How Flight Works

Regardless of the organism, flow must take on different velocities above and below the body or wing, according to Bernoulli's principle, whereby flow is understood in terms of conservation of energy. What this means is that in an ideal fluid where there is no friction (that is, no viscosity), if the fluid accelerates, its pressure goes down. Conversely, when the velocity is reduced, the pressure goes up. While this may be counterintuitive, it nonetheless provides a basis for understanding flight. Thus, wings are not necessary to fly, but rather an organism needs to create a surface that is longer on top than it is on the bottom. A concave body form might possibly provide lift by its shape alone in an air streamline. Wings can assume such a shape by twisting themselves, as in insect wings, or creating a curvature with feathers, as in birds. In this situation, air flows faster above than below the structure, and lift is produced perpendicular to the upper surface.

This only works because fluids follow the law of continuity: if a streamline of air is split by an airfoil, the streamline will flow both over and under the structure. Both the upper and lower streamline must theoretically meet at the end of the structure. Thus, a curved structure or a structure that is inclined at an angle to the oncoming flow will create a longer upper surface than lower surface, hence the differential velocity as the streamlines race to the rear edge of the structure. If the aerodynamic structure is inclined downward, the lifting force can now be separated into a force that drives the structure forward and upward.

This picture of flow is very basic, and it is more complicated in practice. The flow over wings circulates around the wing in circles. Bernoulli's principle may still be applied to the circulating flow to understand how lift is generated. This circulation is shed off the wings at the tips in particular patterns based on the movements of the

The feathers on bird wings create sufficient curvature to produce lift and allow the bird to fly. (Corbis)

From Dinosaurs to Birds

Paleontologists have suggested that ground-dwelling bipedal dinosaurs gave rise to birds, and thus avian flight developed from the ground up. This viewpoint is flawed, since the dinosaurian proavis would have had to overcome gravity by running, which would not be energy-efficient. Moreover, bipedal dinosaurs, by virtue of their well-developed hindlimbs, had their center of mass in the pelvis, a situation which would create an unbalanced torque that would flip the animal attempting to fly. Any lift generation in the chest would act vertically at the forelimb area. The pelvic center of mass would act as a downward force in the rear of the animal, resulting in a rotation of the body. Flying birds have their center of mass and center of lift in roughly the same place, and thus rotations of this kind do not occur. It is likely that birds originated from arboreal reptilian ancestors that were quadrupeds. Jumping or falling from a tree would create a cost-free air flow about the body surface to create lift and thus extend a glide between trees. Quadrupeds have a center of mass close to the pectoral area, unlike bipeds, and thus have less problems with unbalanced rotational forces, such as torques. In fact, those land vertebrates that glide today are all quadrupeds.

wing or (in the case of most fishes) the tail. This circulation of fluid around the wing must be generated for lift and thrust to be generated. These circulating rings of fluid are shed off the wings or oscillating tail as vortex rings. This why aircraft are spaced apart during landings, as these vortex rings may cause such turbulence that the aircraft flying behind may experience loss of lift.

Laminar flow is a flow whose constituent pattern is in one direction, an even flow. Turbulent flow occurs when areas within a flow become chaotic, causing heat production and a loss of velocity. Worse than this is a condition when the turbulence becomes so great that the flow no longer adheres to the aerodynamic surface and departs from the structure, causing a loss of lift. This can happen for a variety of reasons. If the angle of attack of a wing becomes too steep, the flow may become turbulent and separate off the structure. If there is no circulation on the wing, there is no lift, a stall develops, and gravity takes over, with dire consequences. In addition, if the velocity is too great, the flow will become turbulent and unable to stay on the surface.

Shape also may contribute to the production of turbulence. Surface roughness may cause turbulence to occur through collisions with the streamlines. In addition, convexities and concavities can cause turbulence to form and prevent the adherence of the fluid on the surface of the object. While this has practical applications in design, it points to the fact that aerodynamic structures are streamlined, having tapered ends that preclude the necessity of fluids having to adhere to abrupt curvatures and creating potentially turbulent flows.

What has been described here is large-scale turbulence, where separation of flow from the object's surface occurs. Small-scale turbulence can actually benefit the lift on the aerodynamic structure, since the longer the flow adheres to the airfoil, the more lift and thrust the structure can generate. Small-scale turbulence may actually maintain the flow on a surface, and thus the lift produced far outweighs the drag force produced by the turbulence.

Flight in Animals

The evolution of flight in birds is centered mainly on the evolution of feathers. Feathers are complex epidermal structures that may have been derived via a developmental program alteration of scales. Feathers are the most complex epidermal structure found in vertebrates. They have a central strut, called a rachis, and a series of barbs emanating from both sides of the rachis in pinnate fashion to form the feather vane. These barbs are hooked together by a series of hooklets that act very much like Velcro. Feathers form the major aerodynamic surface in a bird. They are lightweight, but very strong. Contour feathers maintain a uniform surface for the bird so that there are no abrupt curvatures that may create turbulence. The long flight feathers, known as primaries, secondaries, and tertiaries, form the wing. Long, narrow wings, termed high aspect-ratio wings, consume less power when flapped than broad or low aspect-ratio wings. The bird wing is cambered and so creates lift in an airflow. Shore birds, such as gulls, are seen lifting out of the water just by holding out their wings in a breeze without the need of flapping. Flapping the wings faster than the velocity of the air increases the lift and thrust imparted to the air. Birds are able to fly because they can generate more lift than their body weight, and it has taken them considerable evolutionary time to perfect the weight reduction necessary for flapping flight. Penguins use their wings to fly underwater. They are extremely maneuverable and use their agility and speed to catch fish. The wing beat does not proceed through the same distance as aerial flying birds because of the greater viscosity of water.

Bats are also evolved from a quadrupedal ancestor. In their case, a skin membrane is stretched between the elongated fingers. In this way the camber and aspect ratio of the wing can change quickly. Many bats retain a membrane between the legs, the uropatgium, that increases the lifting surface of the body. Bats are agile and rapid flyers and, equipped with ultrasonic pulses, can locate a variety of prey from insects to frogs. Mammals have evolved gliding forms in much the same way across other taxa. A wing membrane is stretched between the fore and hindlimbs in marsupials such as sugar gliders, and among placental mammals such as flying squirrels (rodents) and the so-called flying lemur (*Cynocephalus*).

Pterosaurs also used a skin membrane stretched between the elongated fourth digit and the hindlimb. This design worked well for over a hundred million years, but a tear in the membrane would destroy the lift-generating ability of the wing. While most pterosaurs were small, some giant forms evolved with wing spans of over forty feet. Lizards have never evolved powered flight, but have generated gliders and parachutists. In the Triassic and Cretaceous periods as well as in the present day, lizards evolved a flight membrane supported by the ribs. The ribs can be folded against the body when the lizard is climbing among the branches in search of insect prey. Other lizards, such as geckos, have evolved body fringes of skin and the ability to flatten themselves to create an aerodynamic surface. Some species of snakes launch themselves into the air, and some frogs use their expanded webbed hands and feet for gliding.

Although fishes essentially fly with the tail, and many flap the pectoral fins like bird wings, some fish have taken to the air. Flying fish will gain speed underwater using their tail and then leap out of the water spreading their large pectoral fins. These fishes can glide for some distance before reentering the water. The flight strategy is associated with escape behavior from predaceous fish.

There is controversy surrounding the origin of insect flight. Some postulate that insect wings developed for temperature control, as wing beating would heat the organism. Moreover, wings could be used to collect or dissipate heat depending upon exposure to the sun or wind. Others contend that insect wings evolved from lateral extensions of the exoskeletal tergites to aid in the stabilization of jumps. However it began, insects are the only invertebrate to evolve aerial powered flight. Normally insects have two pairs of wings, the first pair essentially acting as covers for the posterior wings involved in lift and thrust generation. Some insects have two functional pairs of wings, such as dragonflies. The wings are operated by muscles that have short contraction lengths to obtain rapid wing movements. As is the case in birds, small insects have the highest wing beat frequencies, reaching over one thousand beats per second. Muscles attach either directly to the wing bases, or indirectly to a specialized part of the dorsal carapace termed the notum. The deflection of the notum moves joints that connect to the wings, allowing them to beat in a twisted fashion and create the aerodynamically shaped surfaces.

—Samuel F. Tarsitano

See also: *Archaeopteryx*; Bats; Birds; Feathers; Insects; Locomotion; Mammals; Pterosaurs; Wings.

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FOOD CHAINS AND FOOD WEBS

Types of animal science: Behavior, ecology, geography, physiology, scientific methods
Fields of study: Ecology, environmental science, marine biology, physiology, population biology, wildlife ecology

In the biosphere—the portion of earth that sustains life—organisms including plants, animals, and microbes interact and interconnect with one another through organized and complex networks. Understanding this network, also referred to as a food chain or food web, is vital to the study of many subjects in biology.

Principal Terms

BIOLOGICAL MAGNIFICATION: the increasing accumulation of a toxic substance in progressively higher feeding levels

CONSUMER: an organism that eats other organisms

DECOMPOSERS: microbes such as fungi and bacteria that digest food outside their bodies by secreting digestive enzymes into the environment

DETRITUS FEEDERS: an array of small and often unnoticed animals and protists that live off the refuse of other living beings

ENERGY PYRAMID: a graphical representation of the energy contained in succeeding trophic levels, with maximum energy at the base (producers) and steadily diminishing amounts at higher levels

NUTRIENT CYCLE: a description of the pathways of a specific nutrient (such as carbon, nitrogen, or water) through the living and nonliving portions of an ecosystem

PRODUCERS: organisms that produce food for themselves as well as for nearly all other forms of life, including plants, plantlike protists, and cyanobacteria

TROPHIC LEVEL: the categories of organisms in a community, and the position of an organism in a food chain, defined by the organism's source of energy

All activities of life are powered, whether directly or indirectly, by a single source of energy: sunlight. The energy enters the biosphere through primary producers, which trap and convert solar energy into chemical energy, first in form of sugars and ultimately in other complex organic molecules. Energy in its chemical form is then passed along from one type of organism to another through a complex feeding relationship. Two fundamental laws underlie this function: Energy moves through ecosystems in a one-way street, while nutrients cycle and recycle. Each time the energy is used, some of it is lost as heat. Energy needs constant replenishment from an outside source, the sun. In contrast to energy, nutrients constantly cycle and recycle in a circular flow. Nutrients enter the system from soil or water or atmosphere through primary producers (plants), and pass along to herbivores, then to carnivores. The wastes and dead bodies or body parts degraded by detritus feeders return nutrients to the ecosystem.

Feeding Relationships Within a Community

Feeding relationships in a community are often defined or described through food chains and food webs. A linear feeding relationship spanning all trophic levels is called a food chain, whereas many interconnecting food chains in a community make up the food web. Obviously, different ecosystems have drastically different food chains. To illustrate who feeds on whom in a community, it is better first to examine some basic laws and structures that govern a community in general. Energy and nutrients are two common elements that sustain all communities and ecosystems. Energy enters communities through the process of photosynthesis, by which plants and other photosynthetic organisms trap a small portion of sunlight and convert it into sugars. Photosynthetic organisms, from the mighty sequoia to the zucchini and tomato plants in a garden to single-celled diatoms in the ocean, are called autotrophs or producers, because they produce food for themselves. They also produce food for nearly all other organisms, called heterotrophs or consumers.

The amount of life a community can support is determined by how much energy the producers within it can capture. Within the community, energy flows from producers, occupying the first trophic level, through several levels of consumers. The consumers that feed directly and exclusively on producers are herbivores, ranging from caterpillars to buffaloes to wheat aphids. These herbivores, also called primary consumers, form the second trophic level. Carnivores, such as the spider, eagle, fox, and birds that eat caterpillars, are meat eaters, feeding primarily on primary consumers. Carnivores are secondary consumers that form the third or higher trophic level. Some consumers, such as the black bear that eats both blueberries and salmon, occupy more than one trophic level.

A food web, however, represents many interconnecting food chains in a community, describing the actual, complex feeding relationships within a given community. A food web also reflects the feeding nature of organisms that occupy more than one trophic level. Animals such as raccoons, bears, rats, and a variety of birds are omnivores, eating at different consumer levels at different times. In addition to producers and consumers, a functional ecosystem also consists of detritus feeders and decomposers that release nutrients for reuse. The extremely diverse network of detritus feeders is made up of earthworms, mites, protists, centepedes, nematodes, worms, some crustaceans and insects, and even a few verte-

Dodos and Bats: Cases of Disrupted Ecosystems

Within complex ecosystems, animals and plants interact with each other in very intricate and dynamic ways. Plants provide animal species with nutritious fruits. In return, animals help to disperse their seeds. These mutually beneficial relationships sustain both plant and animal populations, and ultimately the ecosystem itself.

A pair of organisms, the dodo bird and the tambalacoque tree, coexisted on the island of Mauritius in the Indian Ocean for a long time. When humans arrived at the island, the slow dodos were easy prey. By 1681, humans had hunted the dodo to extinction. The damage, however, reached far beyond just dodos. It turned out that dodos helped disperse the seeds and promote the germination of the tambalacoque trees of Mauritius. Dodos ate the tambalacoque fruit before it had a chance to rot, thoroughly cleaning the seeds and thereby protecting them from infections by destructive fungi. Dodos also dispersed the seeds all over the island, ensuring that some of them reached fertile soil for germination. With the dodos gone, the fruit rapidly rots, the seeds are destroyed by fungi, and the tambalacoque trees are seriously threatened.

In tropical forests, bats serve as the most important agents for seed dispersal. Bats may eat up to twice their weight in fruit in a day. They also fly more than twenty miles per night, defecating the seeds in flight. After passing through bats' digestive tract, seeds have more than a 95 percent germination rate, as compared to 10 percent in seeds planted directly from fruit. As bat populations (and those of other fruit-eating animals) decline dramatically, seed dispersal has stopped or been significantly reduced. Tropical fruits are rotting on the forest floor or sending up doomed sprouts under the shade of their parents and other canopies. Some types of tropical forests may not survive.

brates such as vultures. Except for vultures, these organisms thrive in the garden, and compost by extracting energy stored within dead organic matter, in turn releasing it in a further decomposed state. The excretory products released serve as food for other detritus feeders and decomposers, which are primarily fungi or bacteria. Fungi and bacteria digest food outside their bodies by releasing digestive enzymes into the environment. They then absorb the nutrients they need, and leave the remaining nutrients for recycling. Without detritus feeders and decomposers, nutrients would soon be locked into organic matters, and the ecosystem will cease to be functional.

Energy Transfer and the Nutrient Cycle

One important principle that governs the flow of energy through the ecosystem is that the energy transfer from one trophic level to the next is never efficient. The net transfer of energy between two trophic levels is roughly 10 percent. During the transfer, 90 percent of the energy is lost as heat or in other forms. Of one thousand calories stored in the producer (plants), the caterpillars that consume all plant tissues will obtain one hundred calories, a bird that eats caterpillars will extract ten calories, and when a hawk catches the bird, that portion of the energy is reduced to a mere one calorie. This inefficient energy transfer between trophic levels is called the 10 percent law, or an energy pyramid. This 10 percent law has profound impacts within an ecosystem. Plants have the most energy available to them; the most abundant animals will be those directly feeding on plants, and carnivores will always be relatively rare, especially those of large size that occupy a higher trophic level.

However, when toxic substances pass through trophic levels, the exact opposite is true. While energy diminishes in the process of flowing from lower to higher trophic levels, toxic substances progressively increase in concentration along the food chain. This phenomenon, called biological magnification, was discovered through the study of the use of the pesticide dichloro-diphenyl-trichloroethane (DDT). Tests of water samples following the use of this pesticide showed a trace amount of DDT. Tissue analyses of predatory birds in the same aquatic ecosystem, however, revealed a DDT concentration a million times greater than that in the water. Fish caught from the same waters also contained much higher DDT levels than the water, but substantially lower levels than that of the birds that consumed those fish. DDT has since been confirmed as the cause for population declines of several predatory birds, especially fisheaters such as bald eagles, brown pelicans, and cormorants. Understanding biological magnification is crucial to the prevention of widespread loss of wildlife.

Unlike energy, no mechanism or source exists to allow a constant replenishment of nutrients. The same pool of nutrients has been supporting life from the beginning. Nutrients are elements and small molecules that form all the building blocks of life. Macronutrients are those acquired by organisms in large quantities, including water, carbon, hydrogen, oxygen, nitrogen, phosphorus, sulfur, and calcium. Micronutrients, including zinc, molybdenum, iron, selenium, and iodine, are acquired in trace quantities. Nutrients cycle from producer, to consumer, to detritus feeder and decomposer, and eventually back to producer. The major reservoirs of nutrients are in the nonliving environment, such as soil, rock, water, and atmosphere. In an undisrupted ecosystem, nutrients have cycled and recycled in a sustainable manner for thousands of years. However, human intervention, either through industry or agriculture, has created enormous problems for sustainable nutrient cycling. One example is the nitrogen cycle. Although plants may obtain nitrogen from soil, the primary source of nitrogen is the atmosphere. Nitrogen gas (mainly N) makes up over 70 percent of the air. N may be extracted by some plants or converted by lightning into useable forms that drop as rainfall. Through industrial production and use of nitrogen fertilizers in agriculture, humans have overcharged the nitrogen cycle, causing acid rains and surface water and groundwater contamination, which pose a serious threat to natural ecosystems.

Why Preserve Biodiversity?

Biodiversity is defined as the total number of species within an ecosystem, and also as the resulting complexity of interactions among them. It measures the "richness" of an ecological community. Among an estimated eight to ten million unique and irreplaceable species existing on Earth, fewer than 1.6 million have been named. A tiny fraction of this number has been studied. Over thousands of years, organisms in a community have been molded by forces of natural selection exerted by other living species, as well as by the nonliving environment that surrounds them. The result is a highly complex web of interdependent species whose interactions sustain one another and provide the basis for the very existence of human life as well. Thus, it is easy to see why biodiversity should be preserved.

Loss of biodiversity poses a serious challenge to the sustenance of many communities and ecosystems. For example, the destruction of tropical rain forests by clearcut logging produces high rates of extinction of many species. Most of these species have never been named, and many never even discovered. As species are eliminated, the communities of which they were a part may change and become unstable and more vulnerable to damage by diseases or adverse environmental conditions. Aside from disrupting the natural food webs, potential sources of medicine, food, and raw materials for industry are also lost. As Harvard professor Edward O. Wilson once said, "The loss of species is the folly our descendants are least likely to forgive us."

Food Chains and Food Webs in a Terrestrial Ecosystem

Since different ecosystems have drastically different food chains and food webs, they can be better illustrated using examples of different communities. The first example is a land community, to provide an overview of terrestrial food chains and food webs. Plants such as maple trees and squash are the producers that occupy the first trophic level. Aphids, caterpillars, grasshoppers, and other animals that forage directly plants or plant tissues are primary consumers that occupy the second trophic level. Birds, spiders, and other insects that feed on primary consumers are secondary consumers occupying the third trophic level. Large birds, such as eagles, owls, and hawks, that eat secondary consumers are tertiary consumers making up the fourth trophic level. This food chain can go on to even higher trophic levels.

However, natural communities rarely contain well-defined groups of primary, secondary, and tertiary consumers in a linear pattern. In reality, a food web showing many interconnecting food chains in a community describes much more accurately the actual feeding relationships within a given land community. This is in part due to the omnivorous, or "eating all" nature of some animals. These animals include but are not limited to bears, rats, and raccoons. They act as primary, secondary, and even tertiary consumers at different times. Many carnivores will eat either herbivores or other carnivores, thus acting as secondary or tertiary consumers, respectively. An owl, for instance, is a secondary consumer when it eats a mouse, which feeds on plants, but a tertiary consumer when it eats a shrew, which feeds on insects. Once a shrew eats carnivorous insects, it is by itself a tertiary consumer, making the owl that feeds on the shrew a quaternary consumer that occupies the fifth trophic level. Since organisms are interlocked in such complex yet organized networks, disruption at any particular point of the food web (damage to one group of organisms) might have far-reaching effects on a whole community or ecosystem.

Food Chains and Food Webs in a Marine Ecosystem

Coral reefs will be used as an example for marine ecosystem. Reefs are created by concerted efforts of producers—algae—and consumers—corals. In warm tropical waters, with just the right combination of bottom depth, wave action, and nutrients, specialized algae and corals build reefs from their own calcium carbonate skeletons. The reef-building corals grow best at depths of less than forty meters, where light can penetrate and allow their algal partners to photosynthesize. Algae and corals are involved in a mutualistic relationship, where algae benefit from the high nitrogen, phosphorus, and carbon dioxide levels in the coral tissues. In return, algae provide food for the coral and help produce calcium carbonate, which forms the coral skeleton.

Coral reefs provide an anchoring place for many other algae, a home for bottom-dwelling animals, and shelter and food for the most diverse collection of invertebrates and fish in the oceans. In essence, algae is the producer that occupies the first trophic level. Corals that feed on algae are primary consumers sitting at the second trophic level. Many fish (such as blue tang) that feed on corals are secondary consumers occupying the third trophic level. Larger fish, such as sharks that eat small

Ecosystem Energetics

The diverse forms of life in all ecosystems are powered by a single energy source, sunlight, which enters the biosphere through a process called photosynthesis. Organisms such as plants and algae capture a small fraction of sunlight's energy, storing it as chemical energy in sugar or other complex organic molecules. The energy then passes through an ecosystem via different feeding (trophic) levels. Each time the energy is passed on, a portion of it is lost as heat. Thus, energy needs constant replenishment from the original source, the Sun.

How does energy flow through communities? It flows through ecosystem energetics. Of the energy that reaches Earth, much is either reflected or absorbed as heat by the atmosphere and Earth's surface, leaving only about 1 percent to power all life. Of this 1 percent, green plants capture 3 percent or less. All life on this planet is therefore supported by less than 0.03 percent of the energy reaching Earth from the Sun. Photosynthetic organisms are called autotrophs, or producers, because they produce food for themselves. Directly or indirectly, they produce food for nearly all other forms of life as well. Organisms that cannot photosynthesize are called heterotrophs, or consumers, because they must acquire energy prepackaged in the molecules of the bodies of other organisms.

There are three basic principles that govern ecosystem energetics. First, the amount of life an ecosystem can support is defined by the energy captured by the producers. This energy, made available to consumers over a given period, is called net primary productivity. It is usually measured in units of energy stored per unit area in a given period, or measured as biomass, the dry weight of the total organic material added to the ecosystem per unit area in a given time span. The net primary productivity is influenced by a variety of environmental factors, including the amount of sunlight, the availability of water, the amount of nutrients available to producers, and the temperature. Among all environmental variables, the most limiting variable is the one that determines net primary productivity, for instance, water in the desert or light in the deep ocean.

Second, within the community, energy is passed from one feeding level to another. Energy flow moves from producers to primary consumers to secondary and tertiary consumers. Primary consumers are normally herbivores that directly consume producers. Secondary and tertiary consumers are typically carnivores that eat meat of other consumers. Certain consumers may occupy more than one feeding level. As energy is passed through feeding levels via food chains or food webs, the transfer is never efficient. This is the third basic principle of ecosystem energetics. Each time the energy is transferred to the next feeding level, the bulk of it is lost as heat. On average, only 10 percent of the energy is transferred from one feeding level to the next. In other words, the higher the feeding level an organism occupies, the less energy is available to it. This so-called 10 percent law or energy pyramid puts a cap on how much life a particular ecosystem can sustain.

—Ming Y. Zheng

fishes, are tertiary consumers at the fourth trophic level. A vast array of zooplanktons, invertebrates such as sponges, the poisonous blue-ringed octopus, and so on, also live in coral reef ecosystems to make extremely complex marine food webs. For example, the Great Barrier Reef in Australia is home to more than two hundred species of coral, and a single reef may harbor three thousand species of fish, invertebrates, and algae.

Similar to terrestrial ecosystems, aquatic ecosystems are also prone to human disturbance. Of all aquatic or marine ecosystems, coral reefs are probably most sensitive to certain types of disturbance, especially silt caused by soil eroding from nearby land. As silt clouds the water, light is diminished and photosynthesis reduced, hampering the growth of the corals. Furthermore, as mud accumulates, reefs may eventually become buried and the entire magnificent community of diverse organisms destroyed. Another hazard is sewage and runoff from agriculture. The dramatic rise in fertilizer in near-shore water causes eutrophication, by which excessive growth of algae blocks sunlight from the corals, deprives corals of nutrients, and suffocates corals and other organisms. A third threat to coral reefs, overfishing, is also strictly a result of human interference. It is estimated that in over eighty countries, an array of species, including mollusks, turtles, fish, crustaceans, and even corals, are being harvested much faster than they can replace themselves. Collectively, these human activities had destroyed over 30 percent of coral reefs worldwide by year 2000. Assuming no effective measure is taken to preserve or restore coral reef ecosystems, another 50 percent of reefs will disappear by year 2030. The message is clear: Once humans disturb an ecosystem, through damaging one or more species in an intricately networked food web, balance and sustainability within the whole system is affected. The price for such disruption is high and far-reaching.

—Ming Y. Zheng

See also: Biodiversity; Biogeography; Carnivores; Chaparral; Digestion; Digestive tract; Ecosystems; Forests, coniferous; Forests, deciduous; Grasslands and prairies; Habitats and biomes; Herbivores; Ingestion; Lakes and rivers; Marine biology; Mountains; Nutrient requirements; Omnivores; Predation; Rain forests; Savannas; Symbiosis; Tidepools and beaches; Tundra.

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FORESTS, CONIFEROUS

Types of animal science: Ecology, geography
Fields of study: Conservation biology, ecology, environmental science

Coniferous forests are those in which the predominant species of trees carry their seeds in cones. Although conifers are often associated with cooler climates, they have wide global distribution. Conifers form the plant phylum Pinophyta and include such well-known species as sequoias, spruces, and cedars.

Principal Terms

CONIFER: member of the phylum Pinophyta, characterized by carrying seeds in cones and often having needlelike foliage

DECIDUOUS: trees which lose their leaves annually, such as maples and elms

GYMNOSPERM: a plant whose seeds are borne on seed scales arranged in cones

NAVAL STORES: conifers used for production of turpentine, pitch, and other materials once considered necessary for maintenance of navy vessels

TOLERANCE: ability of a tree to grow in the shade of other trees

Forests in which the dominant species of tree are members of the plant phylum Pinophyta are referred to as coniferous forests. Coniferous forests are often associated with cooler climates, such as the boreal forest stretching across northern Europe, Asia, and North America, but conifers are actually found in a wide range of climates and locations. Conifers are sometimes referred to as evergreens, meaning that the trees seemingly never lose their leaves, but not all conifers are evergreen, nor are all evergreens conifers.

Conifers do, in fact, lose their leaves, but with the exception of the larches (also known as tamaracks), which change color uniformly and shed their leaves seasonally, needle drop is a gradual process. Depending on the species, leaves will remain green and on the tree for many years rather than being replaced annually. The new growth replaces the dropped needles gradually enough that often only the thick mulch of dead needles at the base of pines, spruces, and other conifers provide definitive evidence that needle drop occurs. In some coniferous forests, the thick carpeting of needles on the woodland floor chokes out shade-tolerant species of vegetation, while the evergreen canopy blocking the sun discourages intolerant species from sprouting. Over time a pure stand of conifers may emerge, in which few other species of trees grow and even smaller trees of the same species are crowded out. Many conifers are highly shade intolerant, so a coniferous forest will thin itself naturally. The spreading branches of the taller trees will block the light needed by smaller ones. A mature stand of red pine, for example, will eventually be composed of so many trees of similar size and even spacing that natural red pine forests can be mistaken for artificially planted commercial stands.

Physical Characteristics of Conifers

Conifers take their name from the fact that their seeds are carried in cones and from the observation that many of the most widely recognized coniferous trees, such as spruces and pines, present a rather conical appearance, broad-based at the bottom and tapering symmetrically to a pointed top. The trunks of conifers rarely fork, but instead form a straight central trunk with branches radiating from it. In the event a conifer loses its tip, or leader, a branch near the break may shift its orientation to grow upward to replace the lost leader, while other branches will continue to radiate out horizontally. Not all conifers form such a neat appearance, however. The bristlecone pine is noted for its twisted, gnarled appearance, and many junipers and yews tend to sprawl rather than grow upright. The narrow, needlelike leaves of many conifers are another easily identifiable characteristic, although some conifers, such as the cedars, have leaves that are small and scalelike rather than needle-shaped.

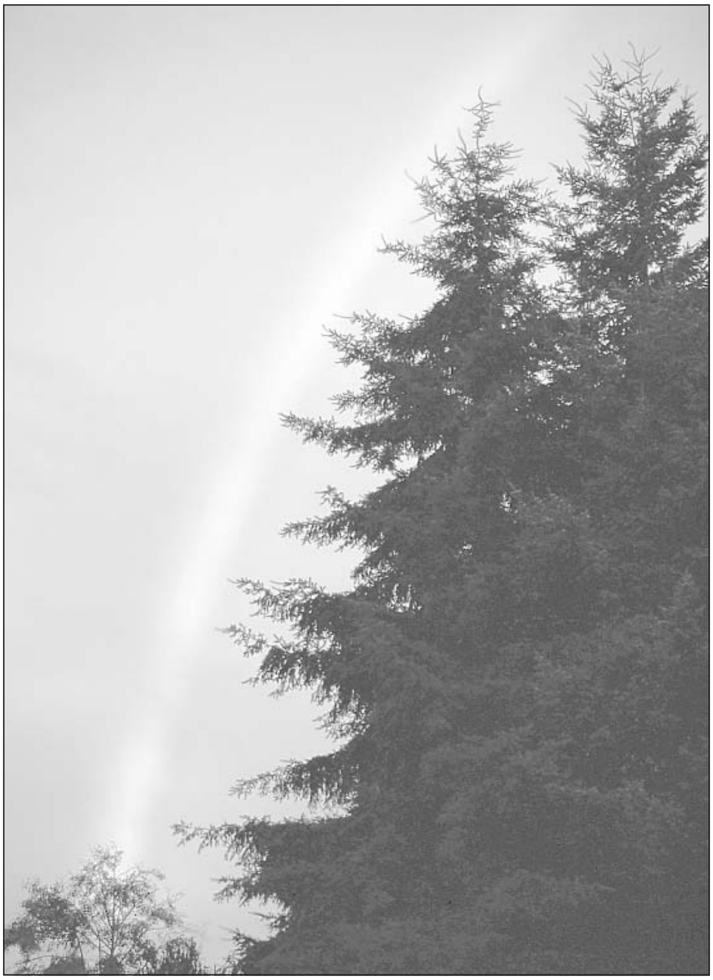
The long, straight trunk of many conifers has contributed to the trees being valued as a source of building materials. During past centuries, millions of acres of white pine forest in North America were cut, first for use as masts on sailing ships, and later for lumber for general construction. Species such as western red cedar, redwoods, and bald cypress continue to be prized for their natural resistance to rot and water damage, while Douglas fir and white spruce are important sources of construction lumber.

In addition to being cut for lumber, conifers are harvested for pulp and the production of chemicals. Prior to the introduction of petroleum products, sailing ships required huge quantities of pine tar. Governments would set aside forest reserves as naval stores, which meant that the trees were not to be cut for lumber. The conifers were instead reserved as a source for turpentine and pine tar, which were produced from the sap of conifers such as pitch pine. The bark of the trees were slashed to allow sap to run into pans for collection. The sap was then distilled into turpentine and pine tar.

Conifer Range

Although coniferous forests dominate the cooler regions of the globe, conifers are also found in tropical and desert regions. Cypress trees thrive in warm, swampy areas, such as the bayous of Louisiana, while piñons and other pines constitute the dominant species on the desert plateaus of the American southwest. The thin, waxy needles of conifers conserve moisture while allowing photosynthesis to occur year-round, an adaptation that serves conifers equally well in the harsh conditions of a subalpine mountain slope or during long Canadian winters.

Some mature conifers are also noted for their extremely thick bark, which reduces their vulnerability to fire. As recently as the 1990's, foresters continued to use fire routinely as a management tool in plantations of loblolly and southern yellow



Coniferous forests are composed of very tall trees with relatively little undergrowth. (Corbis) pines. Controlled burns removed the undesirable broadleaf species, such as rhododendrons, from the understory, while leaving the taller, thick-barked pines unharmed. Other species have evolved so that natural fire is a necessary part of the reproductive cycle. Until humanity began suppressing forest fires, fires triggered by lightning strikes were a common occurrence in many coniferous forests. The litter of dead needles and fallen branches on the ground rarely built up to catastrophic levels, and low intensity fires remained on the ground where they did little long-term harm to the forest. Lodgepole pine, for example, bears seed cones that will remain tightly closed for many years, until exposed to extreme heat. When fire sweeps through an area, it both clears the ground of competing species and opens the lodgepole pine cones, allowing for a new generation of trees to sprout.

Conifer Size and Age

Species of trees found in coniferous forests range from the stunted-looking spruces growing in the arctic taiga, where the boreal forest merges into the tundra, to the giant sequoias (*Sequoiadendron giganteum*) in the mountains of southern California. In far northern regions, spruce trees hundreds of years old may stand barely ten feet tall and be only a few inches in diameter. Sequoias, in contrast, are the most massive trees on earth, as they attain heights of 275 feet and diameters as large as 30 feet. Young sequoias present a pleasing symmetrical appearance, the typical cone shape of many conifers, but as the trees mature they often lose their tops to lightning strikes and become rather ragged and uneven looking. The largest sequoia on record measured 293 feet in height, with a diameter of 37 feet. Once widespread throughout North America, giant sequoias are now found only in isolated groves high in the mountains of California. A closely related species, the redwood (*Sequoia sempervirens*) is the dominant species in the forests along the Pacific coast in northern California and Oregon. Although redwoods grow as tall as sequoias, they do not achieve as a large a diameter, nor are they as long-lived. Redwoods are considered mature at 400 years and may live to 1,500. No sequoia is known to have died of old age, although mature trees have been killed by lightning strikes and fire.

The oldest known living examples of conifers, however, are not the mammoth redwoods and sequoias, but bristlecone pines found in the mountains of the North American West. Scientists have identified individual bristlecone trees over four thousand years old. Unlike the sequoias and the bristlecone pines, which may live for millennia, other conifers, such as balsam fir, are relatively short-lived, reaching maturity in only a few decades and dying off while less than a century old.

Based on the fossil record, scientists believe conifers have existed on earth much longer than the broad-leaved species of trees. Botanists speculate that conifers evolved from the giant fern trees common during the days when dinosaurs roamed the earth. Broad leaf trees, such as maples, are angiosperms, or plants whose flowers contain both male and female parts. Angiosperms are the most common plants on earth, with hundreds of thousands of different species growing in a wide range of environments. Angiosperms encase seeds within fruits, such as acorns, that both protect the seed and provide food for the embryonic plant. In contrast, the flowers of gymnosperms will be either male or female, never both at once, and seeds are set on scales arranged in cones. Although the flowers of gymnosperms are less complex than angiosperms, gymnosperms may have both male and female flowers on the same plant. Just as the needles of many conifers may remain on the tree for five or more years, so too do the cones of some species cling to the tree through many seasons. Sequoias, for example, will hold cones for as long as twenty years, with the cones remaining green and seemingly recently formed the entire time they are on the tree. Gymnosperms such as the conifers number fewer than one thousand species globally and are more limited in range than angiosperms.

Conifers as Habitat

All forests provide wildlife habitat on multiple levels, with some animals living on or under the forest floor, others taking advantage of resources available in the lower sections of the trees, and still others living in the canopy. Coniferous forests are no exception. Small rodents, such as chipmunks and mice, live in underground burrows, subsisting on seeds gathered from fallen cones. While the needles on conifers may not appear palatable to humans, deer, elk, and moose depend on conifers for winter browse. Moose, in particular, rely on conifers such as balsam fir as a primary food. Squirrels often thrive in dense spruce and balsam stands, building their nests high in the trees and rarely setting foot on the ground. A wide variety of small birds and mammals often dwell in coniferous forests, as the evergreen canopy provides a protective cover from large birds of prey such as eagles. Kirtland's warbler, the marbled murrelet, and the spotted owl are only a few examples of birds that call coniferous forests home.

—Nancy Farm Männikkö

See also: Chaparral; Ecosystems; Forests, deciduous; Grasslands and prairies; Habitats and biomes; Lakes and rivers; Mountains; Rain forests; Savannas; Tundra.

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FORESTS, DECIDUOUS

Types of animal science: Classification, ecology, reproduction
Fields of study: Anatomy, ecology, zoology

Deciduous forests contain trees that shed their leaves. Temperate deciduous forests shed their leaves in autumn, and monsoon or tropical deciduous forests do so in the dry season. They hold many animal species, including predators, omnivores, and herbivores.

Principal Terms

CARNIVORE: animal that eats other animals
DECIDUOUS: shedding or losing leaves at the end of a growing season
GESTATION: the term of pregnancy
HERBIVORE: animal that eats plants
OMNIVORE: animal that eats plants and animals

A forest is an aggregate of vegetation, mostly trees and other woody plants, on land that may encompass many square miles. Forests exist relatively unchanged over very long time periods, having in them lasting populations of specific trees, shrubs, grasses, and animals. The interactions of these creatures with each other and with the forest helps to maintain the status quo. The climate, soil, and geography of the region where a forest occurs determine the main tree types it contains and their locations in the aggregate. Within any section of a forest, dominant trees help to control the specific shrubs, herbs, and grasses that are present.

Forests are divided into ten types on the basis of tree leaf types and ambient climate. Two are deciduous temperate and deciduous monsoon or tropical forests. Deciduous temperate forests are exemplified by the typical forest of the eastern and midwestern United States, Balkan forests, and Scandinavian forests such as the ones in Norway. Deciduous temperate forests hold trees which lose their leaves in autumn, when the weather turns cold. Deciduous monsoon or tropical forests include those of Southeast Asia, western coastal Mexico, and Central America. The climate in those areas varies between long periods of heavy daily rainfall and dry periods during which trees shed their leaves.

Temperate Deciduous Forests

Typical temperate deciduous forests are those occurring in the mountains of southeastern Europe's Balkan Peninsula. These mountains begin at the western Romanian border and run south to the Bulgarian border. In Bulgaria, they turn east and run toward the Black Sea. The Balkans contain deciduous forests whose trees are mostly oak, ash, beech, birch, hazel, and maple. Elk, deer, foxes, wolves, badgers, weasels, martens, wild boar, lynx, bear, and roe deer are among larger animals found in them.

In the United States, over 40 percent of Wisconsin's land is forest. The southern part of the state has huge deciduous forests composed largely of maple, basswood, oak, elm, and hickory trees. Many animals inhabit the forests, including white-tailed deer, black bears, badgers, foxes, hares, porcupines, woodchucks, coyotes, skunks, mink, beavers, muskrats, wolves, martens, copperhead snakes, rattlesnakes, and lynx. In addition, wild birds include pheasant, ruffed grouse, partridges, robins, wrens, swallows, owls, chickadees, and eagles.

Forests also cover about one third of Norway. Scandinavian deciduous forests occur near the south and southwest coasts. The main trees in the forests are oak, ash, birch, hazel, elm, and maple. Elk, deer, foxes, otters, wolves, martens, pit vipers, other reptiles, and many birds inhabit the forests.

Fauna of Temperate Deciduous Forests
Among the interesting organisms in temperate deciduous forests are carnivores, including the weasel family (mustelids). These furry mammals weigh from a few ounces to one hundred pounds. They include weasels, martens, otters, skunks, and badgers. All have short legs and paws with five toes and sharp claws for grasping prey and burrowing. Beautiful mustelid fur is used in expensive fur garments. Mustelids have glands that make musks, which produce odors to mark territory or enable self-defense. Mustelid musk is most offensive in skunks, who use it in self-defense. Male and female mustelids live alone, except when mating. Mating seasons, gestation (two to nine months), and litter size (up to ten young) depend upon species. Life spans of those mustelids that reach old age are up to twenty-five years.

Lynx, also carnivores, are cats. They have very long legs and large paws, are found all through temperate and subarctic regions of the northern hemisphere, and can grow to three feet long. Most have hair tufts at each ear tip and are agile climbers, spending much of their time on the limbs of trees, waiting to ambush passing prey. Lynx live in caves and hollow trees. Their litters contain two to four offspring. The lynx of Europe, the United States, and Canada are different species.

Wolves belong to the dog family. The two wolf species are the gray (timber) wolves of Europe, Asia, and the New World and the red wolves of Texas and Louisiana. An adult timber wolf has a maximum body length of 6.5 feet and a weight of 185 pounds. These wolves are usually reddish-yellow to yellowish-gray, with white underbodies. Red wolves are smaller and darker colored. All wolves have powerful teeth and bushy tails. They live on prairies, in forests, and on mountains. In winter, their packs seek small animals, birds, and large mammals as prey. Wolves den in caves, hollow trees, or holes they dig. Breeding season is the spring, and a female has three to nine cubs, which stay with parents until the following winter.

Monsoon or Tropical Deciduous Forests
Deciduous monsoon or tropical forests, with their broadleaf trees, occur in southern Brazil and along highland slopes of the Andes, South America, Central America, and the lowlands of Mexico, a neotropical region. Its animals are quite varied and differ from those of all other continents, including North America north of Mexico's plateau region.

Deer and Elk

Deer and elk inhabit all temperate forests. The name deer denotes hoofed, artiodactyl mammals of the family Cervidae, whose males have bony, branching antlers that are shed and regrown annually. There are forty cervid species in the Americas, Asia, Europe, and North Africa. Most inhabit forests, especially deciduous forests. Deer species range in size from moose, seven feet tall at shoulder height, to tiny species only a foot tall.

Deer and elk eat the twigs, leaves, bark, and buds of bushes and trees, as well as grasses. They feed mostly at twilight. Does (or female moose) birth one or three offspring each year, after six- to ten-month gestations. In the United States, the most common deer is the white-tailed deer, known for a tail with a white underside. The American elk, or wapiti, is called the red deer in Europe. Moose—the largest deer in the world—found throughout the United States, are known as elk in Europe.

Dear and elk have compact bodies and long, powerful legs suited for woodland terrain. They are also fine swimmers. They are herbivorous ruminants (cud chewers). Also, their solid and bony antlers, unlike the hollow, permanent horns of other ruminants, form only in males. The antlers are used to make territorial markings and threaten or combat other males. Male moose have the largest antlers, which can be six feet wide and weigh fifty pounds.

Deciduous forests are usually composed of a wide variety of trees of different sizes, with a lot of undergrowth. (PhotoDisc)

Found throughout tropical deciduous forests, as well as in rainforests, are mammals confined to the neotropical region, such as monkeys different from those seen elsewhere. Ruminants such as cameloid llamas and alpacas graze forest meadows and carnivorous puma or jaguar eat them. Many neotropical birds such as tanagers, macaws, hawks, and condors also live in or seek prey in the deciduous forests and their open meadows. Reptiles include boas, bushmasters, fer-de-lance, and other poisonous snakes. Also present in these forests are peccaries, tapirs, capybaras, and agoutis.

Jaguars are the largest, most powerful American big cats. Found in Mexico and throughout Central and South America, they are most abundant in Central America and Brazil. Jaguars are the only big cats absent in Africa and Asia. They inhabit forests, swamps, and grasslands. Mature jaguars have lengths of seven feet, shoulder heights of two feet, and weights of 275 pounds. Their yellow coats are spotted with black rosettes, each a circle of spots around a central spot. Adept climbers and swimmers, jaguars eat a wide range of animals, such as peccaries, deer, tapirs, monkeys, agoutis, capybaras, birds, fish, and rodents.

Jaguars of either sex live alone except when mating, each maintaining a hunting territory. They have no set breeding season and gestation is about 3.5 months. Mothers give birth to two to four babies. They mate at age two years and have life spans up to twenty-two years. Jaguars are close to the top of the food chain in their environment.

Among the interesting animals that are prey for jaguars and pumas are tapirs. Brazilian tapirs have stocky bodies, short necks, and sturdy legs built to push through forests. They have short trunks with flexible "fingers" at the trunk tips. Trunk fingers bring leaves to their mouths. Nocturnal animals, Brazilian tapirs have short, stiff neck manes which provide some protection from predators. Tapirs have thick brown skins, and can attain lengths of 6 feet, heights of 2.5 feet, and weights of five hundred pounds. These herbivores eat grass, aquatic plants, leaves, buds, twigs, and fruit. They are solitary except when mating or nursing young. Mating occurs year round and gestation is 12.5 months. A mother births one offspring, which cannot mate until age two to three. Tapirs can live for over thirty years.

Peccaries, forest-dwelling pigs, are also prey for big cats. They inhabit high-altitude forests from Mexico to South America. These artiodactyls reach lengths of four feet, heights of two feet, and weights of one hundred pounds. They are gray-black to brown, have slender legs, and can run quite fast. Omnivorous, peccaries eat roots, seeds, fruits, and insects. They have tusks, which they use to dig and cut roots. Peccaries live in herds of up to one hundred. After mating, gestation is six months and produces two or three young, dependent on their mother for six months. Peccaries can mate at a year old and can live for up to ten years in the wild or twenty years in captivity.

Damaging Deciduous Forests

A deciduous forest is a self-sustaining ecosystem. In it, interactions of trees, shrubs, and grasses help to maintain viability and forest identity. Added to this, appropriate interaction of plants and resident herbivores help to assure that plant species do not overgrow and damage the balance or severely change the status quo that gives the forest its identity. In addition, predation by forest carnivores adds to the picture by assuring that herbivores do not become so plentiful that they overgraze the forest and alter its identity.

Any untoward alteration of the population of an animal species in a deciduous forest has a ripple effect which profoundly alters the sum of relationships that, taken together, lead to forest continuity of identity. For example, decreasing numbers of wolves in deciduous forests due to their hunting by humans has damaged food webs in forests, where their predation helped to prevent overpopulation of herbivores such as deer. Deer overpopulation, in turn, caused overgrazing of many forest areas, followed by starvation of the excessive number of deer. The overgrazing also has damaged the lives of many other plant and animal species because of the lack of the ability of such forests to provide for their needs. Thus it is crucial to assure that appropriate numbers of all plants and animals inhabit deciduous forests by suitable monitoring and conservation measures, if it is desired to maintain them in their primal states.

—*Sanford S. Singer*

See also: Chaparral; Ecosystems; Forests, coniferous; Grasslands and prairies; Habitats and biomes; Lakes and rivers; Mountains; Rain forests; Savannas; Tundra.

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FOSSILS

Types of animal science: Classification, evolution
Fields of study: Evolutionary science, paleontology, systematics (taxonomy)

Fossils are the preserved remains of once-living organisms or the traces left by biological activity. They provide a record of the development of life through time and are used extensively in evolutionary studies as well as in the dating of rocks and the interpretation of past environments.

Principal Terms

BIOSTRATIGRAPHY: the dating of rocks using fossils
CAMBRIAN: the period of time between 544 and 505 million years ago
ICHNOLOGY: the study of trace fossils
PALEONTOLOGISTS: scientists who study fossils
TAPHONOMY: the study of the processes that lead to fossilisation
ZONE FOSSILS: fossils that characterize a period of time and can be used to provide a relative date for a rock

Fossils are now recognized as the remains of once-living organisms; however, in the past the term was not so restricted and included anything dug out of the ground (Latin *fossilis*, "to dig up"). Thus minerals, gems, and archaeological remains were all included as fossils. The record of fossils goes back 3.4 billion years to preserved single-celled organisms such as bacteria and blue-green algae. Complex organisms or metazoans did not appear until about 700 million years ago, and hard parts were not preserved until about 544 million years ago, at the base of the Cambrian when there was a tremendous development of organisms often called the Cambrian Explosion. Since then, a diverse assemblage of fossil organisms is available for study by paleontologists.

Recognition of Fossils

Early ideas about the source of fossils were that they were the remains of mythical animals or that they had grown in the rocks like crystals. Aristotle suggested that the fossils of fish were the remains of sea animals that had swum into cracks in the rocks and become stranded, while others thought that they developed from seeds or grew from fish spawn washed into cracks during Noah's Flood. These ideas remained an important influence until the Renaissance, when Leonardo da Vinci recognized that fossil shells in the Apennines represented ancient marine life, and Nicolaus Steno in the mid 1600's showed that "tongue stones," thought to be the petrified tongues of dragons, were actually ancient shark teeth. At about the same time that Steno was writing, the British scientist Robert Hooke studied and described fossils and used early microscopes to study their cellular structure. However, their ideas were slow to become accepted, and it was not until the mid 1700's that naturalistic concepts of fossils began to prevail; when Linnaeus published his classification of all organisms, the *Systema Naturae* (1735; *A General System of Nature*, 1800-1801), fossils were treated as living organisms. By 1800, Baron Georges Cuvier was able to apply comparative anatomy to fossil organisms, both showing their relation to modern organisms and arguing that they must represent extinct animals, as they had not been found living on even the most remote continents. Prior to this, the fact of extinction was not accepted, as it went against the view that

God would not allow any of his creations to become extinct. Cuvier also recognized that fossils occur in a regular succession and can thus be used to date the sediments in which they are found. At about the same time, this fact was also recognized by William Smith in England, who developed it to the point that he was able to produce geological maps of England and Wales in 1815. This was the basis of dating and mapping rocks, and by the time of the publication of Charles Darwin's *On the Origin of Species* in 1859, the understanding of the fossil record had reached the point where few scholars took biblical ideas about the history and evolution of life literally.

Fossilization

Fossilization is a rare occurrence, and it has been estimated that of the more than one million living species, only 10 percent are likely to be preserved as fossils. A single square meter of seafloor could, during a few million years, produce enough sea shells to swamp the museums of the world if they were all preserved. It must be appreciated, therefore, that the fossil record is selective and thus may be incomplete and biased. This is because some organisms with hard parts, such as shells or skeletons, tend to fossilize readily, and therefore much is known about their past. Others are soft-bodied and rarely if ever fossilize, so their fossil record is minimal. The study of how organisms become fossils, the study of death and decay, is called taphonomy. This is now an important area of paleontology, because to understand and interpret the fossil record it is necessary to understand the processes that have resulted in fossilization. Once an organism dies, its remains are subject to

Image Not Available

decay and perhaps transport and mechanical breakdown before they are buried. The more of that lost information that can be reconstructed, the more reliable the final hypothesis about the original community will be.

Preservation is dependent on a number of factors, of which the most important are the composition and structure of the organism, its abundance, the sedimentary environment in which it lives, and the postdepositional changes that occur. All organisms are composed of delicate tissues, known as soft parts, but many also have more resistant tissues, referred to as hard parts. The hard parts may be mineralized, as in the shell of bivalves, or composed of organic material, such as the chitin that makes up the exoskeleton of arthropods. Although in general the possession of mineralized hard parts is a prerequisite for fossilization, soft-part preservation can occur, and some fossil groups have only organic soft parts.

In a few exceptional cases, organisms are preserved entire, and this results from unusual preservational circumstances. Woolly mammoths have been preserved by freeze-drying, so that their soft tissues and even their last meals are preserved, and humans have been found completely preserved in peat bogs. Preservation in amber occurs when small organisms are trapped by tree resin that subsequently hardens around them, and in some cases the preservation is so good that original biomolecules can be extracted and deoxyribonucleic acid (DNA) sequencing carried out. Although this was the premise of the film *Jurassic Park* (1993), it is clear that the genetic material is so incomplete that it will never be possible to reconstruct a complete organism in this way.

In most cases, the soft tissue has been lost and some change has taken place to the hard tissues during the process of fossilization. Permineralization is the process by which the natural pores in wood, bone, or shell are filled with minerals by groundwater that percolates through them in the sediment. In this case, none of the original material is lost, and even in petrified wood there is still some of the original material, although the logs have been completely permeated by silica. Only part of the original material is preserved in carbonization, a process in which most of the volatile organic materials disperse, leaving a black carbon film. This may result in exceptional preservation in insects, for instance, or ichthyosaurs (marine reptiles) in which the outline of the body is preserved as a carbon film. More frequently, the hard tissues are recrystallized or are replaced by some other mineral. Recrystallization results in the loss of internal detail, and the same is true of replacement, as in both cases none of the detailed structure is left. However, replacement by more resistant minerals, such as the replacement of a calcite shell by silica, can improve the survival potential of a fossil and preserve delicate structures, such as spines, that might otherwise be lost.

Preservation Potential

The preservation potential of an organism is affected by a number of factors that operate at different stages in the process of fossilization. Necrolysis, or the breakup and decay of an organism after death, reduces the potential for preservation of all but the most resistant organisms, and it has been estimated that only 20 to 30 percent of shallow marine organisms are likely to be preserved. The numerical abundance of organisms is generally considered to be important as, all other things being equal, abundant organisms would seem to be more likely to be preserved than rare ones. However, in a number of cases this has been shown not to be true, and this differential preservation is often related to the preservability of the hard tissues. Mobile organisms tend to have lighter and less durable skeletons that would be more easily destroyed than those of static animals such as corals, in which the skeleton is formed of a solid mass of calcite.

A number of agents may operate to destroy even resistant skeletons. Biological agents include scavengers, which may break up shells and bones to extract nutrition, and burrowing organisms, which may use the hard tissues as a substrate and thus weaken them. Mechanical agents such as wind, waves, and currents can also be very effective, particularly in shallow environments where

Lagerstätten

Although generally only a small proportion of organisms become fossilized, there are a number of examples in the fossil record in which there are unusual concentrations of fossils or in which the fossils are remarkably well preserved. These are termed "fossil *Lagerstätten*," a term that derives from the German mining tradition in which *Lagerstätte* are rocks containing constituents of economic interest. These exceptional fossil occurrences are separated into concentration *Lagerstätten*, in which there are uncommon concentrations of fossils, although their preservation may be unremarkable, and conservation *Lagerstätten*, in which the individual quality of preservation is unusual. Concentration deposits often occur in situations in which fossils have been preserved initially in an unconsolidated sediment and then eroded and redeposited together with more recent material. Conservation deposits include some of the most celebrated and famous fossil occurrences, including the Late Jurassic Solnhofen Limestone in Germany, which has yielded fossils of *Archaeopteryx*, the earliest known bird, and the Burgess Shale in the Canadian Rockies, which provides a window on the development of organisms during the Cambrian, 530 million years ago. In the Burgess Shale, the organisms were transported from a carbonate bank area into deep, anoxic waters by submarine landslides, where they were buried in fine muds and thus protected from decay. This has resulted in the preservation of soft-bodied organisms as well as those with hard parts, and has provided evidence for the presence of many unique and sometimes bizarre animals that would otherwise be completely unknown. Although most of these fossils can be assigned to existing phyla, many are considered to be evolutionary experiments that did not survive into later periods, thus demonstrating that there was a great deal of experimentation in body plans during the Cambrian, most of which did not survive.

energy is highest. Experiments in which shells were tumbled with pebbles have shown that thin-shelled organisms break up quickly, while thicker shells last longer. Similar studies for terrestrial vertebrates have shown that the least durable parts of a skeleton are the ribs and vertebrae, while the skull, jaws, and particularly the teeth are the most resistant to breakdown. In general, it appears that the shape, density, and thickness of the bone or shell are the most important factors in determining its survival during mechanical transport.

Many apparently unfossiliferous rocks may have had fossils at one time but lost them during the changes that take place in sediments after deposition. Many snails and bivalves have shells composed of the unstable form of calcite called aragonite, and this may dissolve early, leaving no trace of the fossil, while other organisms composed of more stable calcite will not be dissolved. In these cases, therefore, the representation of the original community will be biased more by the chemical composition of shells than by their mechanical durability or by their relative abundance.

Trace Fossils

Trace fossils (or ichnofossils, from the Greek *ichnos*, "track") are sedimentary structures created by organisms and, therefore, reflect their behavior. They include tracks, trails, burrows, and borings and may occur in sediments that contain no body fossils, thus providing the only record of life and certainly the only record of soft-bodied organisms that are not normally preserved. One important aspect of trace fossils is that they are almost always preserved in place, as reworking would result in their destruction, and thus they can always be directly related to the sediments in which they are found. Because of this, trace fossils are particularly important in understanding and reconstructing paleoenvironments.

Trace fossils are difficult to classify, as they represent behavior rather than the remains of an animal. They are also difficult to relate to the animal that formed them, as traces are rarely found with the organism that made them, different organisms may form similar traces, and the same organism may form a variety of different traces in different circumstances. Because of these problems, traces are organized within behavioral categories, including dwelling structures made by organisms that feed outside their burrows; mining structures that are formed by animals feeding in the sediment; grazing traces made by animals feeding across a surface; locomotion traces formed by animals during travel; and resting traces formed by an animal during a temporary stop. Thus, dinosaur tracks would come within the locomotion category and the burrow of a filter-feeding worm would be recognized as a dwelling structure.

Understanding the behavioral genesis of trace fossils has enabled their use in reconstructing past environments. They are grouped in recurrent ichnofacies (traces reflecting a particular environment), and these are in turn linked to a set of environmental parameters, such as salinity, light level, and temperature, that are generally correlated with depth. This approach has been particularly valuable in recognizing shallow marine facies and has the advantage of being independent of time, as particular environments and, therefore, behavior persist through time, although the trace formers themselves may change.

The study of marine traces is relatively recent; however, terrestrial traces have been studied for much longer, as the first dinosaur tracks were reported in 1802, although they were misidentified as bird tracks at that time. Terrestrial trackways can give a considerable amount of information about the locomotion and behavior of the trace former, and can lead to quite precise information about speed, as well as insights into posture, activity levels, and metabolism. Relative speed is related to the length of the leg and the stride length (the distance between one foot impression and the next by the same foot). Hip height (calculated from foot length) is divided into the stride length (measured from the trackway) to give a proportional estimate of the speed. At 2.0 an animal moves from walking to trotting, and above 2.9 it is running, information that has been used in studies of dinosaur locomotion. In addition, the fact that trackways show dinosaurs moving together in herds has been used to suggest a level of social organization greater than that demonstrated by any modern reptiles.

Fossils and Time

In geology, both relative time and measured time are recognized. Measured time is obtained from the decay rates of certain radioactive minerals in rocks and gives a date in years. Relative time refers only to the sequence of strata, showing that some beds are older or younger than others. Although the relative age of rocks can be obtained from their sequence, as those lower in the sequence are older and those higher in the sequence are younger, the lithology of the rocks cannot be carried laterally, because sedimentary environments change over distance. This problem was resolved in the late 1700's in England by William Smith, who recognized that there was a sequence to the fossils in the sedimentary record and that this could be used to characterize the rocks and correlate them to each other over a distance. This recognition of "faunal succession," which represents the successive preservation of organisms as they evolved through time, has been extremely important in the development of the study of biostratigraphy, in which fossils are used to provide dates for rocks. In this system, the basic unit is the zone, which is represented by zone or index fossils that characterize a period of time. The potential of different organisms as zone fossils will vary, and to be most useful they should embody certain characteristics. They must have a high preservation potential, be relatively common, and also be distinctive, so that accurate identification is possible. They must also have a wide lateral distribution but a short vertical range, so that they characterize a short time period over a wide area. It is also helpful if they are independent of environment. Because of this and because most sediments are marine in origin, the organisms used are often planktonic, that is, they float near the surface of the ocean but will be preserved in various sedimentary environments when they die. Microfossils, such as spores and pollen, are very useful because they are wind-borne and thus may be found in both terrestrial and aquatic environments.

—David K. Elliott

See also: *Allosaurus*; *Apatosaurus*; *Archaeopteryx*; Dinosaurs; Evolution: Animal life; Extinction; Hadrosaurs, Ichthyosaurs; Paleoecology; Paleontology; Prehistoric animals; Pterosaurs; Sauropods; Stegosaurs; *Triceratops*; *Tyrannosaurus;* Velociraptors.

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FOXES

Type of animal science: Classification
Fields of study: Anatomy, ecology, evolutionary science, physiology, reproduction science, systematics (taxonomy), wildlife ecology, zoology

There are approximately twenty-one species of fox, in the order Carnivora. Foxes constitute only 0.5 percent of the four thousand mammalian species, but play a very important role in the environment.

Principal Terms

CANID: doglike in appearance
ESTRUS: the period of maximum sexual receptivity
TEMPERATE: moderate with respect to temperature
TERRITORY: the area of land that an animal defends against intruders
VIXEN: a female fox

The fox is a canid, related to coyotes, jackals, and wolves. The fox is the smallest member of the dog family. It is also the most numerous and widespread carnivore in the world. Although primarily carnivorous, foxes will also eat fruits and grains. Foxes hold territories, the size of which depends on habitat. A dog fox, a vixen, and their cubs occupy each territory. A differing number of chromosomes eliminate the possibility of foxes interbreeding with other canids.

Fox populations fluctuate along with the population cycles of their prey. In many cases, availability of dens and secure sites for hiding will also play an important role in population size. Foxes have few natural predators. However, in mountainous regions, coyotes and cougars will sometimes attack foxes. In arid lands, wild dogs, large cats, and hyenas are problematic, and will often compete with foxes for food. In arctic regions, the wolf can also be a dangerous competitor.

Foxes appear to have characteristics of both dogs and cats. Some of their catlike characteristics include vertical slit eyes, partially retractable claws, light body weight, and a stalking and pouncing style of hunting. Foxes are also good tree climbers. Fox coloration varies among black, red, silver, silver-gray and white.

The Life Cycle of Foxes

During December and January, vixens leave scent marks that tell the male fox she is in estrus. The dog will follow the marks until he finds her. The courtship is very short, since the vixen is only fertile for about one week each year. Litter sizes are normally one to six. The dog fox helps the vixen

Fox Facts

Classification:
Kingdom: Animalia
Subkingdom: Deuterostomia
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Subclass: Eutheria
Order: Carnivora
Family: Canidae
Genus: Vulpes, with twelve species
Geographical location: All continents except Antarctica
Habitat: Temperate climates, although some live in desert and Arctic regions; generally next to water, meadows, and forests
Gestational period: Fifty to sixty days
Life span: Up to six years in the wild; up to thirteen years in captivity
Special anatomy: Pointy muzzles, large ears, long thin bodies, long legs, long bushy tails

Foxes are territorial and will drive off outsiders who intrude on their range. (Corbis)

raise the cubs during the first two months. For the first month or so, the vixen depends entirely on the dog fox to bring her food. In the first two weeks, the cubs are unable to see or hear anything. They are fed by the mother's milk. The fur is short and black. After three weeks, the fur will slowly turn dark brown on the head, and gray on the body. The teeth break through the gum, and the cub starts to chew on anything. Soon the cub starts to show the first signs of social behavior, and the first fights are fought between the siblings. After four weeks, the cubs start exploring the world outside the den for the first time. Later, they start to follow their mother when she goes hunting. In the summer, the young foxes get more and more independent from the mother fox. After about three months, the dog fox will go back to his solitary lifestyle, but he will try to find the same vixen again when the mating season comes back. In the fall, the young foxes come into puberty and become sexually mature. It is then that the vixen begins to force the cubs out of the den.

Destructive and Beneficial Foxes

Foxes may cause serious problems for farmers. Losses may be heavy in small farm flocks of chickens, ducks, and geese. Damage by foxes can be difficult to detect because the prey is usually carried from the kill site to a den, or uneaten parts are buried. Foxes will also scavenge carcasses, making the actual cause of death difficult to determine.

Like other scavengers, foxes will clean up carcasses, or kill dying or weak animals for food. In this manner they are a major contributor to the processes of natural selection.

—*Jason A. Hubbart*

See also: Carnivores; Cats; Dogs, wolves, and coyotes; Predation; Scavengers; Urban and suburban wildlife.

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FROGS AND TOADS

Types of animal science: Anatomy, classification
Fields of study: Anatomy, conservation biology, herpetology, systematics (taxonomy)

The more than four thousand living species of frogs and toads are classified in the order Anura. Most species have a biphasic life cycle, in which a larval stage, the tadpole, develops in water (or land, in some species) and undergoes an abrupt metamorphosis into the adult body form.

Principal Terms

EXTERNAL FERTILIZATION: the union of eggs and sperm in the environment, rather than in the female's body

GRANULAR GLANDS: one of many kinds of glands in the skin of frogs and toads; granular glands secrete toxins for defense from predators

METAMORPHOSIS: an abrupt change from a larval body form, accompanied by many physiological changes, into an adult body form

REPRODUCTIVE MODE: a combination of life-history characteristics, including egg-deposition site and type of parental care

TADPOLE: the larval stage of frogs and toads

Frogs and toads, the Anura, are amphibians, a group of vertebrates that first evolved in the Devonian era, about 400 million years ago. Two other groups of amphibians are the Caudata, salamanders and newts, and the Gymnophiona, caecilians. More than four thousand species of frogs and toads currently inhabit the planet. In contrast, about 400 species of salamanders and newts and 165 species of caecilians are extant. Frogs and toads thus account for approximately 88 percent of all living amphibians.

Amphibians have many unique characteristics that separate them from other vertebrates. In terms of skeletal features, the skull articulates with the vertebral column by a specialized vertebra called the atlas, and ribs are lacking in most frogs and toads. Many amphibians have a two-phase life history, an aquatic larval stage and a terrestrial adult stage, although some species may be entirely terrestrial or entirely aquatic. Amphibian skin is unlike that of other vertebrates in that it is glandular and lacks scales, feathers, or hair. Respiration is by means of the skin, which is porous, freely permitting the exchange of oxygen and carbon dioxide, with gills in aquatic larvae and adults, and lungs in terrestrial species.

Scientists classify frogs and toads into twenty-five families. Although the terms "frog" and "toad" are commonly used, toads are simply a specialized group of frogs. The true toads are in the family Bufonidae. They are distinguished from other families by a number of osteological (bony) features, and they also typically have thick, glandular skin with wartlike pustules. Many species have large parotoid glands that produce toxic secretions located on the back of the head. In contrast, most frogs have smooth skin and no parotoid glands. Toads in the family Bufonidae can generally withstand drier conditions than frogs. Other kinds of frogs have common names that include the word "toad," such as spadefoot toads, which are in the family Pelobatidae, or narrow-mouth toads, which are in the family Microhylidae.

Anatomy of Adult Frogs and Toads

Frogs and toads are tailless amphibians. In general, they are small animals; the largest has a body length of about three hundred millimeters, whereas the smallest is under ten millimeters.

They have a truncated body with a greatly reduced number of vertebrae and elongated hindlimbs. The vertebrae in the lower part of the body are fused into a rodlike structure, which provides rigidity for their jumping mode of locomotion.

Two types of glands are present in the skin of all adult amphibians: mucous and granular. Mucous glands continuously secrete mucopolysaccharides, which function to keep the skin moist so that cutaneous respiration can occur. All amphibians, including frogs and toads, have granular or poison glands in their skin, and these glands produce a variety of toxic or noxious chemicals used for defense. The chemicals are broadly classified into four major groups, of which alkaloids are one. The great majority of these chemicals are not harmful or deadly to humans, but they can be irritating. For example, if a secretion from one of the tree frogs found in the eastern United States is rubbed into the eyes, an intense burning sensation will be felt for a short time. If a frog or toad is grabbed by a predator, such as a bird or a snake, it may be quickly released because of the bad-tasting secretion. Some predators have evolved an immunity to the secretions, however, so frogs and toads are not free from predation.

Anatomy of Tadpoles

Frogs and toads are unique among amphibians in that the young, called tadpoles, are very different from adults in morphology and physiology. Tadpoles typically have a round, globular body, with a long tapering tail. After a period of time that varies from one to two weeks to several years, depending on species, the larval forms undergo metamorphosis and change into adult frogs. Many radical changes, initiated by the hormone thyroxin, occur during this period. The most obvious of these is the loss of the tail, which is gradually absorbed, and the growth of the limbs. The hindlimbs begin to develop early in the tadpole stage, but are held flat against the body and are not used until they are quite large. The front limbs develop at the same rate, but they are hidden beneath the operculum, a thin layer of skin that covers the gills. At metamorphosis, as the tail is absorbed, the hindlimbs enlarge and the forelimbs break through the operculum.

The tadpoles of most species of frogs are herbivorous or detritivorous, and the digestive system consists of a long, coiled intestine. At transformation, the digestive system undergoes a radical modification,

Frog and Toad Facts

Classification:
Kingdom: Animalia
Phylum: Vertebrata
Class: Amphibia
Subclass: Lepospondyli
Order: Anura
Families: Twenty-five, including Ascaphidae (tailed frogs), Bufonidae (true toads), Centrolenidae (glass frogs), Dendrobatidae (poison frogs), Hylidae (treefrogs), Leptodactylidae (tropical frogs), Microhylidae (narrowmouth toads), Pelobatidae (spadefoot toads), Ranidae (true frogs)

Geographical location: Throughout the world, except for the Arctic, Antarctica, some oceanic islands, and some very dry deserts

Habitat: Many habitats, including forests, savannas, prairies, freshwater ponds and streams, and ephemeral pools

Gestational period: Varies among species; some toads and spadefoot toads have a tadpole stage that lasts only for ten days to two weeks; in other species, such as bullfrogs, the tadpole stage may last for three years; in many species, the tadpole stage extends for about two months

Life span: Varies among species; less than a year in many species to as much as six to thirty-six years in some species, particularly for individuals kept in captivity

Special anatomy: Truncated head and body with no neck; long back legs that facilitate jumping; tadpole anatomy, globose body with long tail, very different from adult body shape

Declines in frog populations may be linked to pollutants in the water where they live. (Adobe)

and the long, coiled intestine becomes greatly shortened and divided into a distinct esophagus, stomach, small intestine, and large intestine. The internal gills of the tadpole are lost, and the lungs become fully functional. In many species, the lungs begin to develop and become partially functional long before metamorphosis. Tadpoles of these species are frequently seen rising to the surface of the water to gulp air.

Tadpoles have unusual mouthparts, consisting of a fleshy disc surrounded by small papillae; the disc has rows of small "teeth" that are not the same as the teeth of the adult. The actual opening of the mouth is surrounded by beaklike structures that have sharp, serrated edges. The rows of teeth serve to anchor the disc, and the beak is used to scrape algae and other detritus from the substrate. The food is captured by strands of mucus in the mouth that carry it into the digestive tract. At metamorphosis, the tadpole's mouthparts are completely shed and the adult mouth develops.

Life History of Frogs and Toads

The life history of frogs and toads includes four stages: egg, larva, juvenile, and adult. Eggs consist of an egg cell supplied with yolk surrounded by a varying number of mucoid capsules. Because the eggs have no shells and are susceptible to drying out, they must remain in water or in a humid environment.

In temperate zones (nontropical areas), frogs and toads generally breed in the spring and summer when temperature and moisture conditions are suitable. Some, such as chorus frogs, spring peepers, and wood frogs, begin breeding very early, usually in February, while ponds are still covered with ice. Others, such as American toads and leopard frogs, breed later in the spring, and

Reproductive Modes of Frogs

Gladiator frogs are large treefrogs that construct nests in which eggs are deposited. Nests are made by males, who pivot around in soft sand or mud at the edge of a pond or stream to make a depression that fills with water. Eggs are deposited as a surface film in the nest.

Glass frogs deposit a small clutch of eggs on a leaf overhanging a small stream or river. When the eggs hatch, the tadpoles fall into the water below.

Leptodactylus frogs construct foam nests for their eggs. An amplexing male and female rotate their legs rapidly and secretions emitted with the eggs and sperm are whipped into a meringuelike froth. Eggs and tadpoles develop entirely within the foam; most predators cannot enter the sticky foam.

Poison frogs deposit their small clutches of eggs on land. The male (but sometimes the female) guards them. After the eggs hatch, the parent transports the tadpoles on his or her back to a small pool or stream where the tadpoles undergo the rest of their development.

Eleutherodactylus frogs deposit small clutches of eggs on land. Development of the egg to a small froglet occurs entirely within the egg capsule.

Gastric-brooding frogs swallow their eggs, and development of the tadpoles occurs in the mother's stomach. A chemical secreted by the developing tadpoles inhibits the production of gastric fluids so that the tadpoles are not digested.

still others, such as bullfrogs and cricket frogs, breed primarily in the summer months.

Most temperate-zone frogs migrate to ponds during rains to breed. Males arrive first and begin calling to attract females. Each species of frog and toad has a unique call, so it can be identified only by sound. Frogs make more than one kind of call. The most common calls, termed advertisement calls, are of three kinds: the courtship call, which is used to attract females; the territorial call, used in response to the call of a nearby male that may be intruding on the caller's territory; and the encounter call, used when two males in a breeding chorus are very close. The latter call may be accompanied by grappling or fighting between the two males.

Although female frogs do not make advertisement calls, those of some species (and males, too) can produce a very dramatic distress call when grabbed by a predator. This call is produced with the mouth wide open and is a very loud piercing scream. Some types of predators are startled by this call and will release the frog. Snakes, however, have no ears and do not seem to be affected by the distress call.

Frogs and toads have external fertilization. When a female approaches and nudges a calling male, he will climb atop her and clasp her with his arms behind her arms; this position is called amplexus. The pair floats in the water and simultaneously expels eggs and sperm in the water; thus, fertilization of the eggs occurs outside the female's body.

Eggs generally require several days to one week to hatch, depending on temperature and the species of frog or toad. After hatching, tadpoles of most species disperse throughout the pond to feed and grow. Tadpoles of some species, however, congregate together in schools, similar to fish. Many species of toads, for example, have small, black tadpoles that form tight schools in shallow water at the edges of ponds. Most tadpoles eat algae and other kinds of detritus that they scrape from the substrate of ponds or streams in which they live. A few kinds of tadpoles are predaceous and eat other tadpoles or mosquito larvae and other small aquatic insects. Tadpoles undergo a period of development and then metamorphose into the adult body shape.

Frogs and toads have evolved numerous ways of removing their eggs or tadpoles from aquatic situations, where, presumably, density of egg and tadpole predators is high. Scientists have identified thirty kinds of reproductive modes in frogs and toads, mostly in tropical species. Because tropical regions have high rainfall and warm temperatures, frogs can deposit their eggs on land without risk of desiccation.

Declining Amphibian Populations

Populations of frogs and toads in many parts of the world, even in pristine (undisturbed) locations, are declining and disappearing. The causes of these declines are numerous, and many scientists are now conducting research to determine the causes of the declines. Some of the causes are obvious. For example, habitat destruction is a major cause of loss of many animals and plants, not just amphibians. Most recently, frogs and toads of many species in rain forests in Central America and Australia are reported to have been killed by a type of fungus called a chytrid. The fungus normally infects decaying matter, so why it is now infecting frogs is not yet understood. One theory is that frogs are being stressed by some other environmental problem not yet identified; this stress may reduce the ability of their immune systems to fight disease.

Also being investigated as possible causes of frog population declines are the use of agricultural chemicals and pesticides, acid rain, ozone depletion leading to a rise in ultraviolet (UV-B) radiation, environmental estrogens, and introduction of fish that prey on eggs and tadpoles. It is possible that at any one location, one or several of these factors may be interacting.

—Janalee P. Caldwell

See also: Amphibians; Chameleons; Communication; Defense mechanisms; Ecosystems; Metamorphosis; Salamanders and newts; Vocalizations.

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FUR AND HAIR

Type of animal science: Anatomy
Fields of study: Physiology, zoology

Fur is the hairy covering of the skin of a mammal. This covering is called fur when its individual hairs are fine and spaced closely together; when the hair is soft, kinky, and matted together, it is called wool, which grows in a fleece, and when it consists of coarse, stiff hairs, it is called bristles, or when pointed, spines or quills. Its primary role is as protection, insulation, and ornamentation.

Principal Terms

CORTEX: the main part of a hair, made of pigment-containing cells, surrounding a central medulla

CUTICLE: the outermost layer of a hair, made of scales

EPIDERMIS: the dead, outermost portion of the skin

FOLLICLE: the saclike organ from which a hair grows; its blood vessels nourish the hair

KERATIN: a tough fibrous protein, seen in large quantities in epidermal structures such as hair

MEDULLA: the innermost layer of a hair

SHAFT: the main hair part, made of dead cells arranged in a complex fashion

The term fur is used in several ways. All are related to its being the hairy covering of the skin of a mammal. In its most common usage, fur is the dense, hairy body covering of a mammal. However, even the sparse hair covering on the arms and legs of humans may be viewed as fur, since it is the hairy covering of the skin of a mammal.

Each individual hair in a mammal is a threadlike epidermis outgrowth. Collectively, hairs form the body coverings (or pelage) of all mammals. Each hair is made mostly of a fibrous, sulfur-containing protein called keratin. The pelage is most correctly called fur when its individual hairs are fine and spaced closely together. In cases where the hair is soft, kinky, and matted together, the pelage is wool, which grows in a fleece. Coarse, stiff hairs are bristles, and when pointed (as in porcupines) they are spines or quills. Hair grows on most parts of the bodies of mammals. As their body covering, its primary role is as protection, insulation, and ornamentation, like bird feathers and reptile scales.

The Structure of a Hair

Any hair consists of two main parts, the root and the shaft. The shaft is the hair part outside of the skin. It contains the hair's unattached end. Hair shaft cross-sections range from round to flattened. Due to their composition, round and flat hairs are straight and curly, respectively. Hair shafts consist of dead epithelial cells, arranged in columns which surround a central medulla (or core), covered with flat scales. The scales—a hair's cuticle—overlap like roof shingles, but their free ends face upward, away from the hair's root. Beneath the cuticle is a second layer of dead cells, the cortex, which surrounds a central core made of yet other dead cells (the medulla).

The cortex, which makes up most of each hair, consists of many dead, longitudinally arranged, keratin-rich, spindle-shaped cells which are tightly attached to each other. Hair color results from pigments in cortex cells and light reflected from the medulla. The medulla is less dense than the cortex and its cells are only loosely attached to one another.

Wool and Woolens

Wool denotes soft, curly fleece fibers from domesticated sheep. It differs from hair in that its scales are more numerous, smaller, and pointy. Curliness makes wool very resilient. This high tensile strength and elasticity help wool fabrics to retain their shape. These properties, wool's lightness, and its fine insulating ability make wool fabrics desirable.

Wild sheep have sparse, woolly undercoats and coarse hair, useless in fabrics. The hair has been bred out in domestic breeds. Sheep fleeces are usually shorn annually, from late spring to early summer. The wool is cut off very close to the skin and removed in one piece, weighing nine to eleven pounds. Wool from different fleece parts varies in its fiber length, fineness, and structure. The shoulder and sides yield the best fibers. Merino sheep yield the best overall wool. It makes up 40 percent of all wool produced commercially. Crossbreeds of merino sheep and strains that produce longer, coarser wool yield most of the rest. Some apparel wool comes from alpacas, goats, and llamas.

Woolen cloth manufacture begins by pulling fleeces apart and choosing the best fibers for given uses. Next, fibers are cleaned to remove lanolin and dried-on sweat. The clean fibers are disentangled and drawn straight by carding, which entails passing them between rotating cylinders to yield a thin film or web. Web processing varies, depending on whether it will be used in tweed or worsted yarn. Tweeds, woven from bulky yarn made of short, randomly arranged fibers, are thick and fuzzy. Worsted fabrics such as gabardines are woven from web made of longer, thinner fibers, tightly twisted for smoothness.

At every hair's base is a saclike hair follicle. The hair grows from the bottom of the follicle, nourished by blood vessels in a structure called a papilla. The papilla extends into the follicle and into the hair's root. A tiny muscle is attached to each hair follicle. Action of the nervous system can cause the muscle to contract to make hair "stand on end."

Hair Growth and Replacement

A hair forms from cells that grow from the surface of the papilla, which means that it grows from the root, not the free end. As new cells develop, they push forward old ones, which become part of the shaft. Hair growth continues as long as follicle and papilla are functional. The lifetime of a hair from start of growth until it is shed depends upon the organism which produces it. When an old hair falls out a new one takes its place.

Hair follicles produce hairs in cycles of hair growth, in which the hair follicle and the shaft pass through a complex series of morphological changes. During hair growth, the follicle penetrates into the dermis, and cells of the shaft are joined together. In addition, the follicle's melanocyte cells deposit pigment into shaft cells. Once a hair shaft attains its characteristic length, the follicle contracts and a "dead" hair protrudes from it. The growth period of a single hair ranges from three years in humans to around two weeks in rodents.

Hairs are continually replaced, or shed, throughout the life of a mammal. However, their development and loss occur asynchronously, so mammals are never completely naked of pelage. In rodents, replacement is in waves, across the body. In primates, each follicle passes through the growth cycle, independent of those around it. Hormones control hair growth; however, there are other, as yet unknown components that must also affect the process, because hormones are carried in the blood, and if they acted alone they would simultaneously affect all follicles in the body. This would be disastrous, because if all follicles grew in together, at the same rate, all hairs would be shed at the same time. Then the mammal involved would have naked periods where it was deprived of hair's protection and insulation. Continuous growth of hairs can also be hazardous. For example, in merino sheep, long growth phases produce long-stranded wool. However, if these sheep strayed, were not minded well, or were sheared irregularly, they might starve to death from becoming entangled in underbrush.

Hair Origin and Function

Hair in the pelage of contemporary mammals acts mainly to insulate against temperature variation. It has been proposed that mammal hair evolved into pelage from "prehair" which had the same functions. One theory of hair origin is that it evolved from epidermal mechanoreceptors, a concept supported to some extent by the existence of sinus hairs in mammals. These hairs, whiskers (vibrissae) in mammals such as felines and rodents, have blood-filled sinuses in the skin around the follicle. This tissue, together with associated nerve fibers, engenders mechanoreception, which facilitates nocturnal movement. However, most mammal body hairs lack nerves and only insulate and protect. The basis for hair evolution from vibrissae is therefore unclear.

Certainly, mammalian hair has other functions today. For instance, it can serve the unusual protective function of the quills of porcupines, and perhaps it may more generally serve to attract mates. It seems possible that the change of prehairs into attractive pelage drove development into these main contemporary forms.

Protecting Endangered Fur-Bearers

The desire on the part of humans for fur garments has led to atrocities committed on many mammal species which have gorgeous pelage. One of many examples is clubbing young fur seals to death. Beyond that, many species have been hounded to near extinction by hunters. Classic examples of such endangered species are the big cats, such as

Domesticated sheep have been bred to produce the type of very soft, kinky hair called wool. (PhotoDisc)

The Unusual Porcupine

Porcupines, whose name derives from a French word meaning "spiny pig," are animals that possess very unusual hair coverings. Included in these coverings are quills, which are used for defense against predators. A coat of regular hairs serves the porcupine as thermal insulation.

An adult porcupine possesses between twenty-five thousand and thirty-five thousand quills. Each of the quills is actually a group of long, stiff hairs that have grown together very tightly. The quills range in length from three to eighteen inches, depending upon the porcupine species and the body positions of the quills. Quills have sharp barbs on their ends.

When a porcupine is attacked or otherwise disturbed, it arches its back and makes the quills stand up straight. Attacking predators are very likely to impale themselves painfully on the quills, which pull out of the porcupine's body quite easily. A porcupine can also swing its quill-filled tail at a predator. When the tail connects with the aggressor, quills enter the flesh of that animal deeply and are bound to do damage. When a quill hits an attacker's eye, it may cause blindness. If quills enter its jaw, they may prevent eating and lead to the predator's death by starvation. Porcupines grow new quills, as needed.

tigers and leopards, and rodents, such as the beaver. Many other mammals are threatened species, likely to become endangered in the foreseeable future.

Fortunately, several organizations have sought to protect these fur-bearing mammals. Efforts of organizations such as the World Wildlife Fund have focused public opinion and led to animal conservation legislation. Preeminent are the Endangered Species Act of 1973, and a 1977 Convention, signed by eighty nations, including the United States. These actions have led to agreement that furs will not move interstate or between signatory countries without proof that the species from which they were harvested is not threatened or endangered. This bodes well for the future of hair.

—Sanford S. Singer

See also: Claws, nails, and hooves; Exoskeletons; Feathers; Horns and antlers; Molting and shedding; Scales; Shells; Skin; Teeth, fangs, and tusks.

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GAMETOGENESIS

Types of animal science: Development, reproduction
Fields of study: Cell biology, developmental biology, embryology, genetics, reproduction science

Gametogenesis is the process of sex cell formation. It includes the events that lead to a reduction in chromosome number so that the sex cells will have one-half the chromosomes that are found in normal body cells.

Principal Terms

DIPLOID: the number of chromosomes or the amount of genetic material normally found in the nucleus of body cells; this number is constant for a particular species of animal

GAMETE: a sex cell; the egg or ovum in the female and the sperm in the male

HAPLOID: one-half of the diploid number; the number of chromosomes or the amount of genetic material found in a gamete

MEIOSIS: reduction division of the genetic material in the nucleus to the haploid condition; it is the process used by animal cells to form the gametes

OOGENESIS: gamete formation in the female; it occurs in the female gonads, or ovaries

SPERMATOGENESIS: gamete formation in the male; it occurs in the male gonads, or testes

SPERMIOGENESIS: the structural and functional changes of a spermatid that lead to the formation of a mature sperm cell

Sexual reproduction is the predominant mode of reproduction in animals. Sexual reproduction involves the production of gametes: the eggs and sperm. In most animals, these gametes are produced in specialized organs called gonads (ovaries and testes). The sex cells in most animals are separate—that is, each individual animal contains either testes or ovaries, but not both. Such animals are said to be dioecious. In dioecious animals, the sex cells from two different individuals (one male and one female) will fuse together in a process known as fertilization to form the offspring. The advantage of sexual reproduction seems to be in its potential to produce variability in the gametes and therefore in the new organism.

Gametes are highly specialized cells that are adapted for reproduction. These egg and sperm cells develop by a process of gametogenesis, or gamete formation. Sperm cells are relatively small cells that are specialized for motility (movement); egg cells are larger, nonmotile cells that, in many species, contain considerable amounts of stored materials that are used in the early development of the zygote (fertilized egg).

In animals, gametogenesis consists of two major events. One involves the structural and functional changes in the formation of the gamete. The other involves the process of meiosis. Animal body cells normally contain the diploid amount of genetic material. Each species of animal has a characteristic diploid number that remains the same from generation to generation. Because fertilization involves the fusion of the egg and the sperm, bringing together each cell's set of genetic material, some mechanism must reduce the amount of genetic information in the gamete, or it would double every generation. Meiosis is a special nuclear division whereby the genetic material is reassorted and reduced to form haploid cells. Therefore, gametes are haploid, and gamete fusion during fertilization reestablishes the diploid content in the zygote.

Sperm

Sperm are highly motile cells that have reduced much of their cellular contents and are little more than a nucleus. Sperm are produced in the testes from a population of stem cells called spermatogonia. Spermatogonia are large diploid cells that reproduce by an equal division process called meiosis. Spermatogenesis is the process by which these relatively unspecialized diploid cells will become haploid cells; it is a continuous process that occurs throughout the sexually mature male's life. When a spermatogonium is ready to become sperm, it will stop dividing mitotically, enlarge, and begin the reduction division process of meiosis. These large diploid cells that begin to divide meiotically are known as primary spermatocytes.

The first step in the division process involves each primary spermatocyte dividing to form two secondary spermatocytes. Each secondary spermatocyte continues to divide, and each forms two spermatids. These spermatids are haploid cells. For each primary spermatocyte that undergoes spermatogenesis, four spermatids are formed. The spermatids are fairly ordinary cells; they must go through a process that will form them into functional sperm. The transformation process of a spermatid into a sperm is called spermiogenesis and involves several changes within the cell. The genetic material present in the nucleus begins to condense, while much of the cytoplasm and its subcellular structures are lost. The major exception to this latter event is the retention of mitochondria, cytoplasmic structures involved in energy production. The mature sperm has three main structural subdivisions: the head, the neck (or midpiece), and the tail. All are contained within the cell's membrane. The oval head has two main parts, the haploid nucleus and the acrosome. The acrosome comes in various shapes but generally forms a cap over the sperm nucleus. The acrosome functions differently in various animals, but generally its functions are associated with the fertilization process (union and subsequent fusion of egg nucleus and sperm nucleus). Acrosomes contain powerful digestive enzymes (organic substances that speed the breakdown of specific structures and substances) that allow the sperm to reach the egg's membrane. The midpiece of the sperm contains numerous mitochondria, which provide the energy for the sperm's movement. The tail, which has the same general organization as flagella or cilia (subcellular structures used for locomotion or movement of materials), uses a whiplike action to propel the sperm forward during locomotion. The structural changes that occur during spermiogenesis are meant to streamline and pare down the sperm cell for action of a special sort and of a limited duration. The sperm's function is to "swim" to the egg, to fuse with the egg's surface, and to introduce its haploid nucleus into the egg's interior.

Eggs

The female gamete, the egg or ovum, is produced by a process known as oogenesis. This process occurs in the female gonads, the ovaries. At first glance, oogenesis and spermatogenesis appear to be very similar, but there are some striking differences. The major similarity is that both processes form gametes, which contain genetic material that has been reduced to the haploid condition. To understand oogenesis, one must consider that its goal is to produce a cell that is capable of development. The mature egg in all animal cells is large in comparison with other cells, particularly with the sperm. There are two important features of the egg that must be considered: the presence of a blueprint for development and the means to construct an embryo from that blueprint. In other words, the egg must be programmed and packaged during oogenesis. The programming refers to the information that is coded within the structure of the egg. This information includes the genetic material as well as the cytoplasmic information. Together, the nucleus and cytoplasm provide the egg with the potential to transform a simple cell into a complex preadult form. Since it is within the egg that this transformation occurs, the programming must be within the organization of the egg, and the directions for development must be within that organization. The packaging refers to the presence of all the material necessary to build embryonic structures, to nourish this developing embryo, and to provide its energy until it can obtain nourishment on its own.

As happens in spermatogenesis, the potential eggs are formed from unspecialized stem cells, in this case called oogonia. Oogonia contain the diploid amount of genetic material and divide by the process of mitosis. At some point in their life, oogonia stop dividing mitotically, enlarge, and prepare to become eggs—that is, they begin meiosis. The cell that begins this reduction division process is called the primary oocyte. Each primary oocyte divides into two cells—one large cell, the secondary oocyte, and a very small cell, the first polar body. The secondary oocyte continues the final reduction phase of meiosis and forms two cells, one large one (the ovum) and one very small one (the second polar body). The first and second polar bodies are nonfunctional by-products of meiosis. The one functional cell, the mature egg, contains most of the cytoplasm of the primary oocyte and one-half of its genetic material. In many animals (primarily the vertebrates), all oogonia present in the ovaries enter meiosis at the same time; the initial events of oogenesis are synchronous within the animal. Oogenesis in many animals is not a continuous process, as is spermatogenesis in the male. Rather, the primary oocytes in the first stages of reduction division may remain inactivated for a long time—in some cases, for several decades. Therefore, in female animals with this format of oogenesis, a primary oocyte population is maintained, and eggs will mature as they are needed.

Thus far it appears that the egg's formation differs from the sperm's in three ways. First, in many female animals, there is a limited number of primary oocytes capable of going on to form eggs; second, this egg formation is not necessarily a continuous process; third, one primary oocyte yields one mature egg at the end of meiosis. Although these are three very important differences, there are other distinctly egg events that deal with the developmental programming and the packaging of materials in this potential gamete.

Eggs and RNA

Little is known about the egg's storage of developmental directions or the actual programming of information, but developmental and molecular biologists are beginning to elucidate events that occur during oogenesis that are concerned with function of the egg. One such event, fairly widespread among the animal kingdom, is the formation of so-called lampbrush chromosomes during oogenesis. The chromosome's backbone unravels at many sites so that regions, composed of specific genes, loop outward from the backbone. These loops give the chromosome its distinctive lampbrushlike appearance. Large amounts of a nucleic acid known as messenger ribonucleic acid (mRNA) are being made on each loop. This mRNA is then processed and sent into the developing eggs's cytoplasm, where most of it will be stored for use during early development. After fertilization, these maternal (egg-derived) mRNAs can be used to make specific proteins necessary for the embryo.

Another event present in some developing eggs is the mass production of another type of RNA known as ribosomal RNA (rRNA). Most of this rRNA will also be stored until fertilization. After fertilization, these rRNA particles will help form cytoplasmic structures called ribosomes (the sites of protein synthesis). In addition to these egg products, many animal eggs must become filled with yolk. Yolk is the general term that covers the major storage of material in the egg.

Because the maternal proteins (yolk and other protein components) and nucleic acids (various RNAs) form the bulk of the egg cytoplasm, they have profound influences on the development of the embryo. In particular, the positions of maternal mRNAs, ribosomes, and proteins affect the organization of the embryo. It is evident, then, that the maternal genetic information and the arrangement of the products of this information provide crucial developmental information that will control much of the course of embryonic development. Therefore, the egg contributes considerably more than a haploid nucleus to the zygote.

Studying Gametogenesis

There are several approaches to the study of gametogenesis. Early biologists employed cytological techniques (methods of preparing cells for the study of their structure and function) and microscopy to study gamete formation. These early studies were, in fact, observations of the actual events themselves. Although these early descriptive approaches gave much information about the cells involved at each stage of gamete formation, they did not provide any information about the control mechanisms for this process. Biochemical studies have contributed to the understanding of certain regulatory substances and how they function in gametogenesis. By enhancing or inhibiting the presence of these regulatory substances in the organism, investigators have been able to elucidate many of the normal events of gametogenesis.

Beginning at puberty, the hormones (substances released from endocrine glands, generally functioning to regulate specific body activity) of the hypothalamus, the pituitary gland, and the gonads interact to establish and regulate gametogenesis in the organism. Gonadotropin-releasing hormone (GnRH) from the hypothalamus stimulates the release of follicle-stimulating hormone (FSH) and luteinizing hormone (LH) from the anterior portion of the pituitary gland. All three of these hormones are necessary for spermatogenesis and oogenesis.

Surgical removal of the mammalian pituitary gland (hypophysectomy) in the male leads to degeneration of the testes. Testicular function can be restored in these hypophysectomized animals by administering the hormones FSH and LH. These studies suggest that FSH and LH are necessary for normal functioning of the testes. LH appears to stimulate the release of testosterone (male hormone) by certain cells (Leydig cells) of the testes. Both testosterone and FSH are necessary for spermatogenesis, but the exact role that each of these hormones plays in male sexual physiology has yet to be determined.

Oogenesis in the female has been the subject of intense investigation. At the beginning of each ovarian cycle, from puberty to menopause, one primary oocyte present in the female's ovaries is activated to continue the process of gamete formation. Release of GnRH from the hypothalamus at the beginning of each cycle stimulates the anterior portion of the pituitary gland to release FSH. FSH, in turn, affects the ovaries: It stimulates a primary oocyte to mature to the point that it can be released from the ovary, as a secondary oocyte, and it causes certain cells (follicle cells) in the ovary to produce estrogens, female hormones. High estrogen levels will cause the pituitary to inhibit FSH release, a negative feedback mechanism, and stimulate LH release. These estrogen-mediated events occur at approximately the middle of the ovarian cycle. LH also affects the ovaries. LH, however, is responsible for ovulation (the release of the oocyte from the ovaries) and for the formation of a cellular structure called the corpus luteum. LH also stimulates the corpus luteum to produce progesterone, another female hormone. Eventually, high levels of progesterone will inhibit LH release from the pituitary gland, and the cycle begins anew.

—Geri Seitchik

See also: Aging; Asexual reproduction; Cell types; Cleavage, gastrulation, and neurulation; Determination and differentiation; Embryology; Fertilization; Growth; Parthenogenesis; Pregnancy and prenatal development; Regeneration; Reproduction; Reproductive system of female mammals; Reproductive system of male mammals; Sex differences: Evolutionary origins.

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GAS EXCHANGE

Type of animal science: Physiology
Fields of study: Biochemistry, biophysics, cell biology

Gas exchange refers to the processes used by animals to take up oxygen and eliminate carbon dioxide. These processes are the basis for understanding how animals breathe, particularly in diverse conditions.

Principal Terms

DIFFUSION: the passive movement of a gas across a membrane from a region of high pressure to one of low pressure

EPITHELIUM: a thin layer of cells that lines a body surface, such as the lining of the lungs or the intestines

PARTIAL PRESSURE: that part of the atmospheric pressure caused by only a single gas of many in a mixture; it is determined by how much of the gas is present in the mixture

PERMEABILITY: the tendency, in this case of a membrane, to permit the movement of a gas across that membrane

RESPIRATORY MEDIUM: the water or air that contains the oxygen used by an animal to carry out biochemical reactions

VENTILATION: the movement of the respiratory medium to and across the site of gas exchange

Gas exchange is the uptake of oxygen and the loss (or elimination or excretion) of carbon dioxide. It refers to two major steps in the overall oxygen consumption (or carbon dioxide excretion) by the whole animal. These two steps are the movement of the respiratory medium (containing oxygen) past the site of gas exchange, known as ventilation, and the diffusion of oxygen across the gas-exchange surface into the animal. The final step in diffusion of oxygen into an animal always involves diffusion from a liquid into a liquid, even in air breathers. Both ventilation and diffusion depend on the design of the structures as well as the way in which the systems and structures work. The additional steps in the whole respiratory system are the internal counterparts to ventilation and diffusion. These are perfusion, or blood flow, and diffusion from the blood to the tissues.

Basically, gas exchange takes place at a respiratory surface where the source of oxygen, the respiratory medium, is brought into contact with the surface. Oxygen diffuses into the animal, carbon dioxide diffuses out, and the spent or used respiratory medium is removed. The movement of the respiratory medium is termed ventilation. Once oxygen is in the animal, it is transported to the site of oxygen utilization, the tissues. Carbon dioxide, on the other hand, must be transported from the tissues to the site of gas exchange for excretion in gaseous form.

Gas-Exchange Organs

Animals have three basic types of gas-exchange organs: skin, invaginations (inpocketings of the epithelium), and evaginations (outpocketings of the epithelium). All three show modifications to improve the conditions of gas exchange. Skin always permits gas exchange unless it is coated with some material that limits diffusion. The skin of a snake or a turtle is so coated and permits very little gas exchange. The skin of a worm or an octopus, on the other hand, is quite thin and permits gas exchange quite freely. Invaginations of the external epithelium are basically what lungs and insect tracheas are, but in a highly modified condition. Evaginations of the skin are represented by the gills of aquatic animals; even when inside a cavity, as are fish and crab gills, they are still evaginations.

There is only one way that animals take up oxygen from the external medium, regardless of whether that medium is air or water. Gas must passively diffuse across the membrane that separates the animal from its environment. That membrane is a type of tissue called epithelium and is similar in nature and structure to the tissue that lines other body surfaces. The different types of epithelia are classified according to their locations and functions; those lining gills, lungs, and certain other organs of gas exchange are all known as respiratory epithelia. The respiratory epithelium not only separates the internal and external fluids but also represents a barrier to the movement of materials such as gas.

Gas Diffusion

Diffusion of a gas across a membrane occurs according to the laws of physics. The driving force for gas diffusion is the difference in the partial pressure of the gas across the membrane. A high external partial pressure and low internal partial pressure will provide a large difference and will enhance diffusion. Oxygen makes up 20.9 percent of the air, so that 20.9 percent of the atmospheric pressure at sea level (14.72 pounds per square inch) is attributable to oxygen (3.08 pounds per square inch). At higher altitudes, atmospheric pressure and partial pressure of oxygen are reduced.

The other factors that determine the diffusion of a gas are the thickness of the membrane across which it diffuses, the membrane's total surface area, and the nature or composition of the membrane. Obviously, a thick membrane will retard diffusion of gas because the gas must move across a greater distance. The distance the gas must diffuse is known as the diffusion distance. Additionally, the total surface area of the membrane available for diffusion has a direct effect on the rate of diffusion from one place to another. The greater the surface area, the greater the quantity of gas that can diffuse in a given time. Finally, the composition of the membrane is of critical importance in determining the diffusion of a gas. The nature of the membrane is referred to as the permeability of the membrane to the gas in question. The greater the permeability, the more easily gas diffuses. A membrane with a layer of minerals (calcium, for example) on the cells will not be as permeable as one without such a layer.

A very important point to note is that gases diffuse according to the difference in the partial pressure of the gas and not according to the concentration of the gas in the liquid. Several scientists have proved this by constructing artificial systems with two dissimilar fluids separated by a membrane. The movement of oxygen is always from high partial pressure to low and not from a high concentration to low. The reason is that pressure is a measure of molecular energy, but concentration of a gas in a liquid depends on the amount of that gas that can dissolve in the liquid—its solubility.

A Fluid-Fluid Boundary

All gas exchange occurs across a fluid-fluid boundary—that is, from one liquid to another—even in air breathers. The explanation for this is that all respiratory epithelia are moist and are kept so by the cells that line the surface. If the surface were to dry out, the permeability to gases (and other materials) would be substantially reduced. Thus, in air breathers, oxygen must first dissolve in the thin fluid layer lining the surface before diffusion across the epithelium takes place.

Organs of gas exchange work as do radiators, except that a gas is exchanged instead of heat. In this system, there are two liquids, one the source and the other the sink for the transferred material, the gas. The source is the external supply, and the sink is the blood or other internal fluid. Both fluids are contained in vessels or tubes that channel and direct it, with a thin layer of epithelium between the two. In the most efficient transfer systems, both the source and the sink flow, and they flow in opposite directions. If they did not flow, then the two fluids would simply come to an equilibrium, with oxygen partial pressure the same in both of the fluids. By moving in opposite directions, each is renewed, and the difference between them is always maximized. This type of exchange system is a "countercurrent system," because the two fluids flow in opposite directions. The most efficient of the gas-exchange organs function this way.

Two other types of gas-exchange systems are based on fluids flowing in directions other than perfectly opposite to each other. Birds have a respiratory system in which blood and air do not flow in opposite directions; rather, the blood flows perpendicularly to the direction of the air flow. This is referred to as crosscurrent flow. While not as efficient as countercurrent flow, it provides for an acceptably high level of efficiency. A system in which the respiratory medium is not channeled, but the blood is instead in vessels, is known as a mixed volume system. The mammalian lung functions in this way; the air is pumped into sacs that are lined with tiny blood vessels, but the air does not flow.

Ventilation

Ventilation of gas-exchange organs is accomplished by a pumping mechanism that brings the respiratory medium to and across the gas-exchange surface. Both water and air breathers use ventilatory pumps, but water breathers must move a much heavier and denser medium than air breathers. Pumping mechanisms may be located at the inflowing end of the system or at the outflowing end. The former are positive pressure pumps that push respiratory medium, and the latter are negative pressure pumps that pull respiratory medium into the cavity. Negative pressure is used in mammalian lungs, insect tracheas, and crab gills, while positive pressure is used in some fish that push water from the mouth into the gill chamber.

There are two basic patterns of flow of the respiratory medium through gas-exchange organs: one-way and tidal. One-way flow is found in fish, crabs, clams, and a number of other aquatic animals. Interestingly enough, the bird respiratory system also uses one-way flow. In one-way flow systems, the medium is always moving and passes over the gas exchange surface only once. In tidal-flow systems, the respiratory medium moves in and out (like the tide) through the same passages and tubes. The mammalian and insect respiratory systems both utilize tidal ventilation. The respiratory medium is not always moving, and when it is exhaled, there is some amount remaining in the cavity. The remaining respiratory medium will contain more carbon dioxide and less oxygen than fresh respiratory medium, with which it will mix upon inhalation.

Measuring Gas Exchange

The total amount of oxygen used by an animal is a gross measure of gas exchange known as oxygen uptake or oxygen consumption. Its counterpart for carbon dioxide is carbon dioxide excretion. Oxygen uptake is expressed as the amount of oxygen used per minute per kilogram of animal mass. Carbon dioxide excretion is expressed in the same terms. In theory, oxygen uptake and carbon dioxide excretion will be numerically the same, but in live animals there are several circumstances that cause the two to differ. Measurement of both rates is accomplished in similar ways. One method is the use of a respirometer and involves placing an animal in a sealed container and measuring the rate at which oxygen is depleted or carbon dioxide produced by an animal. Alternatively, respiratory medium, either air or water, is pumped through the respirometer and the oxygen or carbon dioxide measured in the inflowing and outflowing medium; the difference will be the amount used by the animal. The flow rate of the air or water must also be known for the calculations. The use of a respirometer is preferable but may not be practical for large animals, such as a horse.

In the case of animals too large to use a respirometer, oxygen uptake or carbon dioxide excretion is determined by measuring the rate of flow of the respiratory medium through the gas exchange organ and measuring the oxygen in the inspired and expired air or water. The result is the ventilation rate and the amount of oxygen extraction, the product of which is the oxygen consumption rate. This measurement is straightforward in animals with one opening for inspired and another for expired respiratory medium, such as a fish or a crab. In animals that inhale and exhale through the same organ, however, there are complications that make the measurements more difficult. Still, it is possible to measure the flow of air in and out of a lung and to collect at least some of the gas and measure either the oxygen or carbon dioxide in that air.

There is an additional advantage to the latter technique, measuring ventilation and the oxygen in the water or air. That advantage is that another measure of gas exchange is provided in these measurements. The difference between the amount of oxygen in inspired and expired water or air is the extraction (the amount taken out) and assesses the efficiency of the gas exchange organ. The efficiency is usually given as the percentage of oxygen taken out of the respiratory medium (the amount removed divided by the amount in inspired air or water). There are numerous factors that affect extraction, and measuring the efficiency provides one piece of information.

Studies of gas exchange encompass all levels of organization of animals, from the cellular to the whole animal. One of the most important levels concerns the structure of the organ and the parts of the organ. For this, it is necessary to see the spatial relationships among the parts, measure distances and areas, and count structures. The surface area, the volume, the number of structures or substructures, and the diffusion distances must all be measured. The results describe the morphology and morphometrics of the organ. Both whole, intact animals, and preserved specimens are used to make these measurements. The techniques are those used in surgery and dissection, and the results are critical to an understanding of the basic function of the respiratory organ. The electron microscope has been a powerful tool in this regard, permitting the accurate measurement of cellular-level distances, such as the diffusion distance.

Measuring Partial Pressure Difference

Measuring the partial pressure difference between the inside and outside of the animal is critical because of the role that this pressure difference has in gas exchange. Partial pressure of oxygen may be measured in two ways: in the intact animal or in a sample removed from the animal and injected into an instrument. The instrument most commonly used for measuring oxygen or carbon dioxide partial pressure is an electrode that changes electrical output when oxygen diffuses across an artificial membrane into a salt solution. Some of these electrons have been miniaturized and are only four millimeters across, and they will fit in a syringe needle. Still, it is difficult to use one of these in an intact mammal. The other way to measure partial pressure of oxygen or carbon dioxide on either side of the respiratory epithelium is to withdraw a sample of the air or water on the outside or the blood from the vessels on the inside. This procedure may be routine (in animals such as fish and crabs) or somewhat difficult (as in a mammal). A small tube is threaded into the lung to withdraw the air sample.

Measuring Ventilation

The movement of the respiratory medium, ventilation, is an important measure in determining the rate at which oxygen is brought to the respiratory surface. The blood flow (perfusion) on the inside is the counterpart to ventilation and is equally important. Ventilation can be measured either indirectly (meaning it is calculated) or directly. Indirect determinations require measuring other functions and then calculating ventilation based on known equations. If the rate of oxygen uptake and the extraction are measured, for example, then ventilation can be calculated.

Direct measures of ventilation use an electronic sensing device to determine the flow of water or air at the site of intake or outflow of respiratory medium on the animal. A human subject can simply breathe into such an electronic or mechanical device. Nonhuman mammals are more difficult and frequently require indirect techniques.

Direct measures may be the flow rate of the respiratory medium, the frequency of breathing, the hydrostatic pressure in the respiratory chamber, or a change in shape and size of the respiratory chamber. Any of these measures can be used to monitor routine respiratory function, but all are needed to assess gas exchange completely and accurately.

It is also necessary to know the general pattern of water or air movement at the respiratory surface. To do so often requires some invasive technique and the use of an indicator, such as a dye in the respiratory medium. The movement of the medium can then be visualized to determine the pattern. In some animals, video cameras can be used to photograph flow patterns of dyed medium, particularly water.

Uses of Gas Exchange Study

Gas exchange is studied by researchers and health practitioners both to assess basic function and to determine the source and nature of limitations of the systems of the body. These two areas may seem quite different at first; one is applied research, and the other is considered basic research. Both, however, have the same bases and use the same equations and principles. Only the animals or conditions differ.

One of the clinical applications, or contexts, in which gas exchange is studied is in respiratory distress or pulmonary (lung) disease. In these cases, the respiratory epithelium may become inflamed and thickened. This will increase the diffusion distance and retard, or limit, oxygen uptake and carbon dioxide release at the lung. Secretion of mucus by a respiratory epithelium may have a similar result for the same reasons. Mucus secretion occurs in several diseases and also takes place in fish gills when irritated by noxious chemicals in the water.

Gas exchange is also studied in diverse animals to understand evolutionary trends and pressures. Animals that live at high altitudes, for example, are constantly faced with low oxygen pressure in the air, and therefore some adjustment must be made by the animal. Scientists study the respiratory systems of these animals to determine if one of the other factors that affects gas exchange, such as diffusion distance or total surface area, is altered to compensate for the lower pressure difference.

All animals have similar basic physiological needs, including a need for oxygen to fuel the conversion of food materials into energy and other substances. Many animals have unique or specific forms or structures enabling them to survive in a particular habitat. Some of these forms affect the respiratory system—as in the differences between the respiratory surface in land animals compared with similar species that live in water. Scientists have compared the gas-exchange systems in aquatic and terrestrial species to learn more about evolutionary processes.

—Peter L. deFur

See also: Cell types; Circulatory systems of invertebrates; Circulatory systems of vertebrates; Hibernation; Lungs, gills, and tracheas; Metabolic rates; Respiration: Adaptation to low oxygen; Respiration in birds; Respiratory system.

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GEESE

Type of animal science: Classification
Fields of study: Anatomy, ornithology, physiology, zoology

Geese are migratory water birds. Over two dozen species of geese have been identified; seven live in North America.

Principal Terms

BANDING: attachment of identification tags to individual birds
CLUTCH: number of eggs in the nest
COVERTS: feathers covering the bases of the large feathers of the wings and tail
FLEDGLING: young bird still unable to fly
LAMELLAE: toothlike structures in the beak, forming a strainer that permits birds to retain food particles while still enabling water to flow from the closed mouth
MANDIBLES: upper and lower beak parts
MOLTING: the loss of feathers that will be succeeded by new growth

Relatively difficult to identify, geese are perhaps best known for their migration, being harbingers of both summer and winter. Geese live comfortably at the intersection of water and land, eating a vegetarian diet of grasses, seeds, roots, berries, and aquatic plants. Unlike many birds, geese pair-bond and mate for life, building a simple nest in the ground and lining it with down. Depending on their species, geese lay a clutch of four to nine eggs, and fledglings remain grounded for forty to seventy-three days. Geese molt once a year after the breeding season; during this period the bird is unable to fly for four to five weeks.

Physical Characteristics of Geese

Geese are medium- to large-sized birds, between the size of ducks and swans. They have long necks and short legs in the center of their bodies. Because of this leg placement, geese do not waddle as much as other waterfowl when moving about on land. Their feet are webbed, which enables them to swim rapidly.

The bills of geese have serrations on the mandibles called lamellae; these are useful, because most geese gather some of their food while submerged. Because the bill is equipped with a horny covering at the tip of the upper mandible and because of the curved shape of the bill, geese can easily clip grasses, grains, or other foods.

Most species of geese are blackish in color, although many species have considerable white

Geese Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Class: Aves
Order: Anseriformes
Family: Anatidae
Subfamily: Anserinae
Tribe: Anserini (swans and geese, four genera, thirty-six species)
Geographical location: Primarily the Northern Hemisphere
Habitat: Land (fields, prairies, tundra, forests) and water (ponds, lakes, rivers, streams, inlets, tidal areas, oceans)
Gestational period: From three to four weeks
Life span: Most geese live about twenty years; can (rarely) reach fifty-five years
Special anatomy: Webbed feet, long necks, large bills

Migrating geese make stopovers en route, forming huge, seasonal flocks on lakes along their flyways. (PhotoDisc)

markings in their plumage, often restricted to their bellies or lower tail coverts. Even though each species has distinguishing physical characteristics, it is often difficult to identify a particular species in the field. Even Canada geese, which are probably the easiest to identify with their white chin straps, can be a source of frustration for bird watchers attempting to distinguish between the dozen or so subspecies of Canada geese. Male and female geese of each species resemble each other.

Goose Migration

Many species of birds migrate, but geese, because they are so visible, epitomize this phenomenon to most people. Geese migrate for survival: Their northern breeding grounds become inhospitable when water areas freeze over, making food unattainable, and their southern grounds cannot sustain large populations of birds year around. In the United States, geese migrate northward from February to March and southward from September to November.

Geese, like many birds, often return to the same summer and winter areas year after year. Clearly, geese make use of visual landmarks when migrating; even at night some landmarks, such as large bodies of water, can be seen from the air. Young geese learn about these landmarks, as well as about traditional migratory stopping places, from their elders. Landscape alone, however, is not all that helps geese navigate. The position of the sun and stars can help them, as can the wind and the earth's magnetic field.

Most species of geese fly in some sort of V-formation. Flocks of snow geese, for example, form U's, checkmarks, or irregular masses. Only Canada geese fly in an almost perfect V. These formations have less to do with aesthetics than aerodynamics. Just as bicycle racers will draft lead bikers by riding slightly behind and to the side of them, so a goose will draft the lead bird, the one doing most of the work by breaking the wind's resistance for the birds that follow. Lead birds change during a flight. Geese normally fly at about forty miles per hour, a speed that can change if the bird is in a hurry or being chased.

By plotting the origins and destinations of banded birds, biologists have discovered four main flyways used by geese in the United States: the Atlantic Flyway, the Mississippi Flyway, the Central Flyway and the Pacific Flyway. Banding geese in order to study them is more than an academic exercise. Knowing migration paths has allowed experts to make decisions on hunting quotas and on the location of wildlife refuges.

—Cassandra Kircher

See also: Beaks and bills; Birds; Domestication; Feathers; Flight; Migration; Molting and shedding; Nesting; Pair-bonding; Respiration in birds; Wildlife management; Wings.

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GENE FLOW

Type of animal science: Evolutionary science
Fields of study: Anthropology, ecology, genetics

In biology, "migration" refers to the movement of a member or many members of a species of animal or plant from one geographic location to another. If other members of the same species interbreed with the migrating species, either along the way or in the new location, an exchange of genes occurs. Biologists call this exchange "gene flow" and consider it to be fundamental to the evolutionary process.

Principal Terms

ALLELE: one of a group of genes that occurs alternately at a given locus

DEME: a local population of closely related living organisms

FOSSIL: a remnant, impression, or trace of an animal or plant of a past geologic age that has been preserved in the earth's crust

GENE POOL: the whole body of genes in an interbreeding population that includes each gene at a certain frequency in relation to other genes

MUTATION: a relatively permanent change in hereditary material involving either a physical change in chromosome relations or a biochemical change in the codons that make up genes

POPULATION: a grouping of interacting individuals of the same species

SPECIATION: the process whereby some members of a species become incapable of breeding with the majority and thus form a new species

SPECIES: a category of biological classification ranking immediately below the genus or subgenus, comprising related organisms or populations capable of interbreeding

Prior to the nineteenth century, religious dogmatism retarded the activities of most scientists investigating the origins and nature of life by insisting on the immutability of species created by God. Despite mounting fossil evidence that many species of flora and fauna that once inhabited the earth had disappeared and that many extant species could not be found in the fossil record, pre-nineteenth century naturalists could find no viable explanation (other than divine intervention) for the disappearance of life-forms and their replacement by other forms. Then, in 1859, Charles Darwin published his epochal *On the Origin of Species*, which proposed the theory that all contemporary life-forms have evolved from simpler forms through a process he called "natural selection."

Many individuals before Darwin had proposed theories of evolution, but Darwin's became the first to be widely accepted by the scientific community. His success resulted from the careful and objective presentation of an overwhelming amount of evidence showing that species can and do change, and his concurrent promulgation of a convincing explanation of the mechanism that produces that change—natural selection. Since Darwin, scientists have modified and added new concepts to his theory, especially concerning the ways in which species change (evolve) over time. One of those new concepts, which was only dimly understood in Darwin's lifetime, is the importance of genetics in evolution, especially the concepts of migration and gene flow.

Genes and Gene Exchange

Genes are elements within the germ plasm of a living organism that control the transmission of a hereditary characteristic by specifying the structure of a particular protein or by controlling the function of other genetic material. Within any breeding population of a species, the exchange of genes is constant among its members, ensuring genetic homogeneity. If a new gene or combination of genes appears in the population, it is rapidly dispersed among all members of the population through inbreeding. New alleles may be introduced into the gene pool of a breeding population (thus contributing to the evolution of that species) in two ways: mutation and migration. Gene flow is integral to both processes.

A mutation is the appearance of a new gene or the almost total alteration of an old one. The exact causes of mutations are not completely understood, but scientists have demonstrated that they can be caused by radiation. Mutations occur constantly in every generation of every species. Most of them, however, are either minor or detrimental to the survival of the individual and thus are of little consequence. A very few mutations may prove valuable to the survival of a species and are spread to all of its members by migration and gene flow.

When immigrants from one population interbreed with members of another, an exchange of genes between the populations ensues. If the exchange is recurrent, biologists call it "gene flow." In nature, gene flow occurs on a more or less regular basis between demes, geographically isolated populations, and even closely related species. Gene flow is more common among the adjacent demes of one species. The amount of migration between such demes is high, thus ensuring that their gene pools will be similar. This sort of gene flow contributes little to the evolutionary process, since it does little to alter gene frequencies or to contribute to variation within the species. Much more significant for the evolutionary process is gene flow between two populations of a species that have not interbred for a prolonged period of time.

Populations of a species separated by geographical barriers often develop very dissimilar gene combinations through the process of natural selection. In isolated populations, dissimilar alleles become fixed or are present in much different frequencies. When circumstances do permit gene flow to occur between two such populations, it results in the breakdown of gene complexes and the alteration of allele frequencies, thereby reducing genetic differences in both. The degree of this homogenization process depends on the continuation of interbreeding between members of the two populations over extended periods of time.

Hybridization

The migration of a few individuals from one breeding population to another may, in some instances, also be a significant source of genetic variation in the host population. Such migration becomes more important in the evolutionary process in direct proportion to the differences in gene frequencies—for example, the differences between distinct species. Biologists call interbreeding between members of separate species "hybridization." Hybridization usually does not lead to gene exchange or gene flow, because hybrids are not often well adapted for survival and because most are sterile. Nevertheless, hybrids are occasionally able to breed (and produce fertile offspring) with members of one or sometimes both the parent species, resulting in the exchange of a few genes or blocks of genes between two distinct species. Biologists refer to this process as "introgressive hybridization." Usually, few genes are exchanged between species in this process, and it might be more properly referred to as "gene trickle" rather than gene flow.

Introgressive hybridization may, however, add new genes and new gene combinations, or even whole chromosomes, to the genetic architecture of some species. It may thus play a role in the evolutionary process. Introgression requires the production of hybrids, a rare occurrence among highly differentiated animal species. Areas where hybridization takes place are known as contact zones or hybrid zones. These zones exist where populations overlap; in some cases of hybridization, the line between what constitutes different species and what constitutes different populations of the same species becomes difficult to draw. The significance of introgression and hybrid zones in the evolutionary process remains an area of some contention among life scientists.

Biologists often explain, at least in part, the poorly understood phenomenon of speciation through migration and gene flow—or rather, by a lack thereof. If some members of a species become geographically isolated from the rest of the species, migration and gene flow cease. The isolated population will not share in any mutations, favorable or unfavorable, nor will any mutations that occur among its own members be transmitted to the general population of the species. Over long periods of time, this genetic isolation will result in the isolated population becoming so genetically different from the parent species that its members can no longer produce fertile progeny should one of them breed with a member of the parent population. The isolated members will have become a new species, and the differences between them and the parent species will continue to grow as more ages pass. Scientists, beginning with Darwin himself, have demonstrated that this sort of speciation has occurred on the various islands of the world's oceans and seas.

Studying Gene Flow

Scientists from many disciplines are currently studying migration and gene flow in a variety of ways. For decades, ornithologists and marine biologists have been placing identifying tags or markers on members of different species of birds, fishes, and marine mammals to determine the range of their migratory habits in order to understand the role of migration and subsequent gene flow in the biology of their subjects. These studies have led, and will continue to lead, to important discoveries. Most studies of migration and gene flow, however, relate to human beings.

Many of the important discoveries concerning the role of gene flow in the evolution of life come from the continuing study of the nature of genes. A gene, in cooperation with such molecules as transfer ribonucleic acid (tRNA) and related enzymes, controls the nature of an organism by specifying amino acid sequences in specific functional proteins. In recent decades, scientists have discovered that what they previously believed to be single pure enzymes are actually groups of closely related enzymes, which they have named "isoenzymes" or "isozymes." Current theory holds that isozymes can serve the needs of a cell or of an entire organism more efficiently and over a wider range of environmental extremes than can a single enzyme. Biologists theorize that isozymes developed through gene flow between populations from climatic extremes and enhance the possibility of adaptation among members of the species when the occasion arises. The combination and recombination of isozymes passed from parent to offspring are apparently determined by deoxyribonucleic acid (DNA). Investigation into the role of DNA in evolution is one of the most promising avenues to an understanding of the nature of life.

A classic example of the importance of understanding migration and gene flow in the animal kingdom is the spread of the so-called killer bees. In the 1950's, a species of ill-tempered African bee was accidentally released in South America. The African bees mated with the more docile wild bees in the area; through migration and gene flow, they transmitted their violent propensity to attack anything approaching their nests. As the African genes slowly migrated northward, they proved to be dominant.

Further research into migration and gene flow promises to provide information indispensable to the attempt to unravel the mysteries of life. Coupled with the concept of mutation, gene flow is a crucial component of evolution.

—*Paul Madden*

See also: Adaptive radiation; Demographics; Ecological niches; Ecology; Evolution: Animal life; Evolution: Historical perspective; Genetics; Habitats and biomes; Hardy-Weinberg law of genetic equilibrium; Natural selection; Population analysis; Population genetics; Punctuated equilibrium and continuous evolution.

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GENETICS

Types of animal science: Evolution, fields of study, reproduction
Fields of study: Biochemisty, cell biology, developmental biology, embryology, evolutionary science, reproduction science

Genetics is the study of inheritance of characteristics from one generation to the next. Humans have been studying genetics since prehistoric times with the first selective breeding of wolves for companion animals. In the 1800's, an Austrian monk, Gregor Mendel, described the basic laws that govern the inheritance of genetic traits. In the twentieth century, the field of molecular genetics was created as biologists determined the actual chemical makeup of genes.

Principal Terms

ALLELE: alternative forms of a single gene
CHROMOSOME: a long strand of DNA with supporting proteins, that contains many genes
DEOXYRIBONUCLEIC ACID (DNA): the chemical polymer that is the genetic material of multicellular organisms
GENE: factors in cells that are responsible for an observable characteristic of an organism
GENOME: all of the genetic material of an organism
GENOTYPE: the actual genetic makeup of an organism
MUTATION: any heritable change in the genetic material
PHENOTYPE: the observable characteristics of an organism (for example, black fur color in a cat)

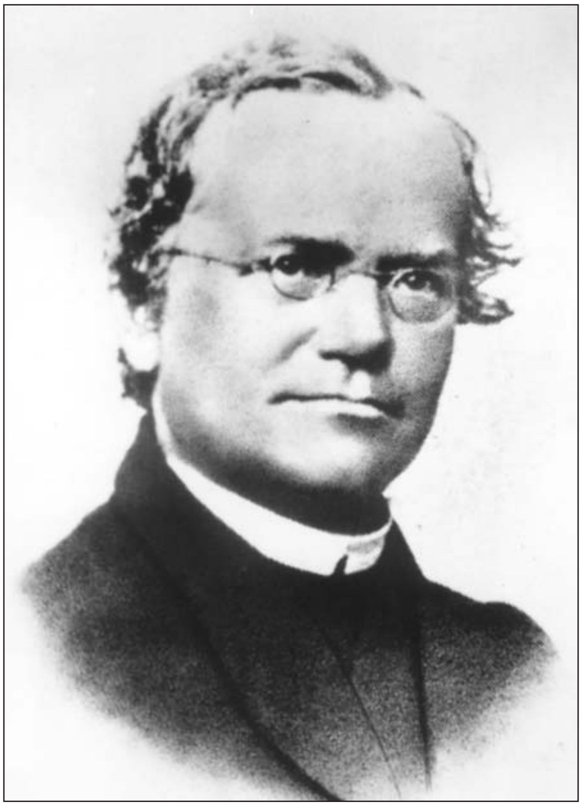
Before any recorded history, ancient man chose alert pups from a litter of wolves for breeding. This practice of selectively breeding the wolves that were good companions eventually gave rise to the domesticated dog. The oldest undisputed dog bones known, excavated from a twenty-thousand-year-old Alaskan settlement, demonstrate that prehistoric humans knew that traits could be passed from one generation to the next, and that selectively breeding animals (or plants) could produce an organism that possessed desired characteristics. This practice of deliberate breeding is known as artificial selection.

Humans have practiced artificial selection on numerous animals, including pigs, cattle, goats, and sheep. Homer and other Greek poets wrote about selective breeding, and part of the wealth of the ancient city of Troy was attributed to its expertise in horse breeding. Although humans had some control over the traits of domesticated animals through selective breeding, the results of matings were not always predictable, and nothing was known about the mechanism through which traits were passed from one generation to another until the mid-1800's.

Mendelian Genetics

Gregor Mendel, an Austrian monk, is the undisputed father of the science of genetics. Working with garden peas, Mendel analyzed thousands of breeding experiments to describe laws that governed the inheritance of traits. Though Mendel studied a plant, his laws for the inheritance of traits apply to all sexually reproducing organisms, including humans.

Mendel chose seven distinct traits to study in his garden peas: flower color, plant height, seed shape, seed color, pod shape, pod color, and flower position. He concluded that each of these



Gregor Mendel's experiments with garden peas laid the foundation for the study of genetics. (National Library of Medicine)

traits was determined by a single, discrete factor called a gene. For instance, there was a gene for flower color and a gene for seed shape. Each gene had several variations, or alleles. The gene for flower color had a white allele that produced white flowers and a purple allele that produced purple flowers.

Mendel's experiments revealed that organisms have two copies of any gene for a trait. Those two copies can be identical, two purple alleles of the flower color gene, for instance; or those two alleles can be different. A pea plant could have one purple allele of the flower color gene and one white allele of the flower color gene. When an organism has two identical alleles of a gene, it is homozygous for that gene. When an organism has two different alleles of a gene, it is heterozygous for that gene.

An organism inherits one allele, or copy of a gene, from one parent and one allele from the other parent. An organism, or cell, that has two copies of all of its genetic information is called diploid. In most sexually reproducing animals, the offspring are formed when a sperm cell from the male parent fertilizes an egg from the female parent. The sperm and the egg only contain half of all the genetic information. They are said to be haploid. However, the new organism they create is diploid because it gets one copy of the genetic information from the sperm and a second copy from the egg.

Mendel's first law, or the law of segregation, states that the two copies of each gene separate during the formation of gametes (eggs and sperm), and that fertilization of the egg by the sperm is a random event. Any sperm containing any allele of a gene can fertilize any egg of the same species, regardless of the allele carried by that egg.

Mendel noted that certain alleles seemed to dominate over others. For instance, when a plant had a purple allele for flower color and a white allele for flower color, the plant always had purple flowers. Mendel called the allele that was seen in the heterozygote, in this case the purple allele, the dominant allele. The allele that was hidden or masked, he called the recessive allele. In order to show a recessive allele, an organism has to have two identical copies of a gene, both containing the same recessive allele. This is known as the homozygous recessive condition. Garden peas that have white flowers are homozygous recessive for the white allele of the flower color gene.

Homozygous recessive describes the organism's genotype, or its genetic makeup. It has two copies of the recessive allele of the gene. The observable characteristic of the organism, having white flowers, is called its phenotype.

Mendel also demonstrated that the segregation of alleles of any one gene is not dependent on the segregation of alleles of any other gene. For instance, a gamete could receive a dominant allele for an eye color gene and a recessive allele for height, or that gamete could receive the recessive alleles for both genes or the dominant alleles of both genes. This is Mendel's second law, the law of independent assortment, and it applies to any genes that are located on separate chromosomes.

Mendel's work was far ahead of its time. Although Mendel published his research in the 1800's, it was not until after his death that his work gained recognition in the scientific community. In 1900, three other scientists, each working separately on inheritance, came across Mendel's work in the course of their research. They gave him credit for his insights, and Mendel's research provided the foundation for the new discipline of genetics.

Genes and Chromosomes

Although Mendel described the gene as the factor that was responsible for a particular trait, nothing was known about the physical makeup of a gene. One of the first questions scientists needed to answer was where genes are found in cells. Early studies in frogs and sea urchins indicated that the nucleus of the sperm and the nucleus of the egg combined with each other during fertilization. This observation suggested that the genetic material that determined how the fertilized egg would develop might reside in the nucleus.

As microscopes improved, scientists were able to distinguish structures within the nuclei of cells. These long, threadlike structures stained blue and were called chromosomes (Greek *chroma*, "color"). Several scientists observed that when animal and plant cells divided, the chromosomes duplicated, then separated, and each daughter cell inherited a complete set of chromosomes. The one exception to this was the cell division that produced the gametes (eggs and sperm). When an egg or a sperm cell was produced, it only contained half the number of chromosomes as the cell that produced it. If genetic information was carried on chromosomes, scientists reasoned that a sperm and an egg could each contribute half of the genetic information to the new organism at fertilization.

Some of the first evidence that chromosomes were linked to observable traits came from the studies of American graduate student Walter S. Sutton. Sutton studied grasshoppers, and his observations indicated that male grasshoppers always had an X and a Y chromosome, whereas female grasshoppers contained two X chromosomes. Several other scientists observed similar things in other organisms, such as fruit flies, and concluded that the physical characteristic of sex was determined by the kind of chromosomes an organism possessed.

Since chromosomes determined the trait of sex, it was possible that chromosomes contained the genes that Mendel had shown to determine physical characteristics. The first scientist to demonstrate that genes were located on chromosomes was Thomas Hunt Morgan, who showed that an eye-color gene in the fruit fly, *Drosophila melanogaster*, was located on the X chromosome.

Next, scientists wanted to know what kind of chemical molecule actually carried the genetic information. Chromosomes contain two kinds of molecules, protein and a weak acid called deoxyribonucleic acid (DNA). Experiments in the early 1930's first demonstrated that DNA is the genetic material. Oswald Avery, Colin MacLeod, and Maclyn McCarty showed that adding DNA to these bacterial cells could change their physical traits. In their experiments, they mixed a harmless strain of bacteria with DNA from bacteria that caused disease in mice. When they did this, the previously harmless bacteria changed (or transformed) into disease-causing bacteria. Two other scientists, Alfred Hershey and Martha Chase, later obtained similar results by studying a virus that infects *E. coli*.

Molecular Genetics

By the 1940's, scientists knew that genetic information was carried by genes made of DNA molecules inside cell nuclei. However, scientists did not know how the genetic information was copied accurately from one generation to the next—from one cell division to the next. Nor did scientists know how the DNA could account for the appearance of inherited changes or mutations. In order to answer these questions, scientists needed to know the precise chemical structure of DNA.

Many scientists contributed to the understanding of the structure of DNA. Erwin Chargaff obtained data that indicated that specific molecular components of the DNA molecule were always present in equal parts. These components were nitrogen-containing molecules (or nitrogenous bases). Chargaff determined that the nitrogen-containing bases adenosine and thymine were always present in a one to one ratio, and the bases guanine and cytosine were always present in a one to one ratio, no matter what species' DNA was analyzed.

Simultaneously, two scientists at Kings College in London, Rosalind Franklin and Maurice Wilkins, were attempting to make X-ray pictures of DNA molecules. Rosalind Franklin obtained an X-ray film that indicated that DNA was a helical molecule. Just previous to Franklin's work, an American chemist, Linus Pauling, had made a breakthrough in solving the structure of the protein alpha helix using a model-building approach.

Two scientists working at Cambridge University in England, James Watson and Francis Crick, decided to use Pauling's method of model building to attempt to solve the structure of the DNA molecule. Combining the data from a variety of sources including the data of Chargaff, Wilkins, and the crucial X-ray crystallography data of Rosalind Frankin, Watson and Crick solved the structure of the DNA molecule.

Watson and Crick created a model of DNA: a double helix, like a twisted ladder. The DNA molecule was a long polymer of repeating nucleotides. Each nucleotide contained three chemical parts: a sugar, a phosphate group, and a nitrogen-containing base. The sides of the double helix ladder were formed by alternating sugars and phosphates, and the rungs were formed on the inside of the helix by specific pairings of the nitrogen-containing bases. Adenine paired with thymine to form one kind of rung. Guanine paired with cytosine to form a second kind of rung.

The order of the bases provided the information within DNA. Certain combinations of bases could form "words" that stood for parts of proteins or other molecules encoded by the DNA. The double helix could unzip like a zipper, each strand serving as a template to guide the construction of a new strand. This provided an accurate means for copying the DNA molecules from a parent cell to a daughter cell.

Animal Model Genetic Organisms

ROUNDWORM (*Caenorhabditis elegans*): This millimeter-long worm allowed scientists to test the concepts of gene therapy, to develop methods for sequencing large amounts of DNA, and provided information about the biology of human diseases such as Alzheimer's disease and cancer. Research on this worm has also enabled scientists to develop effective control measures for plant and animal parasitic roundworms.

FRUIT FLY (*Drosophila melanogaster*): Studies in this organism allowed scientists to determine that genes reside on chromosomes, and gave insight into the nature of mutations. Studies of the development of complex structures such as the eye continue to provide insight into some of the ways cell specialization is regulated and directed by DNA.

ZEBRA FISH (*Danio rerio*): The zebra fish, with its transparent embryos, provides an excellent system in which to study the genes that regulate vertebrate development. Additionally, zebra fish have been used in studies investigating bioaccumulation of organic compounds in the environment.

COMMON MOUSE (*Mus musculus*): Mice are useful for genetic study because of the availability of hundreds of single gene mutations. Studies in mice demonstrated that Gregor Mendel's laws of inheritance were as applicable to mammals as to plants. Transgenic genetic analysis of mice has allowed the creation of mouse strains that mimic human genetic diseases.

Genetic Engineering

The details of how DNA is passed from one generation to the next, of how mutations arise, and of how the information of DNA is actually translated into the activities of cells forms the basis of genetic research at the beginning of the twenty-first century.

One of the most important scientific discoveries that led to modern genetic technology was the discovery of a particular kind of protein, a restriction enzyme, from bacteria that cuts DNA molecules at specific sequences of bases. These restriction enzymes gave scientists the tool they needed to break DNA down into smaller pieces, eventually allowing the isolation of individual genes from the huge amount of DNA inside the nucleus of the cell.

Herbert Boyer and Stanley Cohen combined their knowledge of restriction enzymes and bacterial transformation (getting bacteria to take up DNA from the environment) to clone genes. Gene cloning involves isolating a gene of interest by using a restriction enzyme to cut it away from other DNA, and placing it in a piece of DNA called a vector that can be taken up by bacterial cells. One of the first applications of this technology was the production of human insulin. Scientists isolated the gene that encodes the information for making insulin from human DNA, cloned it into a bacterial vector, and placed the vector with the insulin gene in *E. coli*. The *E. coli* cells were able to produce large quantities of insulin. This new insulin was considerably cheaper and safer than insulin purified from human tissue.

Variations on this technique of taking a piece of DNA from one species and inserting it into the cells of another species are involved in genetic engineering of multicellular organisms. In multicellular organisms such as plants or monkeys, the DNA vector is usually a modified virus. These techniques are the basis of human gene therapy.

In the last decade of the twentieth century, entire organisms have been cloned. In Scotland, Ian Wilmut and colleagues reported the first mammalian cloning of a sheep named Dolly. In Wisconsin and Japan, scientists have cloned cattle. When an organism is cloned, all of its DNA, usually contained within an intact nucleus from a cell of the adult animal, is transferred to an egg cell from which all the genetic information has been removed. The egg is then allowed to develop into a new organism. Although the new organism is young, it has the same DNA as the parent from which the nucleus was obtained.

Scientists have also developed techniques for sequencing DNA, determining the exact order and number of nitrogenous bases within the DNA of an organism's genome. In 2000, the Human Genome Project announced that the entire genome of the human had been sequenced. Many other genomes have been sequenced, including the roundworm, *C. elegans*, several plants, and even baker's yeast. The sequence of an organism gives scientists another tool in answering questions about how DNA regulates and determines the activities of cells.

The ethical consequences of genetic engineering are not clear. DNA forensic evidence is now used to convict or exonerate criminal suspects on a routine basis. The genetic engineering of food crops that are pest resistant or contain additional nutrients is fairly routine. With the cloning of entire organisms now possible, the cloning of a human is not science fiction. Parents can have an embryo tested for devastating genetic diseases before it is born. While many of these advances are clearly positive, many of them are double-edged swords, begging for informed public debate.

—Michele Arduengo

See also: Asexual reproduction; Breeding programs; Cleavage, gastrulation, and neurulation; Cloning of extinct or endangered species; Copulation; Courtship; Determination and differentiation; Development: Evolutionary perspective; Estrus; Fertilization; Gametogenesis; Hermaphrodites; Hydrostatic skeletons; Mating; Parthenogenesis; Pregnancy and prenatal development; Reproduction; Reproductive strategies; Reproductive system of female mammals; Reproductive system of male mammals; Sexual development.

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GIRAFFES

Type of animal science: Classification
Fields of study: Anatomy, behavior, ecology, physiology

Giraffes are even-toed, herbivorous mammals that are found exclusively in Africa. They have long necks and legs, and distinctive brown patches all over their bodies.

Principal Terms

BROWSER: feeds on shoots and leaves
DIURNAL: active during daylight hours
FLEHMEN: behavior involving curling and wrinkling of lips and nostrils, with the activation of the Jacobson's organ
HIERARCHY: a social structure in which animals are dominated by those higher on the linear ladder
JACOBSON'S ORGAN: a sense organ between the roof of the mouth and nasal passages, which detects chemical signals associated with reproduction

Because of their long necks and legs, giraffes are the tallest animals in the world. Patch coloration and shape can vary within their extensive habitat range. Females are distinguished from males in that the females have shorter, inward-curving horns. In both sexes, a long mane of stiff, brushlike hairs extends from the back of the head to the shoulders. Giraffes exhibit a unique, fluid gait. When walking, the fore and hind legs on the same side appear to move almost in unison. Swift and fleeting, giraffes can gallop up to thirty-three miles per hour. Their gallop can be described as a motion in which the front legs move together and their hind legs move forward and outward, enveloping the forelegs in a unique rhythmic pattern. Long and graceful, their sleek necks swing back and forth rhythmically with their legs. The neck has remarkable range of motion. A system of blood vessels and valves in the neck protects the brain and reduces blood pressure when the animal lowers its head.

Diet

Although some may feed at night, giraffes are classified as herbivorous diurnal eaters. They are browsers, and competition for food is greatly reduced because of the height at which they feed. The male feeds at greater heights, with his head stretched upward, whereas the female feeds at lower heights, often bending her head and neck to reach the leaves. Giraffes feed mainly on the highly nutritious leaves, fruit, and flowers of acacia trees. Their long, dexterous tongues strip leaves from the acacia twigs. Giraffes often consume soil and bones to balance the phosphorus and calcium in their blood. When feeding on sprouted vegetation and when drinking water, giraffes splay their front legs and bend their knees. In such a position, they are vulnerable to predators, especially lions. Giraffes can go without water for days.

Protection, Defense, and Communication

Generally docile creatures, giraffes may kill other animals with a kick of a fore or hind hoof. Their heads, used like a knight's mace, land formidable blows on the body or legs of opponents. The effective use of their heads as weapons is enhanced by the physical structure of horns and knobs. The skull bone is solid and thick, so that its force can result in a fatal blow. The giraffe's own head is protected by extensive sinuses, which absorb shock. Giraffes snort, grunt, bleat, bellow, and

Giraffe Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Artiodactyla
Family: Giraffidae
Genus and species: Giraffa camelopardalis, with nine subspecies

Geographical location: Africa, south of the Sahara

Habitat: Dry, open savanna biomes, covered with bush and acacia trees

Gestational period: About 450 days

Life span: Up to twenty-five years in the wild; up to twenty-eight years in captivity

Special anatomy: A long neck with seven vertebrae (characteristic of all mammals); adult height of between fifteen and eighteen feet; chestnut brown patches of various sizes and shapes; sloping back ending in a long, tufted tail; a pair of horns on top of the head

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GOATS

Types of animal science: Anatomy, classification, reproduction
Fields of study: Anatomy, zoology

Goats, artiodactyls similar to sheep, can live on hills and mountains where sheep would starve. They were domesticated to provide meat, milk, and leather.

Principal Terms

ARTIODACTYLS: hoofed mammals with an even numbers of toes

GESTATION: pregnancy

HERBIVORE: an animal that eats only plants

KERATIN: a tough, fibrous major component of hair, nails, hooves, horns

RUMINANT: a herbivore that chews and swallows plants, which enter its stomach for partial digestion, are regurgitated and chewed again, and reenter the stomach for more digestion.

UNGULATE: any hoofed mammal

Goats are herbivorous artiodactyls—even-toed ungulates—of the family Bovidae, genus *Capra*, which usually have hooves and hollow horns. They are also ruminants, chewing and swallowing food, regurgitating it, and chewing and swallowing it again. This cud chewing allows them to get the most nutrients possible from the low-quality foods they eat.

Wild goats are mountain dwellers, adept at leaping between rocks, sure-footed due to their hoofs. The hoofs have a hard outer layer and a softer, inner layer that wears away quickly and leaves hard edges useful for climbing. Domesticated goats, raised for milk, meat, and leather, retain many of these characteristics. Swiss goats, the most common domesticated variety, have pointy ears and horns, while Nubians are hornless.

Physical Characteristics of Goats

Most adult goats weigh up to 125 pounds. They are not as large as sheep, which they resemble. Their horns are twisted flat and turn backward. Their hoofs are divided in two (cloven). Males are called rams or billies, while females are called does or nannies. Males emit strong odors during mating season. Males and most females have chin beards, leading to the name "goatee" for the similar style of facial hair in men. Goats are normally covered with straight hair, but some grow wool, such as angora goats. Their coats are red, brown, tan, or white. Goats find enough to eat on poor, dry land where horses, cows, and sheep would starve. Adult female goats reach lengths of 2.5 to 3.5 feet and are approximately 4 feet at the shoulder; they weigh between 100 and 120 pounds. Males are 20 percent larger and heavier than females and have longer horns.

Domesticated goats derive from ten wild goat species. They live on hills and mountains and are either goat antelope or true goats. All except the Rocky Mountain goat inhabit Europe and the Asian Himalayas. Rocky Mountain goats and chamois are goat antelope, having physical characteristics of both goats and antelope.

Types of Goats

Rocky Mountain goats are goat antelope inhabiting mountains from the American Northwest to Alaska. They live in snowy, craggy habitats and are excellent climbers, due to hoofs having soft pads with hard rims that work well on snow, ice, or rock. Rocky Mountain goats are about three moo to communicate. Because of their height, giraffes' sense of smell is not as keen as other animals. However, their sensitivity to sound and their visual acuity more than compensate for their underdeveloped sense of smell.

Reproduction and Birth

Mixed herds of variable numbers have been recorded in the field. Old males are often solitary. About a day before mating, the female becomes sexually attractive. At the onset of mating, the male licks the female's genitals and catches her urine on his tongue. Chemical signals in her urine are detected by flehmen as the male's Jacobson's organ becomes activated. The male remains with the female in heat unless he is displaced by a higher-ranking challenger. The female gives birth in cover, with her back legs bent to reduce the height from which the calf falls. Initially, the mother is alone with her calf, but later she may form a nursery group assisted by other females. The calf stands within five minutes of birth and suckles within the hour. The calf becomes independent of the mother around the sixteenth month. Play behavior, called nose-to-nose sniffing, between the young cements social bonds between them.

—William P. Carew

See also: Defense mechanisms; Fauna: Africa; Herbivores; Horns and antlers.

Giraffes are the tallest animals in the world, with long necks that allow them to eat leaves from the tops of trees unreachable by other herbivores. (Corbis)

Goat Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Artiodactyla
Family: Bovidae
Subfamily: Caprinae
Tribes: Rupicaprini (four genera, five species); Ovibonini (two genera, two species); Caprini (five genera, seventeen species)
Geographical location: Asia, Europe, North America, Africa, New Zealand, Australia
Habitat: Dry mountains or hills
Gestational period: Around 5.5 months
Life span: Fourteen to twenty years
Special anatomy: Permanent, hollow horns, ruminant stomach, very tough hooves

feet tall at the shoulder, with black horns, white, shaggy pelage, and goatees. They eat any plants available and are solitary, except during mating.

Chamois goat antelope have light brown pelage in the summer, which turns dark in winter. The males' deadly curved horns are eight inches long. Chamois are about the same size as Rocky Mountain goats and have similar hoofs. They live above mountain tree lines in Europe, Asia, and New Zealand and prefer eating grass and lichens. During winter, they eat pine needles and bark. Females form herds of up to one hundred, while males live alone except to mate. Chamois battle for mates, and defeated males often die after their belly and throat are ripped open by the victor's horns.

Angora goats, true goats, have body shapes like domesticated Swiss goats. They inhabit Turkey, South Africa, the United States, Argentina, Australia, and New Zealand. Horned and bearded, their long, thick, hair is used in mohair cloth. Angora goats grow approximately 80 percent of the size of Rocky Mountain goats. They live on hillsides, eating woody vegetation and grass.

Nubian goats, hornless true goats, have short hair and droopy ears, and the males have goatees. Adult males weigh up to 180 pounds, while females weigh up to 140 pounds. Males are about five feet tall at the shoulder. Their coats are black, tan, or red, sometimes with white spots. They eat briars, thistles, and brambles, as needed, with their tough mouths and teeth. Their splayed hooves aid climbing hills. Nubians live in large herds and males fight for mates.

Goat Life

Goats prefer eating leaves and grass, but can eat thistles, briars, and brambles with their tough mouths and teeth. Thus, they can survive where soft vegetation is scarce and other herbivores starve. Goats are sociable and live in groups of from a dozen to thousands of individuals.

Mountain goats are adept at leaping from rock to rock, balancing on their hooves. (PhotoDisc)

In the wild, males fight for mates and may die in such battles. Mating usually occurs in the spring among domesticated goats, while wild goats generally mate in the fall. The goat gestation period is about 5.5 months and yields one to four young, nursed for six months. Young goats are born with hair, eyes open, and can run and jump within twelve hours of birth. Goats can live for fourteen to twenty years.

A number of goat breeds are raised for meat, milk, leather. Goats are fine milk producers, and the milk is often used to make cheese. Their milk is sweet, nourishing, and easy to digest. It also has more fat and protein than cow milk and is helpful to persons with digestive troubles. More people throughout the world use goat milk than cow milk. Toggenburg and Saanen Swiss goat imports are popular milk goats in the United States. Toggenburgs are brown, with light side stripes, while Saanens are short-haired and white or cream-colored; both breeds produce around five quarts of milk per day. Goatskins also make high-grade leather; for instance, "Morocco leather" is chamois skin. Angora and cashmere goats are raised for their coats, which are used to make wool.

—*Sanford S. Singer*

See also: Domestication; Mountains; Ruminants; Sheep; Ungulates.

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GOPHERS

Types of animal science: Anatomy, classification, reproduction
Fields of study: Anatomy, zoology

Gophers are small, burrowing rodents with fur-lined cheek pockets. When they eat bulbs and roots they become agricultural pests, damaging crops.

Principal Terms

GESTATION: time in which mammalian offspring develop in the uterus
HERBIVORE: an animal that only eats plants
INCISOR: a cutting tooth that acts like a scissors or chisel
RODENT: any gnawing animal

Gophers are small, herbivorous rodents. They are rat-sized, but somewhat more rotund than rats. They form the families Geomyidae and Thomomyini, which have eight genera, thirty-five species, and hundreds of subspecies. Gophers burrow in the ground and do not leave their burrows during daylight hours. Different species are found in deserts, shrublands, and grasslands across much of North and Central America, from central and southwestwern Canada through the western and southeastern United States, Mexico and south to the Panama-Colombia border.

Striped gophers (*Citellu tridecemlineatus*, prairie squirrels), which have thirteen body stripes, live from the western plains of the United States to Panama. Camas rats (*Thomomys bulbivorus*) are the largest gophers, reaching body lengths of over one foot. Plains pocket gophers (*Geomys bursarius*) are dark brown, and common in the Mississippi Valley.

French settlers in North America first noticed that gopher burrows honeycombed the soil and named them *gaufres* (French for "honeycomb"). These animals all have pouches (pockets) in their cheeks, and are more correctly called pocket gophers (pouched rats). Pocket gophers are divided into twenty-six Geomyini species and nine Thomomyini species. The main gopher types include eastern pocket gophers, yellow pocket gophers, and western pocket gophers.

Physical Characteristics of Gophers

Gophers are plump, ratlike rodents, up to 1.25 feet long and covered with soft, short, black and red-

Gopher Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Rodentia (rodents)
Family: Geomyidae (gophers)
Tribes: Geomyini (four genera, twenty-five species); Thomomyini (one genus, nine species)
Geographical location: North and Central America, from central and southwestern Canada, western and southeastern United States, Mexico, and south to the Panama-Colombia border
Habitat: Deserts, shrubby land, grasslands, agricultural areas, and tropical lowlands
Gestational period: About three weeks
Life span: Up to four years in the wild; up to six years in captivity
Special anatomy: Fur-lined pockets in cheeks, whiskers, strong incisor teeth, front claws for digging, tactile tails

brown to gray fur. All have whiskers, to help them navigate underground and at night, and two large, fur-lined pockets, one in each cheek. These pockets, used to carry food, lead to the name pocket gopher. The pockets are lined with fur, and a gopher can turn them inside out to clean them.

Gophers have wide, blunt heads, with underdeveloped ears and eyes. Their incisors are large and well designed for gnawing. Gophers have short limbs and feet with powerful claws, longer on the forefeet. They dig tunnels with the claws of the front feet. Their thick, almost hairless tails, about three inches long, are sensitive tactile organs, used to help them find their way around their tunnels when moving backward. Gophers are able to run backward about as quickly as forward. Their body lengths range from 4.5 to 17 inches, and they weigh between 0.75 and 2 pounds.

Gopher Life

Gophers eat leaves, grass, roots, nuts, tubers, buds, and farm vegetables. Their main foods, garnered in their tunnels, are roots and tubers. The other foods are gathered on nocturnal surface forays. They need water to survive, but when water is scarce in arid regions, they eat cacti to obtain it. The gophers store most of their food in the tunnels and chambers of their burrows. They carry the food to their burrows in their cheek pouches.

Gophers are solitary and males are territorial. They come together only to breed. Female gophers can have one or several litters each year. They birth two to ten young, depending on the species. Gestation is about three weeks. The young are totally dependent on their mothers at birth, weaned after a month, and have their own tunnels by age three to four months. Pocket gophers have life spans of one to seven years.

Image Not Available

Western Pocket Gophers

Western pocket gophers—like other gophers—have small, round bodies. They are tan to gray and live in deserts, meadows, and farmlands in Canada, the southwest United States, Mexico, and Central America. They like areas where the soil is easy to dig. These gophers eat plant leaves and underground roots and tubers. In dry areas, they eat cacti to obtain water. They travel on the surface at night, seeking and cutting through underground roots with sharp incisors. Western pocket gophers carry their food in their cheek pouches. They are territorial, and a given male's territory may be up to one thousand square feet.

Western pocket gophers can breed up to four times a year, once during each season of the year. Gestation is approximately three weeks, and young, born completely dependent on their mothers, develop their own burrows and territories within three months. These gophers live for four years in the wild and seven years in captivity.

Gophers are very destructive when they tunnel in farmland such as meadows, farms, and orchards. The tunnels are identified by the mounds of earth left along their courses. Very voracious, gophers eat all vegetation they find underground. They destroy food trees, tuber crops, and flower crops by gnawing roots, tubers, and bulbs.

—Sanford S. Singer

See also: Fauna: Central America; Fauna: North America; Home building; Mice and rats; Nesting; Rodents.

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GORILLAS

Type of animal science: Classification
Field of study: Anatomy

Gorillas, the largest, rarest, most powerful apes, are shy vegetarians living in bands in the wild. They have language and are an endangered species.

Principal Terms

BAND: A gorilla group of five to twenty apes, including males, females, and young

SILVERBACK: An older, male band leader, whose back hair has turned gray

Gorillas, the largest, strongest, rarest apes, look the most human of all other primates. They live in equatorial West African forests, from lowlands near the Cameroon Coast to highland altitudes of 10,000 feet in Rwanda, Zaire, and Uganda. All gorillas are believed to belong to one species, *Gorilla gorilla*.

Physical Characteristics of Gorillas

Males are 5.75 feet tall when on all fours, over six feet when standing erect, and thus are taller than the average man. They are much heavier, weighing three hundred to six hundred pounds. Unsurprisingly, their bone structure is heavier than that of humans. Females, a foot shorter than males, weigh half as much. Gorilla skin is dark and, except for the face and hands, covered with long, coarse, dark brown to black hair. This hair turns gray on the backs of older males, who are then called silverbacks.

Gorillas, especially males, look fierce, although they are timid unless mating, cornered, or threatened. Their fierce looks are due to hulking bodies and somber faces, with dark, hairless, strong jaws and long, powerful teeth. In addition, gorillas have brutish brow ridges which jut out above small eyes. Finally, the face of the male is dominated by a large, flat nose with coarse nostrils. Combined, these features produce what humans perceive as a somber and threatening expression.

Gorilla brain cases and brain sizes are smaller than in humans, promising lower intelligence. As to skeletal structure, the gorilla is similar to humans, but its bones are thicker. Its arms are much longer and its legs are much shorter. Gorilla spines lack the structures needed for a continual erect posture. Therefore, while gorillas can stand upright and walk erect, most often they walk on all fours, using the knuckles of their hands as supports.

Life and Sexual Cycles of Gorillas

Contrary to their legendary savagery, reinforced by their appearance, gorillas are shy, friendly creatures. Once they become used to unthreatening intruders, as Dian Fossey discovered, these individuals are accepted. Initially, males of gorilla groups charge intruders, growling and beating their chests. Intruders who run are often killed. Those who stand their ground and behave in an unthreatening manner are not harmed.

Gorillas live in families and extended families (bands) of five to twenty individuals. A band has a silverback leader, up to three subordinate males who help protect it, several mature females, and numerous young. The silverback drives most young gorilla males away at maturity. At these times all males are fierce and use their strength to attain and maintain supremacy. Males driven off form bachelor groups or join other bands. Silverbacks, challenged and defeated, live alone.

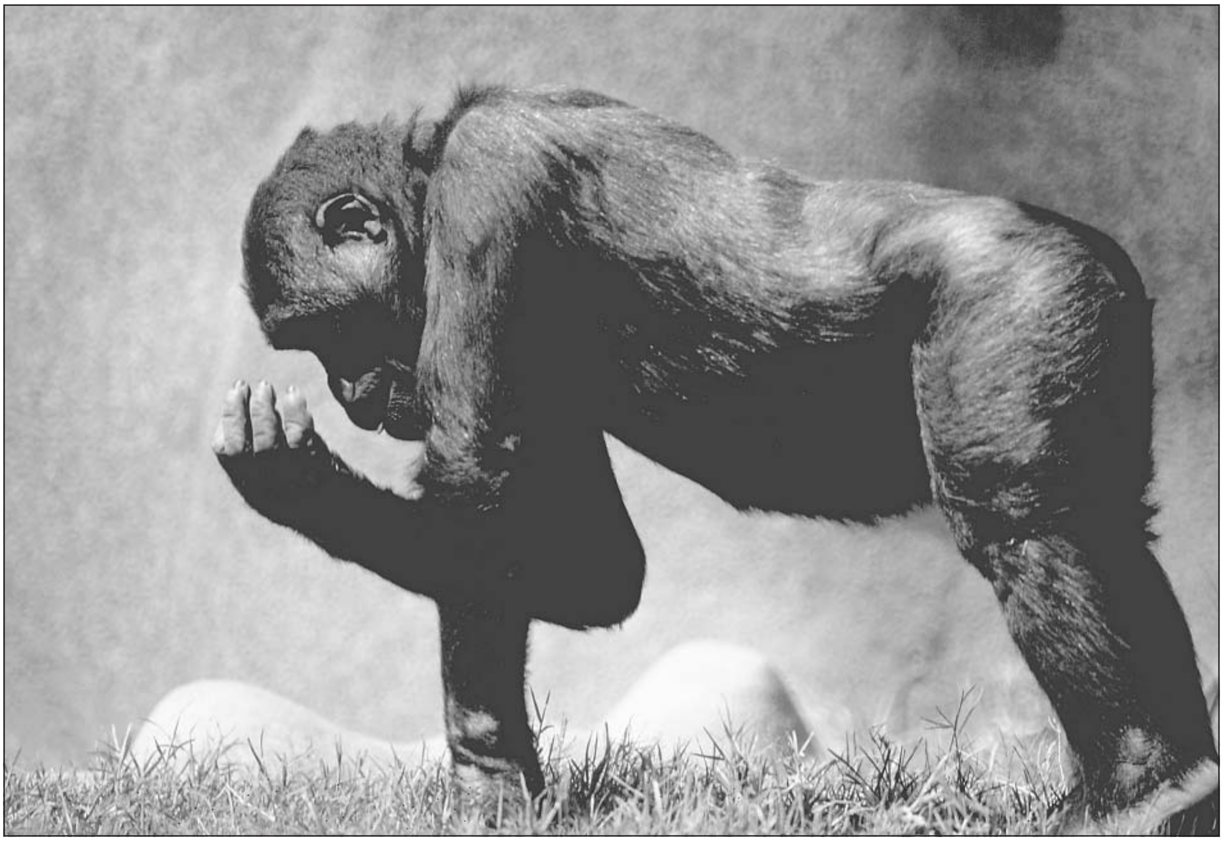
Gorilla bands each have a territory they allow

Gorilla Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Primates (apes, monkeys, and humans)
Family: Pongidae
Genus and species: Gorilla gorilla
Geographical location: Equatorial West Africa
Habitat: Lowland and highland forests
Gestational period: Nine months
Life span: Thirty to forty years in the wild, up to fifty years in captivity
Special anatomy: Long arms used to walk on all fours

others to enter. A band lacks permanent dwellings. Rather, its members build temporary shelters each night after a long day of travel to forage for the honey, eggs, plants, berries, bark, and leaves that make up the gorilla diet. In the wild or in captivity gorillas will eat meat, but do not seek it or kill other animals, except in self defense. When the terrain permits, females and young sleep on tree platforms of branches and leaves. Mature males nest at the bases of trees occupied by other band members.

Female gorillas, like women, menstruate monthly and mate successfully at any time. Pregnancy lasts 9.5 months and yields one or two young. Baby gorillas are suckled for a year. They are adults ten to eleven years later. Wild gorillas live for thirty to forty years. A few captive gorillas have attained more than fifty years.



The gorilla's spine lacks the support structures that would allow it to stand upright, so it usually uses its arms for support, resting on its knuckles. (Corbis)

Dian Fossey

Born: January 16, 1932; San Francisco, California
Died: December 26, 1985; Karisoke Research Center, Rwanda
Fields of study: Anthropology, zoology
Contribution: Fossey, an American zoologist, was a world authority on mountain gorillas.

Dian Fossey was born in San Francisco. After completing elementary and high school, she studied occupational therapy at San Jose State College, graduating in 1954. After this, she worked as a therapist in a children's hospital in Louisville, Kentucky.

In 1963, Fossey traveled to East Africa. There she met the famous anthropologist Louis Leakey and had her first exposure to mountain gorillas. Fossey returned to the United States and to her job, staying there until 1966. Then the persuasive Leakey convinced her to return to East Africa to study mountain gorillas in the wild, from the perspective of a trained therapist. Fossey began to work with these rare, elusive apes, which fascinated her and became her lifework. In 1967, she formalized this fascination by establishing the Karisoke Research Center in the solitude of Rwanda's Virunga Mountains. Initially she carried out her work alone, with no professional staff.

After expending a great deal of effort on the task, Fossey was able to accustom the gorillas to her presence in their midst and to study them quite extensively. The data that Fossey was able to accumulate greatly enlarged the scientific understanding of the mountain gorilla's lifestyle, habits, and methods of communication in the wild. To expand her scientific credentials, Fossey left Rwanda for England in 1970 to work on a doctorate in zoology at venerable Cambridge University. She received her degree in 1974, with a dissertation titled "The Behavior of the Mountain Gorilla."

Fossey soon returned to Rwanda and to her beloved apes. Several volunteer student aides accompanied her. This staff of educated assistants made possible much more extensive research on the mountain gorillas. During the course of her endeavors, one of Fossey's best and most-liked study subjects, the gorilla Digit, was killed by poachers. This motivated her to engage in a pitched battle against the poachers. In 1978, Fossey's efforts to this end began the international media coverage of the issue.

In 1980, she left Rwanda again, accepting a visiting associate professorship at Cornell University in Ithaca, New York. While teaching at Cornell, Fossey completed her well-known book *Gorillas in the Mist* (1983), which was made into a film of the same name (1988). Then she returned to her beloved Rwanda to resume the study of the mountain gorilla. Fossey also increased her campaign against the poachers. Sadly, in 1985 Dr. Fossey's dead body was found in the bush, presumably a murder victim of poachers whose activities she had sought so bravely to stop.

—Sanford S. Singer

Image Not Available

Gorilla Language and Intelligence

Gorilla language is composed of several sounds. Hooting signals alarm or indicates unusual events. Hooting by a silverback gains immediate attention from all band members. Other language sounds include sharp grunts that discipline young gorillas and low growls signifying pleasure. All gorillas beat their chests. In males, this is a symbol of power and intimidates other creatures.

The mental capacity of gorillas was long thought inferior to chimpanzees. Their intelligence is still being explored and testing is changing experimenters' opinions. Different techniques are needed to train gorillas, who are not as curious as chimpanzees. Trained correctly, gorillas have better memories and problem-solving skills than chimpanzees. They also discriminate between geometric shapes better. In addition, it is reported that they are most likely to perform tasks associated with intelligence out of interest, not for rewards. In exploration of communication via American Sign Language (ASL), some gorillas have mastered over one hundred words.

Gorillas' Endangered Status

Gorillas are close to extinction because of intrusion on their habitat of farmers, animal herders, and hunters. In the early 1970's, the estimated gorilla population was one thousand. About 25 percent were in Zaire's Kahuzi-Biega National Park (KBP) and 40 percent in its Mount Virunga area (MVA). The rest were scattered but relatively numerous in Rwanda's Parc des Volcans and Uganda's Gorilla Game Reserve.

In 1980, the number of gorillas in KBP was unchanged and those in MVA had dropped 40 percent. The implied decline, which may be continuing, is explained by increased farming and cattle herding in gorilla habitats. Also, killing and poaching of elephants and buffalo causes these animals to move into gorilla habitats, cutting down food sources for the great apes. The Rwandan Mountain Gorilla Project has slowed the decline in Rwanda. Similar efforts are in place elsewhere.

—Sanford S. Singer

See also: Apes to hominids; Baboons; Cannibalism; Chimpanzees; Communication; Communities; Evolution: Animal life; Evolution: Historical perspective; Fauna: Africa; Groups; Hominids; *Homo sapiens* and human diversification; Human evolution analysis; Infanticide; Intelligence; Language; Learning; Lemurs; Mammalian social systems; Monkeys; Orangutans; Primates.

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GRASSHOPPERS

Types of animal science: Anatomy, classification, reproduction
Fields of study: Anatomy, entomology, invertebrate biology

Grasshoppers, leaping insects of the order Orthoptera, include long-horned and short-horned species. They eat grasses and shrubs, as well as agricultural crops, and some human societies eat them.

Principal Terms

MANDIBLES: insect jaws
MOLTING: shedding an insect shell, to enable continued growth
NYMPH: a grasshopper larva

Grasshoppers, leaping insects of the order Orthoptera, include all locusts. However, not all grasshoppers are locusts. The main difference between the locusts and other grasshoppers is the length of their horns (antennae). Locusts (Acrididae) have shorter antennae than other grasshoppers (Tettigoniidae). The amazing leaps of grasshoppers are due to long, slender hind legs with large thighs. These leaps are each many times the grasshopper's body length.

Most grasshoppers also have large, straight, delicate hindwings, which enable flight. When a grasshopper is at rest, these wings are folded up and protected by tough front wings that cover them entirely. Grasshoppers are found in most areas of the world except for northern Canada, Greenland, northern Asia, northwest Africa, West Australia, and the Arctic and Antarctic regions.

Long-horned grasshoppers are herbivores and found wherever vegetation grows. Their threadlike antennae are longer than their bodies. They are related to katydids. When endangered, they spit out brown liquid called "tobacco juice," and take huge, vigorous leaps to escape. The green color of these grasshoppers conceals them in grass, where they eat pieces of grass leaves and stems.

Long-horned grasshoppers do not usually eat crop plants. Short-horned grasshoppers, locusts, are called true grasshoppers because they live only in grasses and leaves. They are well known for traveling in huge swarms that lay bare whole farms or whole regions of countries. The huge populations of swarms and the destruction they have caused are mentioned in the Bible. *Schistocera perigrina*, a North African locust, may have been the species described in the biblical account of the plagues of Egypt.

Physical Characteristics of Grasshoppers

Grasshoppers are one to eight inches long when fully grown. Some species undergo seasonal color changes, being green at some times and red, olive, or brown at others. Like other insects, the grasshopper body is divided into three parts: head; thorax, or mid-section; and abdomen, or hindsection. A grasshopper's antennae, which have tactile functions, are found on its head.

Each grasshopper has a pair of compound eyes with many lenses, located on the front of its head. Grasshoppers also have three pairs of legs, extending from the thorax. The last pair is much larger and longer than the others and enables jumping. Grasshoppers eat leaves, roots, and stems of grasses, herbs, and shrubs, chewing with strong mandibles (jaws), moving these jaws from side to side to break apart their food.

Most grasshoppers have two pairs of wings along the back of the abdomen. Two hard forewings serve as protection and two membranous hindwings are used to fly. When a grasshopper is not flying, its hindwings fold up and are covered and protected by its forewings. All long-horned

Grasshoppers' long, slender hind legs and strong thighs allow them to make amazing leaps many times the length of their bodies. (Digital Stock)

the process. Mature insects mate, and about a week later, females lay the eggs for the next generation. They die a few weeks after this.

Locusts, such as the Rocky Mountain locust (*Melanoplus spretus*), lay their eggs in holes in the ground in the fall. The eggs hatch in the spring, and young reach maturity in July or August. Those of long-horned grasshoppers, such as meadow grasshoppers (*Orchelimum vulgare*) are laid in low bushes or crevices in tree bark.

Not only do locusts eat human crops, but in turn, humans have eaten them for centuries. For example, Talmudic law exempts locusts and other grasshoppers

grasshoppers "sing" by rubbing the bases of their forewings together. Some male locusts make calls to females by rubbing their hind legs against their wings, and others do so by rubbing their hind legs or forewings against other parts of their bodies.

The hearing organs of long-horned grasshoppers are small growths just beneath the knee joints of their front legs. In short-horned grasshoppers, these ears are clear, circular areas on the abdomen at points just behind the junction of hind legs and body. In females, growths shaped like sickles are located at the rear of the abdomen. These ovipositors drill holes in grass, twigs, or the ground, where eggs are deposited. Ovipositors of short-horned grasshoppers are specially designed to deposit pouches of eggs in the ground.

Grasshopper Life Cycles

In the spring, grasshoppers hatch from eggs as pale, wingless nymphs (larvae). Then, within ninety days, they develop into full-grown locusts, molting four to five times in

Grasshopper Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Arthropoda
Class: Insecta
Order: Orthoptera (grasshoppers and related species)
Families: Include Acrididae (short-horned grasshoppers, locusts), Tettigoniidae (long-horned grasshoppers)

Geographical location: Most world locations, except Arctic and Antarctic regions, northern Canada, Greenland, northern Asia, northwest Africa, and West Australia

Habitat: Grass and shrubbery

Gestational period: Natural gestation time is uncertain, as eggs laid in the fall do not hatch until spring

Life span: A year in temperate to cool climates, indeterminate in the tropics

Special anatomy: Six legs, three on each side of the thorax; two pairs of wings, two hard forewings that serve as protection for two membranous hindwings used in flying; ears on or near legs; compound eyes from the taboo on eating flying or creeping creatures "going on all fours." Also, Shakespeare's play *Othello* mentions food "luscious as locusts." Candied locusts are eaten throughout China and the Philippines. In North Africa, locusts dried and ground into powder are mixed into flour used to bake bread.

—Sanford S. Singer

See also: Antennae; Ears; Insects; Molting and shedding; Wings.

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GRASSLANDS AND PRAIRIES

Type of animal science: Ecology
Fields of study: Conservation biology, ecology, environmental science, wildlife ecology

Grasslands, including the prairies of North America, are a biome characterized by the presence of low plants, mostly grasses, and are distinguished from woodlands, deserts, and tundra. They support a great variety of plants and animals. At present, the remaining grasslands provide grazing for livestock and wildlife.

Principal Terms

BIOMASS: the dry weight of the living material in an organism, population, or community

BIOME: region with a particular climate and a characteristic community of living organisms

CARNIVORE: animal dependent on animal material in its diet

CARRYING CAPACITY: the maximum number of animals that a given area can support indefinitely

DENUDE: strip the covering from, as vegetation from overgrazed grassland

FERAL: once domesticated but no longer under the control of humans

HERBIVORE: animal dependent on plant material in its diet

RUMINANT: animal with four stomach compartments that regurgitates its food and rechews it

Grasslands occupied vast areas of the world over ten thousand years ago, before the development of agriculture, industrialization, and the subsequent explosive growth of the human population. They are characterized by the presence of low plants, mostly grasses, and are distinguished from woodlands, deserts, and tundra. They experience sparse to moderate rainfall and are found in both temperate and tropical climatic zones. The main grasslands of the planet include the prairies of North America, the pampas of South America, the steppes of Eurasia, and the savannas of Africa. Grasslands are intermediate between deserts and woodlands in terms of precipitation and biomass. The warmer tropical savannas average 60 to 150 centimeters (25 to 60 inches) of rain. The temperate grasslands range between twenty-five to seventy-five centimeters (ten to thirty inches) of precipitation, some of which may be in the form of snow. The biomass of grasslands, predominantly grasses, is quantitatively intermediate between that of deserts and woodlands, which produce 10 to 15 percent and 200 to 300 percent, respectively, of the amount of plant material. It should be recognized that the grassland biomes can be subdivided in terms of climate, plant species, and animal species. It should also be noted that grasslands do not always shift abruptly to deserts or woodlands, leading to gradations between them. In addition, grasslands do have scattered trees, often along streams or lakes, and low-lying brush.

Grasses have extensive root systems and the ability to become dormant. These permit them to survive low rainfall, including periodic droughts, or the winter cold typical of temperate regions. Furthermore, grasslands have always been subjected to periodic fires, but the deep root systems of grassland plants also permit them to regrow after fire. Grasses coevolved over millions of years with the grazing animals that depend on them for food. Ten thousand years ago, wild ancestors of cattle and horses, as well as antelope and deer, were on the Eurasian steppes; bison and pronghorn prospered on the North American prairies; wildebeest, gazelle, zebra, and buffalo dominated African savannas; and the kangaroo was the predominant grazer in Australia. Grazing is a symbiotic relationship, whereby animals gain their nourishment from plants, which in turn benefit from the activity. It removes vegetative matter, which is necessary in order for grasses to grow, facilitates seed dispersal, and disrupts mature plants, permitting young plants to take hold. Urine and feces from grazing animals recycle nutrients to the plants. The grassland ecosystem also includes other animals, including worms, insects, birds, reptiles, rodents, and predators. The grasses, grazing animals, and grassland carnivores, such as wolves or large cat species, constitute a food chain.

Humans have been an increasing presence in grassland areas, where over 90 percent of contemporary crop production now occurs and much urbanization and industrialization has taken place. Remaining grassland areas are not used for crops, habitation, or industry because of inadequate water supplies or unsuitable terrain but instead are used for grazing domesticated or wild herbivores. In addition, many woodland areas around the world have been cleared and converted to grasslands for crops, livestock, living, or working.

The Prairies of North America

Originally stretching east from the Rocky Mountains to Indiana and Ohio, and from Alberta, Canada to Texas, the prairies were the major grassland of North America. The short-grass prairie extended about two hundred miles (three hundred kilometers) east of the mountains, and the long-grass prairie bordered the deciduous forest along the eastern edge, while the mixed-grass prairie was between the two. Going from west to east, the amount of precipitation increases, causing changes in plant populations. The short-grass prairie receives only about twenty-five centimeters (ten inches) of precipitation each year, mostly as summer rain, and, as its name suggests, has short grass, less than sixty centimeters (two feet) tall. Today, it is used primarily for grazing because the soil is shallow and unsuited for farming without irrigation. The mixed-grass prairie receives moderate precipitation, ranging from 35 to 60 centimeters (14 to 24 inches) and has medium-height grasses, ranging from 60 to 120 centimeters (2 to 4 feet) tall. Much of it is now used for growing wheat. The tall-grass prairie receives more than 60 centimeters (24 inches) of precipitation, mostly in the summer, and had grasses that grow to over 150 centimeters (5 feet) tall. It has rich soil and has been mostly converted to very productive cropland, primarily for corn and soybeans. The prairies experience very cold winters (down to –45 degrees Celsius, –50 degrees Fahrenheit) and very hot summers (up to 45 degrees Celsius, 110 degrees Fahrenheit). They are often windy and experience severe storms, blizzards in winter, thunderstorms and tornadoes in summer.

Like other biomes, the prairies have a characteristic assortment of animals, herbivores that eat the plants and carnivores that prey on the herbivores. Before 1500 C.E., two ruminants, the bison (commonly but inaccurately called buffalo) and the pronghorn (not a true antelope), were the major grazers on the prairies. The prairie dog, a herbivorous rodent that burrows, lived in large communities on the prairies. The major predators were the wolf and coyote for bison and pronghorn, and the black-footed ferret and fox for prairie dogs. A variety of birds, herbivorous and carnivorous, reptiles, and insects also made their home on the prairie.

Overgrazing Grasslands

While grazing is of mutual benefit to plant and animal, overgrazing is ultimately detrimental to both the plant and animal populations, as well as the environment. Continued heavy grazing leads to deleterious consequences. Removal of leaf tips, even repeated, will not affect regeneration of grasses provided that the basal zone of the plant remains intact. While the upper half of the grass shoot can generally be eaten without deleterious consequences, ingesting the lower half, which sustains the roots and fuels regrowth, will eventually kill the plants. Overgrazing leads to denuding the land, to invasion by less nutritious plant species, to erosion due to decreased absorption of rainwater, and to starvation of the animal species. Because the loss of plant cover changes the reflectance of the land, climate changes can follow and make it virtually impossible for plants to return, with desertification an ultimate consequence. It is not just the number of animals, but the timing of the grazing that can be detrimental. Grasses require time to regenerate, and continuous grazing will inevitably kill them. Consumption too early in the spring can stunt their development.

Semiarid regions are particularly prone to overgrazing because of low and often unpredictable rainfall; regrettably, these are the areas of the world where much grazing has been relegated, because the moister grassland areas have been converted to cropland. Overgrazing has contributed to environmental devastation worldwide. Excessive grazing by cattle, sheep, goats, and camels is partly responsible for the desert of the Middle East, ironically the site of domestication for many animals and plants. Uncontrolled livestock grazing in the late 1800's and early 1900's negatively affected many areas of the American West, where sagebrush and juniper trees have invaded the grasslands. Livestock overgrazing has similarly devastated areas of Africa and Asia. In the early twenty-first century, feral horses in the American West and the Australian outback are damaging those environments. Overgrazing by wildlife can also be deleterious. The 1924 Kaibab Plateau deer disaster in the Grand Canyon National Park and Game Preserve is one such example, where removal of natural predators led to overpopulation, overgrazing, starvation, and large die-offs.

Riparian zones, the strips of land on either side of a river or stream, are particularly susceptible to overgrazing. Because animals naturally congregate in these areas with water, lush vegetation, and shade, they can seriously damage them by preventing grasses from regrowing and young trees from taking root, as well as trampling and compacting the soil and fouling the water course. The ecosystem can be devastated, threatening survival of plant and animal species and leading to serious erosion. While herding and fencing can be used to control animals in these areas, a less expensive method is to disperse the location of water supplies and salt blocks to encourage movement away from rivers or streams. If deprived of salt, grassland animals crave it and will seek it out.

Grassland Management

Grassland areas need not deteriorate if properly managed, whether for livestock, wildlife, or both. Managing grasslands involves controlling the number of animals and enhancing their habitat. Carrying capacity, which is the number of healthy animals that can be grazed indefinitely on a given unit of land, must not be exceeded. Because of year-to-year changes in weather conditions and hence food availability, determining carrying capacity is not simple; worst-case estimates are preferred in order to minimize the chances of exceeding it. The goal should be a healthy grassland achieved by optimizing, not maximizing, the number of animals. For private land, optimizing livestock numbers is in the long-term interest of the landowner, although not always seen as such. For land that is publicly held, managed in common, or with unclear or disputed ownership, restricting animals to the optimum level is particularly difficult to achieve. Personal short-term benefit often leads to long-term disaster, described as the "tragedy of the commons" by biologist Garrett Hardin.

Appropriate management of grasslands involves controlling animal numbers and enhancing grassland plants. Restricting cattle and sheep is physically easy through herding and fencing, although it can be politically difficult and expensive. Much more problematic is controlling charismatic feral animals, such as horses, or wildlife, when natural predators have been eliminated and hunting is severely restricted. As for habitat improvement, the use of chemical, fire, mechanical, and biological approaches can increase carrying capacity for either domesticated or wild herbivores. Removing woody vegetation by burning or mechanical means will increase grass cover, fertilizing can stimulate grass growth, and reseeding with desirable species can enhance the habitat. Plants native to a particular region can be best for preserving that environment. Effective grassland management requires matching animals with the grasses on which they graze.

—*James L. Robinson*

See also: Chaparral; Ecosystems; Forests, coniferous; Forests, deciduous; Habitats and biomes; Lakes and rivers; Rain forests; Savannas; Tundra.

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GRIZZLY BEARS

Type of animal science: Classification
Fields of study: Anatomy, conservation biology, physiology, reproduction science, wildlife ecology

Grizzly bears are a kind of brown bear found in inland North America. Brown bears den during the winter and their reproduction includes a period of delayed implantation. While many brown bears are found in the world, their numbers have been decreasing.

Principal Terms

DELAYED IMPLANTATION: an extended period after fertilization, when an embryo stops developing, and before it attaches to the uterine wall and resumes development

DENNING: the period of winter sleep during which a bear does not eat, drink, urinate, or defecate

DIGITIGRADE: walking on the toes, with the heel raised

PLANTIGRADE: walking on the sole, with the heel touching the ground

Grizzly bear is a loose term used to describe a subspecies of brown bears found in inland North America. Around the world, brown bears vary in color from black to very light brown. Grizzly bears have a brown coat with silver-tipped hairs, which gives them a "grizzled" coloration. Grizzlies vary in weight, usually between four hundred and eight hundred pounds, but are generally smaller than brown bears found on the North American coast. In contrast, the largest brown bears in the world, found in coastal Alaska, sometimes weigh over one thousand pounds. Weight differences in brown bears are probably due to the availability of dietary protein. All brown bears have small, round ears, and large, round, dish-shaped faces with a large brow. They also have a characteristic hump over their shoulder that contains fat, and powerful digging muscles. Five long, nonretractable claws aid their digging. Unlike dogs and cats, which walk on their toes (digitigrade), bears walk flat on their whole foot (plantigrade), as humans do.

Denning

One of the most amazing characteristics of brown bears is their ability to den through the winter. During this time, bears appear to be asleep. Their heart and breathing rates slow dramatically, and their energy use is cut in half. They do not eat, drink, urinate, or defecate for three to five months. Although this is often referred to as hibernation, bears are not true hibernators. Their body temperature only falls a few degrees (to about 90 degrees Fahrenheit) and they are easily awakened.

In order to survive such a long period without eating and drinking, bears break down their fat stores. During the winter, they lose 15 to 30 percent of their body weight. In order to build up the fat needed to make it through the winter, brown bears must eat around ninety pounds of food per day during the fall. Most of this food consists of plant material, such as berries, grasses, nuts, and roots, which they unearth with their powerful digging muscles. They also eat some animal material, as available. This may include fish, deer, or elk, and small mammals, such as squirrels or insects. The denning period allows bears to survive winter, a time of food shortage, by using their own stores. Captive bears that are fed through the winter do not den.

Some scientists believe that understanding bears' denning abilities could aid human medicine. A person who must remain bedridden for several months will suffer from bone and muscle loss. Yet brown bears do this every winter with no ill consequences. They are able to go several months without urinating by reabsorbing water from the bladder and converting wastes back into proteins. Understanding this process could help humans who suffer from kidney diseases.

Reproduction and Distribution

Brown bears mate in the late spring or early summer each year. In the days after mating, the fertilized egg divides and grows into a small cluster of cells. Then, the embryo stops growing and remains free-floating in the uterus until the beginning of winter. This unusual process is known as delayed implantation. In winter, the embryo attaches to the uterine wall, and after a sixty-day pregnancy, cubs are born. Brown bears usually have two to three cubs at a time. The cubs weigh less than two pounds at birth, which is especially small compared to the size of the mother. Yet this is not surprising, because the mother is pregnant during the denning period, when she does not eat.

Brown bears are the most widely distributed species of bear. They are found in North America, Europe, and Asia, from the Canadian tundra to the Iraqi desert. However, brown bears have disappeared from about 50 percent of their original

Grizzly bears are characterized by a fatty lump over their shoulders, which helps sustain them through their winter hibernation. (PhotoDisc)

Grizzly Bear Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Carnivora
Family: Ursidae (bears)
Genus and species: Ursus arctos horribilus
Geographical location: Inland northwestern United States and Canada
Habitat: Varied, including temperate and Arctic grasslands, temperate forests, mountainous regions
Gestational period: A five-to-seven-month embryonic diapause, followed by a sixty-day gestation
Life span: Average twenty to twenty-five years in wild; record, thirty-five years
Special anatomy: A hump above the shoulders

range due to human activities. Accurate census data are difficult to obtain because of their wide distribution, large individual territories and solitary nature. In Japan, the Middle East, and Western Europe, several isolated populations have less than one hundred individuals. Larger populations, of a few thousand, are found in Turkey and Eastern Europe. Most of the world's brown bears live in Russia (around thirty thousand), Alaska (around thirty-five thousand) and Canada (around fifteen thousand). In the lower forty-eight states, brown bears have disappeared from 99 percent of their original habitat and are estimated to number around one thousand. Most of the United States and Canadian brown bears are grizzly bears.

—*Laura A. Clamon*

See also: Bears; Estivation; Fauna: Asia; Fauna: Europe; Fauna: North America; Hibernation; Polar bears; Pregnancy and prenatal development.

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GROOMING

Type of animal science: Behavior
Fields of study: Ethology, zoology

Grooming comprises the various actions by which animals clean and maintain their body surface and is vital to the health of individuals. In many species, grooming also plays an important social role in the interactions of animals and in the maintenance of the social organization of the species.

Principal Terms

ALLOGROOMING: mutual grooming or grooming between two individuals

ALTRUISM: a behavior that increases the fitness of the recipient individual while decreasing the fitness of the performing individual

CONSORTSHIP: a pairing of a male and a female

PHEROMONE: a chemical produced by one individual that influences the behavior of another individual of the group

SYMBIOSIS: a relationship between two species of organisms which is not necessarily advantageous or disadvantageous to either organism

THERMOREGULATION: the process by which animals maintain body temperatures within a certain range

Grooming serves a number of purposes. It is health related in that the activity cares for the skin, feathers, or fur. Grooming also serves a social function. Between members of a community, grooming reduces stress, communicates and signals social status, spreads pheromones, achieves thermoregulation or pain relief, increases or decreases arousal, self-stimulates, and prevents sexually transmitted diseases.

As grooming is similar through the various levels of animal taxa, it has been conjectured that grooming behavior is evolutionarily ancient. Most animals (mammals, birds, and insects) groom by moving their limbs over their own bodies or mouthing or licking their bodies. In some birds, sandbathing is quite common. With fish, a species with no limbs, it is not uncommon to see them rubbing or simply moving against rocks, branches, or sand, generally accomplishing what a sandbath does for a bird.

A bird preening its feathers, a cat licking its paws, or a bear brushing his back against a tree truck are all self-grooming. This is where the animal, alone, takes care of the grooming behavior without help from another animal. However, mutual grooming is quite common. In mammalian species, this is a form a display behavior, which helps to cement the social bonds between members of the group. Yet another kind of cleaning behavior, called cleaning symbiosis, occurs between certain species of fish and shrimp. Here, one species will eat the parasites off another species. The cleaner gets food, the recipient remains debris- and parasite-free.

Grooming as Cleaning Behavior

Observations and experiments performed on laboratory rats showed that pregnant rats spent an increasing proportion of their time grooming their ventral surface, which includes the nipple lines and anogenital areas. When the rats were fitted with collars so they could not reach these regions, their mammary development was inhibited. The conclusion to be drawn from this is that self-stimulating grooming is a necessary part of the preparation process for nursing.

A similar conclusion was reached when looking at the function of grooming in male rats.

Prepubertal males engaged in self-grooming of the anogenital area more than their female counterparts. When collars restricted the rats from grooming, their sexual development was significantly hampered. Again, the conclusion is that male rats needed to perform self-stimulating autogrooming in order to prepare for reproduction.

Another very important fact about self-grooming behavior is the appearance of a grooming pattern. For example, depending on the species, self-grooming may start around the head area and progresses downward until the entire body has been groomed. In experiments, it has been noted that a particular animal will not vary its grooming pattern. Studies on hamsters show that specific grooming tendencies evolve as the animal matures. Certain types of grooming behavior are always the result of some external stimuli, or they are the consequence of an aspect of the animal's natural behavior. A male rat invariably performs genital grooming after copulation. A dog, when aroused by some external stimuli (fear or excitement) will often groom its genitalia for de-arousal. Many animals, when afraid or nervous, will gnaw on their paws. Pigs often chew on other pigs' tails, it is thought, when they are bored or have an excess of nervous energy. The expression "licking one's wounds" originates from the observation that most animals will tend to an injury by licking the area, spreading an antiseptic found in saliva to reduce pain and decrease chances of infection. Insectivores, like solendons and shrews, spend a good deal of time grooming, using only their hind legs, to ensure thermoregulation.

Regardless of the lack of similarity between grooming species, grooming behavior is remarkably similar; reiterating that there has not been a great deal of diversification in the evolution of grooming behavior. Sea lions, seals, and walruses, regardless of whether the pelage is sparse or

Social grooming, where one animal grooms another, promotes social bonds and maintains hierarchies. (PhotoDisc)

Preening—More than Good Looks

Preening, for a human, conjures up a vision of someone preparing and dressing themselves carefully in preparation for a social event. People observing birds preen themselves tend to carry over that interpretation for explaining the observed activity. One function of a bird's preening is to remove various ectoparasites, such as fleas, lice, and ticks, as well as other debris on the body. Nonetheless, not all preening rituals are for cleaning alone. When birds preen themselves, they are actually discharging the secretions of the preen gland, also known as the urophgial or oil gland, onto the surface of the skin through several nipplelike pores. The preen gland is the only prominent skin gland in birds and is most developed in aquatic birds, including ducks and geese. Most birds have the gland, but it is almost completely lacking in the emu, ostrich, and several species of parrots, among others. The most common preening action for a bird is to rub its bill and head over the preen gland pore and then rub the collected oil over the feathers of the wings and body and the skin of the legs and feet. In this way, the down or underplumage, which is buoyant and serves as insulation for the bird, remains water-resistant, thereby allowing for thermoregulation. Some birds may preen themselves more than a dozen times a day. It is thought that the oil from the preen gland contains a chemical that is the antecedent to vitamin D. In the presence of sunlight, this substance is converted to vitamin D and the skin absorbs it. This promotes the health of the bird by preserving the integrity of its feathers, bill, and scales.

dense, spend much time grooming. This is typical of marine mammals. They accomplish this by a doglike scratching motion with their hind flippers and using their fore flipper to rub their head and neck while balancing on the other front flipper. They also nibble on their fur, much like dogs. It is common for these animals to rub against rocks or each other, similar to the activity of bears when they rub up against trees. Fish will also use this rubbing behavior against rocks or coral to scour their bodies free from debris.

Grooming as Social Behavior

Mutual grooming, also called allogrooming or allopreening, is when an animal cares for the body surface of another. Mutual grooming in animals is more a form of communication, a social act, than it is a cleansing one. Researchers have come to this conclusion because the time allocated to mutual grooming exceeds what is necessary for simple cleansing and sanitation. This behavior, especially in primates and social birds, promotes social bonding and establishes and maintains the hierarchy among members of the community.

Mutual grooming also brings attention to whether there is such a thing as animal altruism, which is the selfless delivery of service from one animal to another. Whenever one observes a parent grooming its young, the conclusion is that the motive behind the act is to tend to the health of the infant or young, which promotes the proliferation of the species. Nearly all mammals and many species of birds display this behavior. With marsupial births, the young of the Virginia opossum are in a semiembryonic state. The mother licks the embryon at birth so that the membrane encasing it will break. She then licks a trail from the birth canal to the pouch so that the neonate, using its developed olfactory senses, can find its way to the pouch without further aid by the mother. In altricial and semialtricial placental mammals, the young are usually born naked or with little fur. Most of these animal types, such as cats, dogs, mice, shrew, rats, and hamsters, lick the newborn to remove the birth membrane, break the umbilical cord, and eat the placenta after birth. They lick the newborn to clean the perineal region and to remove urine and feces, also aiding in thermoregulation.

When one observes animal and birds of a similar peer group performing grooming rituals, what appears to be unilateral or altruistic grooming behavior may in fact be mutual aid, in that over the long term, repayment may be expected. It is the expectation of reciprocation that establishes and maintains social status. For example, studies on nonhuman primates (mostly Old World monkeys such as rhesus macaques, stump-tailed macaques, and baboons) have shown that a competition exists among members of a group for animals considered to be excellent groomers. Alliances are formed between groomer and groomed; the groomed may provide excellent protection or be a skilled food gatherer. There is evidence of ranking among members of primate society and mutual grooming appears to assist in maintaining the social order and structure.

In primates that form consortships (Cercepethecines), grooming is important in the copulatory sequence, which is not the case in primates that do not form consortships. In general, sexual grooming serves as a male strategy to increase receptivity of an estrus female. In olive baboons and hamadryas, there is a high correlation between the age of the male and the grooming of the females, implying that this may be an alternative method of securing female cooperation in mating when direct agonistic approaches fail or are no longer an option.

Equids are well-known for mutual grooming. Horses, zebras, and similar animals groom each other by pairing off and standing nose-to-nose or head-to-tail, scratching and nibbling each other's neck, back, and tail with their teeth. The nose-to-nose greeting and rubbing of noses is also typical of tapirs and rhinoceros.

Interspecies Grooming

Humans have successfully exploited the horses' need for bonding by touch and grooming. Trainers often start training horses in spring when the animals are shedding. By brushing and grooming, the trainer develops a friendship and level of trust with the animal. This is an example of interspecies bonding through grooming. This behavior is widely noticed between any combination of humans, dogs, and cats. Sometimes licking another animal or human is simply a show of affection.

Symbiotic grooming, briefly mentioned above, occurs among some species where they pair off to assist one another in the grooming process. Pilot fishes and remoras are commensal fishes (a type of symbiosis) that attach themselves to sharks and other fish. Apart from eating the remnants of the host's meal, they also feed on the external parasites that plague the host fish. Fleas and lice are symbiotic groomers as they eat harmlessly on dead skin or feathers of mammals and birds.

Grooming behavior is an integral part of existence for all higher-order animals. It is such an important part of human behavior that if proper grooming is not taught at an early age and not performed, there are negative repercussions from peers and society in general. Grooming is such an important part of human community, that in the United States alone, the annual sales of men's and women's toiletries is a multibillion dollar industry. Scientists have only recently begun to study grooming behavior closely.

—Donald J. Nash

See also: Altruism; Communication; Copulation; Courtship; Displays; Emotions; Ethology; Habituation and sensitization; Hormones and behavior; Imprinting; Insect societies; Learning; Mammalian social systems; Offspring care; Pair-bonding; Rhythms and behavior; Symbiosis; Territoriality and aggression.

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GROUPS

Types of animal science: Behavior, ecology, classification
Fields of study: Ecology, ethology, zoology

Animals form groups, or aggregations, for a variety of purposes. These groups can be temporary in nature, occurring only during specific seasons, or can last throughout the lifetime of the members and lead to highly organized societies.

Principal Terms

COMPETITION: interactions among individuals that attempt to utilize the same limited resource

CONSPECIFICS: members of the same species

DILUTION EFFECTS: the reduction in per capita probability of death from a predator due to the presence of other group members

ENCOUNTER EFFECTS: the reduction in the probability of death from a predator due to a single group of *N* members being more difficult to locate than an equal number of solitary individuals

INTERFERENCE: the act of impeding others from using some limited resource

PREDATION: the act of killing and consuming another organism

RESOURCE DEFENSE: the control of a resource indirectly or directly

SOCIALITY: the tendency to form and maintain stable groups

Some animals spend most of their time alone because the presence of other conspecifics would interfere with the use of a particular resource or a suite of resources. These animals only come together with another solitary individual to pair for reproduction. Others form groups ranging from pairs of animals to large herds. Finally, some animals are brought together by phenomena over which they have no control (winds, currents, or tides) and are simply clumped in space. Groups formed for whatever reason can be either temporary or permanent, and are generally theorized as being beneficial for a variety of reasons. Some associations are simply the result of congregating around a common food resource. Other associations arise for specific functions, such as finding mates, caring for young, providing for a learning environment for developing young, providing protection from the elements, thermoregulation or huddling, locomotory efficiency (swimming or flight), locating and subduing food items, resource defense against other groups or competing species, division of labor, population regulation, predator vigilance, and reduced predation risk via dilution, confusion, encounter, or group defense effects. While potential benefits can be many, aggregation can also result in distinct disadvantages for individuals making up the group. Such disadvantages include increased competition for resources (such as mates, food, or shelter), increased risk of disease and spread of parasites, and interference in reproductive behaviors.

Reproduction and Rearing Young

Living in groups can increase an individual's chance of finding a mate, but it often results in increased aggression between males who must compete for females. Because all females may come into estrus within a short time period, grouping together at specific mating territories ensures that all females will be mated. In such species, courtship rituals are often common. These rituals serve a dual purpose: They provide the male with information about the sexual receptivity of the female and they allow the female to assess the quality of the male prior to pairing with him. In some cases, the rituals also serve to bind the pair together for a breeding season, or in some species for longer periods of time. In other cases, males simply congregate at display grounds, attract, and court females. Females leave the display grounds after mating to nest elsewhere, while the males remain to court other females. This latter grouping strategy is known as lekking.

In some species, which both aggregate during mating seasons and form pair bonds, both male and female can care for the young. In some cases, a mating pair may have helpers at the nest—other members of the species (usually offspring) which aid the parents in raising the young. Helpers at the nest greatly contribute to the breeding success of the parental birds and gain experience themselves in rearing young. They can then use their experience to be successful parents in the next breeding season. Other examples, such as lions and elephants, include kin groups (generally sisters or a mother and her daughters) that help to raise whatever offspring are present in the group.

Colonial nesting and thus synchronous egg-laying produces offspring in large numbers, who are vulnerable to predators for only a short period of time. In this way, each parent lessens the chance that their offspring will be the ones taken by any predator (dilution effect). However, colonial nesting also presents the possibility that offspring may grow more slowly or run the risk of parasitism from fleas and mites. Some evidence exists that offspring of bank swallows gained weight more slowly if they were from large colonies versus small colonies, suggesting that large colonies were depleting their resources more rapidly. Nests from large colonies were also more often infested with fleas than those in small colonies.

Rearing young in a group gives the young opportunities to learn from more than one adult. It can also provide them with practice in tasks that later prove important when the offspring are on their own. Cooperative hunting can provide young with the opportunity to learn hunting skills from their elders. Generally, this benefit results in longer-lived species that produce only a few young per year.

Survival

Cold temperatures can cause physiological problems, particularly for animals that are ectothermic (relying upon the environment for heat). During the day, such animals can bask in the sun and maintain high body temperatures. At night, however, they may have difficulty staying warm, so many huddle together in large groups. This type of behavior allows ectotherms to continue to digest their food (a process requiring heat).

Ectothermic species are not the only ones that huddle—many birds and mammals do so as well. Some birds flock together on trees on particularly cold nights to reduce the surface area of their body that is exposed to the elements. Voles, which are normally asocial, huddle in groups during the winter to keep warm. Marmots can huddle underground in groups of twenty for up to seven months to avoid freezing temperatures in the mountain regions they occupy.

Lowered individual predation risk is theorized as a primary benefit leading to the evolution of gregarious behavior, particularly in the absence of kinship between group members. Three likely outcomes of grouping that can reduce rates of attack are the dilution effect, the confusion effect, and the encounter effect. In the dilution effect, the probability of a particular individual being killed or injured is reduced by the presence of other group members that might be attacked first. This helps to explain why ostriches lay eggs in communal clutches which only the first laying female incubates. The first female is not necessarily acting in an altruistic manner, because she is diluting the chance that predators will find her eggs and eat them or, after the chicks hatch, that predators will capture her chicks instead of those of another female. Individuals in a group may also benefit by putting other animals between themselves and the predator (the selfish herd effect). Grouping provides the opportunity to decrease the area of danger around each individual. If individuals within the group are acting in a selfish herd manner, the groups formed tend to be tightly clumped, as all individuals attempt to put other individuals on all sides around them.

Confusion effects benefit group members because predators may have difficulty in fixing upon a particular individual for attack. The time it takes for the predator to discern a particular individual from a mass of surrounding individuals may be enough for the entire group to scatter and to further confuse the predator.

In contrast, the encounter effect results when it is more difficult for a predator to find a single group of prey than an equal number of scattered individuals due to the apparent rarity of the grouped individuals. However, the actual result of aggregation may be increased risk of detection if the group becomes a more conspicuous entity, which is detrimental to the individuals making up the group, rather than beneficial.

Groups can also benefit by collective defense, which is seen in animals possessing weaponry such as horns or other piercing appendages. Commonly these groups will form a line (phalanx) or a rosette (circular structure) with weapons pointed outward toward the attacker(s). Common examples of these defensive groups include musk oxen, elephants, and spiny lobsters. The use of weapons in these defensive lines may enhance the probability of survival above that of mere dilution, since each defending animal is capable of inflicting damage on a predator.

An individual has to partition its time between foraging and being vigilant for potential predators. However, if that individual is within a group, it can spend more timing on foraging and less time on vigilance because its scan frequency for predators can decrease proportionate to the number of members of the group. Furthermore, because of the many eyes within the group, detection of predators with subsequent alerting of the danger is enhanced. Some species go so far as to alert other group members to danger by alarm calling. This may have evolved for several reasons: The

Lions are one of the few feline species that live in groups. These prides are composed of related females who share responsibility for raising all the young in the group. (PhotoDisc) caller benefits because it knows where the predator is and can position itself appropriately within the group to avoid being a target; the caller may enhance the probability of becoming the target, but at the same time, it reduces the probability that its kin will be targets (this works in kin groups); and/or the caller may attract attention to itself at the time of the call, but if it survives, it is entitled to a payback at a later date from some other individual in the group doing the same.

Communal Foraging and Hunting

Frequently, food being sought for exploitation is clumped in space. As a result, the animals that feed upon this food are also clumped, and this promotes aggregation into group structures, such as herds. Because animals can observe others of their species feeding, they can follow successful foragers to feeding groups and group for no other reason. This phenomenon may allow such foragers to exploit food resources in a more systematic way. Some evidence suggests that grasses clipped by herbivore herds actually grow faster and are more productive than grasses not so clipped, and by proceeding from one patch to another, the herds actually allow the grasses to grow back in a systematic fashion. This allows the food time to replenish itself before the herd passes by it again, and would be less likely to happen if individuals exploited the resource, isolated in time and space.

Other animals form groups to facilitate hunting and capture success. However, some of these groupings can be highly variable in time, based on the food supply and how a kill is partitioned between group participants. For example, sociality in lions is controlled by food supply. When wildebeests or zebra are especially numerous, lions concentrate their efforts upon capturing them, but solitary hunters are successful only 15 percent of the time, while groups of five are 40 percent successful. Furthermore, groups of five lions are better able to protect their kill from scavengers than are groups of two or three lions, even though a group of two or three lions will maximize their daily intake of food per successful kill, while a group of five will only secure the minimum daily requirement of food. Despite their propensity for sociality, lions will hunt alone or in pairs when the migratory wildebeests or zebras leave and only resident gazelles are left. Again, the success rate for a solitary lion hunting a gazelle is only 15 percent, while that for a pair is 30 percent; however, a gazelle can provide the minimum daily requirement of food for only two lions.

Similarly, groups of dogs (the African wild dog, Asian dhole, dingoes, or wolves) are able to kill prey larger than themselves by cooperatively hunting. These packs are composed of kin (parents and their offspring) and cover large distances in order to hunt their prey. The individual dogs will spread out around the prey in a phalanx and then approach until one member selects a victim and runs after it. Other members of the pack will run after the prey in relays until the prey is exhausted and can be subdued.

Communal spiders build webs larger than a single individual could spin and capture prey larger than any one could capture alone. They communally feed on the captured prey. Most spider species have a short interval after the spiderlings have hatched where they remained clumped in a group and live in a communal web. After a period of several days, the spiderlings disperse to take up a solitary life. In communal species, however, adults of the same species come together to form colonies of up to one thousand individuals.

Coordinated group hunting is also known in marine mammals, particularly killer whales (orcas) and humpback whales. Orcas live in matriarchal societies (pods) of two to twelve members and hunt other marine mammals. Single orcas will charge sea lions in the surf of a beach, while other pod members will wait offshore to ensnare any sea lions that respond to the charge by entering the water. Adults will also train juvenile orcas, in the process of play-stranding, to capture seals or sea lions by throwing a dead seal to a beached juvenile. Orcas will also attack baleen whales by surrounding them and biting and holding the whale underwater so that it will drown. Humpback whales are known for bubble feeding, where members of the pod surround a school of small

Migration and Crowd Control

The urge to migrate is under control of an internal clock that is species-specific and that regulates physiological and behavioral rhythms. While individuals making up a population in a specific locale may be solitary during most of the year, they begin to manifest migratory restlessness at the appropriate time to migrate. This results in all individuals expressing the migratory urge at the same time and causes even nonsocial species to group together in a migratory exodus. Some bird species, as well as monarch butterflies, migrate in large groups to warmer climates to avoid the cold; other birds migrate to colder climates to avoid the heat of summer; and monarch butterflies migrate up into the mountains to avoid the heat in the lowlands. Some fish come together to locate home streams (salmon) or other breeding groups; some pinnipeds form large herds on communal pupping grounds; herds of ungulates follow a specific resource such as water or food. For those groups that follow a food or water resource, there is frequent mixing of several species that all exploit the same resource.

Birds are thought to fly in V-shaped formations as a means of reducing the drag on the birds behind the lead flyers. This may be so, since vortex rings are shed off of the wings during the flight stroke as there exists a circulation pattern of air on the wing. Birds flying behind the lead birds in a flock would be buffeted by these vortex rings, and thus the drag on their bodies would increase. Moreover, the vortex rings may create turbulent patterns of airflow behind the lead birds that would detrimentally affect the laminar flow needed to create lift on the bodies and wings of the birds behind. To avoid this situation, birds will often fly in a V formation that allows birds to avoid the disruptions to the airflow made by their fellow members during migration, when energy expenditures are critical considering the long distances covered. Likewise, the individuals in a fish school are arranged so that one fish does not encounter the vortices shed from the lead fish's tail.

fish and release bubbles while spiraling upward. This bubble net concentrates the terrified fish into a tight ball, which the whales then eat as they approach the surface and open their mouths. Groups of dolphins herd fish into shallow waters and surround them so they can be easily picked off.

Even groups of mixed species are known to cooperatively hunt. This is common in shorebirds, where one species might herd the prey while another species either dives to prevent the prey's escape from below or stabs at the prey to prevent its escape along the banks of the water. Pelicans and cormorants, as well as grebes and egrets, are known to form these associations.

Colonial species, particularly those that are sessile and need space to spread out, need to be able to defend their resources. Among invertebrates, larger colonies may have the competitive advantage in excluding newcomers from unoccupied space, as well as pushing other colonial species out of the way, so that the space once occupied can be overrun. Corals are well known for their warlike actions as the space on a reef becomes scarce—they will use their stinging cells to attack adjacent coral species in an attempt to kill the polyps making up the other colony. Dense colonies of bryozoans are much more able to withstand overgrowth by other invertebrates than are bryozoan colonies that are more spread out. Mussel beds can overrun barnacle colonies in the intertidal zone if their main predator is not present in sufficient numbers to keep the mussel population low.

Division of Labor

In eusocial insects, colony members divide the labor amongst themselves. In worker bees, the labor done is dependent on the age of the bee. After emergence, a worker bee's first job is cleaning the hive. She then tends the brood, builds up the honeycomb, and guards the nest. Her final task is to forage for pollen and nectar. The change in her duties correlates to physiological changes in her nurse glands and wax glands.

Ant colonies comprise thousands of individuals, divided into workers, brood, and queen. In army ants, workers vary in size, and these size differences determine their role in the colony. Smaller workers spend most of their time tending to and feeding the larval broods; medium-sized workers make up the majority of the population and are responsible for making raids on other colonies and locating food. The largest workers are called soldiers because of their powerful jaws; they accompany the raiding parties but carry no food.

Naked mole rats are the only known vertebrate that lives in colonies like those of the social insects. Only one female breeds. Larger individuals remain in the colony and huddle to keep the entire colony warm. Smaller individuals are the worker caste and are responsible for nest building and foraging.

These examples serve to illustrate that grouping behavior of animals can serve a myriad of purposes, or can simply be the result of phenomena beyond the animal's control (patchy food resources, physical forces of nature). The functions that lead to cooperative activities are usually best explained by groups being composed of kin; however, cooperation can also evolve in the absence of kinship, provided the benefits to group members outweigh the costs.

—*Kari L. Lavalli*

See also: Communication; Communities; Competition; Courtship; Defense mechanisms; Ethology; Herds; Hierarchies; Insect societies; Mammalian social systems; Nesting; Offspring care; Pair-bonding; Population analysis; Predation; Symbiosis; Territoriality and aggression; Thermoregulation; Zoos.

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GROWTH

Type of animal science: Development
Fields of study: Cell biology, zoology

Animal development begins with a single cell, the fertilized egg. Continued growth and formation through numerous cellular replications result in the formation of the complex animal body.

Principal Terms

DIFFERENTIATION: the process during development by which cells obtain their unique structure and function

FERTILIZATION: the union of two gametes (egg and sperm) to form a zygote

GAMETE: a functional reproductive cell (egg or sperm) produced by the adult male or female

GROWTH: the increased body mass of an organism that results primarily from an increase in the number of body cells and secondarily from the increase in the size of individual cells

MITOSIS: the process of cellular division in which the nuclear material, including the genes, is distributed equally to two identical daughter cells

ZYGOTE: a fertilized egg

Animal development has been a source of wonder for centuries. Development involves the slow, progressive changes that occur when a single cell—the zygote, or fertilized egg—undergoes mitosis. Mitosis is the process by which a cell divides into identical daughter cells. During development, mitosis occurs repeatedly, forming multiple generations of daughter cells. These cells increase in number and ultimately form all the cells in the body of a multicellular animal, such as a frog, mouse, or elephant. The simple experiment of opening fertile chicken eggs to observe the embryos on successive days of their three-week incubation period illustrates the process of embryonic development. A narrow band of cells can be seen increasing in number and complexity until the body of an entire, but immature, chick is seen.

Animal Growth and Development

An organism's growth occurs because of the increasing number of cells that form as well as because of the increasing size of individual cells. For example, a mouse increases from a single cell, the zygote, to about three billion cells during the period from fertilization to birth. Embryology is the study of the growth and development of an organism occurring before birth. Growth and development, however, continue after birth and throughout adulthood. Growth ceases only at death, when the life of the individual organism is ended. The bone marrow of human adults initiates the formation and development of millions of red blood cells every minute of life. About one gram of old skin cells is lost and replaced by new cells each day.

Development produces two major results: the formation of cellular diversity and the continuity of life. Cellular diversity, or differentiation, is the process that produces and organizes the numerous kinds of body cells. The first cell that determines an individual's unique identity, the zygote, ultimately gives rise to varying types of cells having diverse appearances and functions. Muscle cells, red blood cells, skin cells, neurons, osteocytes (bone cells), and liver cells are all examples of cells that have differentiated from a single zygote.

Reproduction

Morphogenesis is the process by which differentiated cells are organized into tissues and organs. The continued formation of new individual organisms is called reproduction. The major stages of animal development include fertilization, embryology, birth, youth, adulthood—when fertilization of the next generation occurs—and death. A new individual animal is begun by the process of fertilization, when the genetic material from the sperm, produced by the father, and the egg, produced by the mother, are merged into a single cell, the zygote. Fertilization may be external, occurring in freshwater or the sea, or internal, occurring within the female's reproductive tract. While fertilization marks the beginning of a new individual, it is not literally the beginning of life, since both the sperm and egg are already alive. Rather, fertilization ensures the continuation of life through the formation of new individuals. This guarantees that the species of the organism will continue to survive in the future.

Following fertilization, the newly formed zygote undergoes embryological development consisting of cleavage, gastrulation, and organogenesis. Cleavage is a period of rapid mitotic divisions with little individual cell growth. A ball of small cells, called the morula, forms. As mitosis continues, this ball of cells hollows in the middle, forming an internal cavity called the blastocoel. Gastrulation immediately follows cleavage. During gastrulation, individual cell growth as well as initial cell differentiation occur. During this time, three distinct types of cells are formed: an internal layer called the endoderm, a middle layer, the mesoderm, and an external layer, the ectoderm. These cell types, or germ-cell layers, are the parental cells of all future cells of the body.

Cells from the ectoderm form the cells of the nervous system and skin. The mesoderm forms the cells of muscle, bone, connective tissue, and blood. The endoderm forms cells that line the inside of the digestive tract as well as the liver, pancreas, lungs, and thyroid gland. The transformation of these single germ layers into functional organs is called organogenesis. Organogenesis is an extremely complex period of embryological development. During this time, specific cells interact and respond to one another to induce growth, movement, or further differentiation; this cell-to-cell interaction is called induction. Each induction event requires an inducing cell and a responding cell.

In the formation of the brain and spinal cord, selected cells from the ectoderm form a long, thickened plate at the midline of the developing embryo. Through changes in cell shape, the outer edges of this plate fold up and fuse with each other in the middle, forming a tubular structure (a neural tube). This tubelike structure then separates from the remaining ectoderm. At the head region of the embryo, the neural tube enlarges into pockets that ultimately form brain regions.

For differentiation and development to occur, cells must be responsive to regulatory signals. Some of these signals originate within the responding cell; these signals are based in the genetic code found in the cell's own nucleus. Other signals originate outside the cell; they may include physical contact with overlying or underlying cells, specific signal molecules, such as hormones, from distant cells, or specialized structural molecules secreted by neighboring cells that map out the pathway along which a responding cell will migrate.

Postnatal Development

Embryological development climaxes in the formation of functional organs and body systems. This period is concluded by birth (or hatching, in the case of some animals). Following birth, development normally continues. In some animals, such as frogs, newly hatched individuals undergo metamorphosis during which their body structures are dramatically altered. Newly hatched frogs (tadpoles), for example, are transformed from aquatic, legless, fishlike creatures into mature adults with legs that allow them to move freely on land.

In mammals, development and growth occur primarily after birth, as the individual progresses through the stages of infancy, childhood, adolescence, and adulthood. Mature adulthood is attained when the individual can produce his or her own gametes and participate in mating behavior.

Embryonic growth is especially impressive because the rate of cellular mitosis is so enormous. In the case of the mouse embryo, thirty-one cell generations occur during embryonic development. Thus, the zygote divides into two cells, then four, then eight, sixteen, thirty-two, and so on. This results in a newborn mouse consisting of billions of cells—produced in a period of only twenty-one days. When the newborn passes through its life stages to adulthood, its body cells may number more than sixty billion. One marine mammal, the blue whale, begins as a single zygote that is less than one millimeter in diameter and weighs only a small fraction of a gram. The resulting newborn whale (the calf) is about seven meters long and weighs two thousand kilograms: The embryonic growth represents a 200-millionfold increase in weight. Yet, for some animals, impressive growth periods also occur in the juvenile and adolescent stages of life.

In many cases, once an individual animal reaches its typical adult size, the rate of mitosis slows so that the number of new cells simply replaces the number of older, dying cells. At this maintenance stage, the individual no longer grows in overall size even though it continuously produces new cells. Since most of the cells in the mature adult have reached a final differentiated state, the function of mitosis is simply to replace the degenerating, aging cells. The slowing of the rate of cellular mitosis during this time may be attributable to the presence of specialized cell products called chalones. Chalones are thought to be local products of mature cells that inhibit further growth or mitosis.

Studying Growth

Historically, much study of animal development and growth was performed by simple observation. Aristotle, perhaps the first known embryologist, opened chick eggs during varying developmental periods. He observed and sketched what appeared to be the formation of the chick's body from a nondescript substance. With the invention of lenses and microscopes, growth and development could be studied on a cellular level. The concept of cellular differentiation arose, since investigators could see that embryonic muscle cells, for example, looked different from embryonic nerve cells. Again, much of the investigative information was descriptive in nature. Embryologists detailed the existence of the three germ-cell layers in gastrulation as well as the various tissues and primitive cells involved in organogenesis.

Experimentation as a method of investigating animal growth and development began during the nineteenth century. Lower animal species, such as the sea urchin and frog, were frequently investigated; their developmental patterns are simpler than those of mammals, their development occurs outside the maternal body, and they can be found in abundant numbers. Many of these experiments used separation or surgical techniques to isolate or regraft specific tissues or cells of interest. An attempt was made to determine how one tissue type would interact with and influence the development of another tissue type. Thus, the ideas of induction, in which some tissues affect other tissues, came into being. During this time, the descriptive and comparative observations resulting from these experimental manipulations were the major contributions of investigators.

The embryologists of the early twentieth century paid little attention to genetics. They believed that the major influences on development and growth were embryological mechanisms, although genes were thought to provide some nonessential peripheral functions. Chemical analyses of embryos attempted to establish the chemical basis for the cell-to-cell interactions that were seen during development and differentiation. During the middle portion of the twentieth century, geneticists began to investigate the role of the gene in cell function. The function of genes in the cellular manufacturing of specific proteins led to the hypothesis that each kind of cellular protein was the product of one gene. During this time, bacteria and fruit flies (*Drosophila*) were primary organisms of study because of their relatively simple genetic makeups.

In the latter part of the twentieth century, molecular biology techniques were applied to the study of development. Using techniques for transferring and replicating specific genes, researchers have greatly clarified the central importance of genes in development. Scientists came to believe that all the major developmental and differentiation influences that control cell growth are regulated through specific genes that are turned off or on.

Developmental Biology

The combination of molecular biology techniques with embryological investigations has led to a new field of study—developmental biology. New methods have been developed and used. Radioactive tracer technology has allowed the investigator to label particular genes or gene products and trace their movements and influences on cell growth through several generations. Recombinant deoxyribonucleic acid (DNA) technology has allowed the isolation and replication of significant genes that are important in development. Immunochemistry uses specific proteins (antibodies) to bind to differentiating cell products and quantify them. Cell-cell hybridization allows the introduction of specific genes into the nuclei of cells in alternate differentiation pathways.

Developmental biology, with its multidisciplinary approach, is solving many of the fundamental questions of development. As scientists become better able to understand the role of genetics and cell-to-cell interactions, they gain insight into the mechanisms that control cell growth and development. Consequently, the potential to control undesirable growth or to enhance underdeveloped growth is within reach.

The problem of cell aging is also under investigation. Questions about why mature cells stop dividing and growing and what the causes of aging are constitute important areas of developmental research. While various theories have been presented, the fundamental key to cellular aging remains to be discovered. One of the most challenging areas of continuing research is the determination of how developmental patterns guide evolutionary changes. Developmental principles may provide the answer to why evolution has given rise to animal diversity. In addition, developmental biology may give scientists the information needed to predict and determine future evolutionary trends. The individual animal is a growing organism that begins as a zygote and passes through the stages of embryonic development, birth, youth, adulthood, aging, and death. Preservation of the species depends on adult individuals' producing gametes that result in the formation of a future generation of zygotes and individuals. Remarkably, each zygote contains the necessary genetic instructions to regulate the orderly processes of growth and development. Thus, animal life continues from generation to generation.

—Roman J. Miller

See also: Cell types; Cleavage, gastrulation, and neurulation; Cloning of extinct or endangered species; Determination and differentiation; Development: Evolutionary perspective; Embryology; Fertilization; Gametogenesis; Morphogenesis; Multicellularity; Parthenogenesis; Pregnancy and prenatal development; Regeneration; Reproduction.

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HABITATS AND BIOMES

Type of animal science: Ecology
Fields of study: Anthropology, environmental science, invertebrate biology, zoology

The biosphere is the sum total of all habitats on earth that can be occupied by living organisms. Descriptive and experimental studies of habitat components allow scientists to predict how various organisms will respond to changes in their environment, whether caused by humans or nature.

Principal Terms

ABIOTIC: the physical part of an ecosystem or biome, consisting of climate, soil, water, oxygen and carbon dioxide availability, and other physical components

BIOME: one of the widespread types of ecosystem on the earth, such as the Arctic tundra or the desert

BIOSPHERE: the sum of all the occupiable habitats for life on earth

BIOTIC: the living part of an ecosystem or biome, consisting of all organisms

COMMUNITY: a population of plants and animals that live together and make up the biotic part of an ecosystem

ECOSYSTEM: a relatively self-sufficient group of communities and their abiotic environment

ENVIRONMENT: the habitat created by the interaction of the abiotic and biotic parts of an ecosystem

HABITAT: the specific part of the environment occupied by the individuals of a species

POPULATION: a group of all the individuals of one species

SPECIES: a group of similar organisms that are capable of interbreeding and producing fertile offspring

Life in the form of individual organisms composed of one or more living cells is found in a vast array of different places on earth, each with its own distinctive types of organisms. Life on earth has been classified by scientists into units called species, whose individuals appear similar, have the same role in the environment, and breed only among themselves. The space in which each species lives is called its habitat.

Habitats, Communities, Ecosystems, and Biomes

The term "habitat" can refer to specific places with varying degrees of accuracy. For example, rainbow trout can be found in North America from Canada to Mexico, but more specifically they are found in freshwater streams and lakes with an average temperature below 70 degrees Fahrenheit and a large oxygen supply. The former example describes the macrohabitat of the rainbow trout, which is a broad, easily recognized area. The latter example describes its microhabitat—the specific part of its macrohabitat in which it is found. Similarly, the macrohabitat of one species can refer to small or large areas of its habitat. The macrohabitat of rainbow trout may refer to the habitat of a local population, the entire range of the species, or (most often) an area intermediate to those extremes. While "habitat," therefore, refers to the place an organism lives, it is not a precise term unless a well-defined microhabitat is intended. The total population of each species has one or more local populations, which are all the individuals in a specific geographic area that share a common gene pool; that is, they commonly interbreed. For example, rainbow trout of two adjacent states will not normally interbreed unless they are part of local populations that are very close to one another. The entire geographic distribution of a species, its range, may be composed of many local populations.

On a larger organizational scale, there is more than only one local population of one species in any habitat. Indeed, it is natural and necessary for many species to live together in an area, each with its own micro- and macrohabitat. The habitat of each local population of each species overlaps the habitat of many others. This collective association of populations in one general area is termed a community, which may consist of thousands of species of animals, plants, fungi, bacteria, and other one-celled organisms.

Groups of communities that are relatively self-sufficient in terms of both recycling nutrients and the flow of energy among them are called ecosystems. An example of an ecosystem could be a broad region of forest community interspersed with meadows and stream communities that share a common geographic area. Some ecosystems are widely distributed across the surface of the earth and are easily recognizable as similar ecosystems known as biomes—deserts, for example. Biomes are usually named for the dominant plant types, which have very similar shapes and macrohabitats. Thus, similar types of organisms inhabit them, though not necessarily ones of the same species. These biomes are easily mapped on the continental scale and represent a broad approach to the distribution of organisms on the face of the earth. One of the more consistent biomes is the northern coniferous forest, which stretches across Canada and northern Eurasia in a latitudinal belt. Here are found needle-leafed evergreen conifer trees adapted to dry, cold, windy conditions in which the soil is frozen during the long winter.

Clear-cutting forests is one of the many causes of habitat loss worldwide. (PhotoDisc)

North American Biomes

The biomes of North America, from north to south, are the polar ice cap, the Arctic tundra, the northern coniferous forest; then, at similar middle latitudes, eastern deciduous forest, prairie grassland, or desert; and last, subtropical rain forest near the equator. Complicating factors that determine the actual distribution of the biomes are altitude, annual rainfall, topography, and major weather patterns. These latter factors, which influence the survival of the living, or biotic, parts of the biome, are called abiotic factors. These are the physical components of the environment for a community of organisms.

The polar ice cap is a hostile place with little evidence of life on the surface except for polar bears and sea mammals that depend on marine animals for food. A distinctive characteristic of the Arctic tundra, just south of the polar ice cap, is its flat topography and permafrost, or permanently frozen soil. Only the top meter or so thaws during the brief Arctic summer to support low-growing mosses, grasses, and the dominant lichens known as reindeer moss. Well-known animals found there are the caribou, musk-ox, lemming, snowy owl, and Arctic fox.

The northern coniferous forest is dominated by tall conifer trees. Familiar animals include the snowshoe hare, lynx, and porcupine. This biome stretches east to west across Canada and south into the Great Lakes region of the United States. It is also found at the higher elevations of the Rocky Mountains and the western coastal mountain ranges. Its upper elevation limit is the "treeline," above which only low-growing grasses and herbaceous plants grow in an alpine tundra community similar to the Arctic tundra. In mountain ranges, the change in biomes with altitude mimics the biome changes with increasing latitude, with tundra being the highest or northernmost.

Approximately the eastern half of the United States was once covered with the eastern deciduous forest biome, named for the dominant broad-leaved trees that shed their leaves in the fall. This biome receives more than seventy-five centimeters of rainfall each year and has a rich diversity of bird species, such as the familiar warblers, chickadees, nuthatches, and woodpeckers. Familiar mammals include the white-tailed deer, cottontail rabbit, and wild turkey. The Great Plains, between the Mississippi River and the Rocky Mountains, receives twenty-five to seventy-five centimeters of rain annually to support an open grassland biome often called the prairie. The many grass species that dominate this biome once supported vast herds of bison and, in the western parts, pronghorn antelope. Seasonal drought and periodic fires are common features of grasslands.

The land between the Rockies and the western coastal mountain ranges is a cold type of desert biome; three types of hotter deserts are found from western Texas west to California and south into Mexico. Deserts receive fewer than twenty-five centimeters of rainfall annually. The hot deserts are dominated by many cactus species and short, thorny shrubs and trees, whereas sagebrush, grass, and small conifer trees dominate the cold desert. These deserts have many lizard and snake species, including poisonous rattlesnakes and the Gila monster. The animals often have nocturnal habits to avoid the hot, dry daytime.

Southern Mexico and the Yucatán Peninsula are covered by evergreen, broad-leaved trees in the tropical rain-forest biome, which receives more than two hundred centimeters of rain per year. Many tree-dwelling animals, such as howler monkeys and tree frogs, spend most of their lives in the tree canopy, seldom reaching the ground.

Aquatic biomes can be broadly categorized into freshwater, marine, and estuarine biomes. Freshwater lakes, reservoirs, and other still-water environments are called lentic, in contrast to lotic, or running-water, environments. Lentic communities are often dominated by planktonic organisms, small, drifting (often transparent) microscopic algae, and the small animals which feed on them. These, in turn, support larger invertebrates and fish. Lotic environments depend more on algae that are attached to the bottoms of streams, but they support equally diverse animal communities. The marine biome is separated into coastal and pelagic, or open-water, environments, which have plant and animal communities somewhat similar to lotic and lentic freshwater environments, respectively. The estuarine biome is a mixing zone where rivers empty into the ocean. These areas have a diverse assemblage of freshwater and marine organisms.

The Biosphere

All the biomes together, both terrestrial and aquatic, constitute the biosphere, which by definition is all the places on earth where life is found. Organisms that live in a biome must interact with one another and must successfully overcome and exploit their abiotic environment. The severity and moderation of the abiotic environments determine whether life can exist in that microhabitat. Such things as minimum and maximum daily and annual temperature, humidity, solar radiation, rainfall, and wind speed directly affect which types of organisms are able to survive. Amazingly, few places on earth are so hostile that no life exists there. An example would be the boiling geyser pools at Yellowstone National Park, but even there, as the water temperature cools at the edges to about 75 degrees Celsius, bacterial colonies begin to appear. There is abundant life in the top meter or two of soil, with plant roots penetrating to twenty-two meters or more in extreme cases. Similarly, the mud and sand bottoms of lakes and oceans contain a rich diversity of life. Birds, bats, and insects exploit the airspace above land and sea up to a height of about 1,200 meters, with bacterial and fungal spores being found much higher. Thus, the biosphere generally extends about 10 to 15 meters below the surface of the earth and about 1,200 meters above it. Beyond that, conditions are too hostile. A common analogy is that if the earth were a basketball, the biosphere would constitute only the thin outer layer.

Studying Habitats and Biomes

Abiotic habitat requirements for a local population or even for an entire species can be determined in the laboratory by testing its range of tolerance for each factor. For example, temperature can be regulated in a laboratory experiment to determine the minimum and maximum survival temperatures as well as an optimal range. The same can be done with humidity, light, shelter, and substrate type: "Substrate preference" refers to the solid or liquid matter in which an organism grows and/or moves—for example, soil or rock. The combination of all ranges of tolerance for abiotic factors should describe a population's actual or potential microhabitat within a community. Furthermore, laboratory experiments can theoretically indicate how much environmental change each population can tolerate before it begins to migrate or die.

Methods to study the interaction of populations with one another or even the interaction of individuals within one local population are much more complicated and are difficult or impossible to bring into a laboratory setting. These studies most often require collecting field data on distribution, abundance, food habits or nutrient requirements, reproduction and death rates, and behavior in order to describe the relationships between individuals and populations within a community. Later stages of these field investigations could involve experimental manipulations in which scientists purposely change one factor, then observe the population or community response. Often, natural events such as a fire, drought, or flood can provide a disturbance in lieu of a manipulation caused by man.

There are obvious limits to how much scientists should tinker with the biosphere merely to see how it works. Populations and even communities in a local area can be manipulated and observed, but it is not practical or advisable to manipulate whole ecosystems or biomes. To a limited extent, scientists can document apparent changes caused by civilization, pollution, and long-term climatic changes. This information, along with population- and community-level data, can be used to construct a mathematical model of a population or community. The model can then be used to predict the changes that would happen if a certain event were to occur. These predictions merely represent the "best guesses" of scientists, based on the knowledge available. Population

Habitat Destruction

One of the leading causes of species extinction or threatened extinction is habitat loss and destruction. Although there are many natural disturbances, such as earthquakes, volcanoes, and predators, that degrade or destroy habitats, the problem is most closely correlated with the increase in human population. Between 1850 and 2000, the population of the world increased from about one billion people to over six billion people. Accompanying that increase was the largest destruction of animal habitats and the largest extinction of animal species in the history of the world.

The greatest number of animal species occur in the tropical countries of Africa, South America, Central America, and Asia. Unfortunately, it is in these countries that human population growth continues at an alarming rate, posing an increasing threat in the form of the loss and destruction of animal habitats. In many tropical islands, most of the original habitats are gone, while over 50 percent of the natural habitats in approximately two-thirds of the countries in Asia and Africa have been destroyed.

Particularly threatened are the habitats in rain forests, wetlands, mangrove forests, and grasslands. Although rain forests occupy a small portion of Earth's surface area, they contain over 50 percent of its plant and animal species. Every year, rain forest area exceeding the size of the state of Florida is being lost to commercial logging, conversion to agriculture, and fuel wood production. At the present rate of loss, it is estimated that there may be no more rain forests by the year 2040.

One of the most important habitats for a large variety of vertebrate species are the wetlands and aquatic areas. In the United States, wetland areas account for about 15 percent of the threatened and endangered species. Many of these areas are being drained worldwide for development projects, agriculture, and dam projects. Over 50 percent of the wetlands that existed in the United States in 1800 are now destroyed.

Many aquatic species rely on mangrove forest habitats as breeding areas. Over 50 percent of the commercial species of fish and shrimp in the tropics depend on these areas, as well as many different species of birds. In addition, these special forest habitats, which exist along shallow intertidal coasts, are very important because they control erosion produced by storms. In order to produce more rice, agricultural products, firewood, and construction materials, many of the mangrove forests are being destroyed. In some countries, over 30 percent of these habitats have been lost or destroyed.

Grassland habitats are extremely important for supporting the biodiversity of many vertebrate species. Because these habitats generally occur in gentle terrain with excellent soils, they are frequently exploited for crop production, grazing land, and livestock production. Consequently, as the human population has grown, these areas have drastically shrunk in size.

Another contributing factor to the destruction of a habitat is the problem of habitat fragmentation. This occurs when contiguous habitats are broken into fragments, producing an increasing number of edge boundaries relative to the original habitat. Since many predators, including wolves, foxes, raccoons, and humans, often concentrate on habitat edges for hunting, more and more species become endangered as habitats are fragmented and eventually destroyed.

—Alvin K. Benson

ecologists often construct reasonably accurate population models that can predict population fluctuations based on changes in food supply, abiotic factors, or habitat. As models begin to encompass communities, ecosystems, and biomes, however, their knowledge bases and predictive powers decline rapidly. Perhaps the most complicating factor in building and testing these large-scale models is that natural changes seldom occur one at a time. Thus, scientists must attempt to build cumulative-effect models that are capable of incorporating multiple changes into a predicted outcome.

The biosphere, then, can be studied at different levels of organization, from the individual level through populations, communities, ecosystems, and biomes to the all-encompassing biosphere. Each level has unique relationships that require different methods of inquiry; in fact, these levels describe many of the subdisciplines within the science of ecology.

Biosphere and Biodiversity

Understanding the organization of the natural world of which man is a part is essential to the continued success of humankind. By understanding the abiotic and biotic relationships within and between each ecological level, from microhabitat to biosphere, scientists can partially explain why so many species of organisms have evolved over the last 3.5 billion years. This study of biodiversity may eventually be a key to maintaining a stable biosphere, in which there would be no drastic changes in climate or community relationships. For example, compare the diversity of microhabitats and species in a natural grassland biome with the established monoculture practices of agriculture, with the latter's emphasis on one species. In a wheat field, there are fewer microhabitats available, but those few are available in abundance. This leads to an increase in the population size of "pest" species that compete with man for an abundant food resource, wheat. Understanding the microhabitat requirements of pest species can lead to the reduction of crop losses.

The goal of the study of habitats, biomes, and the biosphere is the construction of predictive models. Once scientists have a general understanding of natural ecosystem processes, mathematical models may be able to predict future changes in the environment caused by the activities of civilization or natural climatic changes. For example, they may indicate whether increased human population size or increased large-scale agriculture in or near desert biomes will lead to the spread of desertlike conditions. On a biosphere scale, they may show whether the increase in the carbon dioxide content of the atmosphere caused by man's activities will lead to global warming. Both these effects are being predicted by many scientists. Prior to the relatively recent growth in the science of ecology and the general interest in it, man had little concern about the effects of the exploitation of natural resources such as forests, of synthetic chemical pollutants such as dichloro-diphenyl-trichloroethane (DDT), or even of the rapid growth of the human population size. With an increasing knowledge and understanding of habitat requirements, natural community interrelationships, and cycling of nutrients and pollutants within the biosphere, however, scientists have greater predictive power concerning the effects of economic development and human population growth. Ecologists are studying the effects of changing rain forests into agricultural land, the extinction of species, the loss of the ozone layer, and many other phenomena that have the potential to change the abiotic environment and therefore affect the stability of biotic communities. These results will be incorporated into future predictive models, giving them increased accuracy.

The challenge—both to scientists and to human civilization as a whole—is to use an understanding of the biosphere to maintain a level of economic growth that is ecologically sustainable. The study of communities and ecosystems may discover ways that civilization can better adapt to its current environment rather than attempt to mold the environment to fit its own preconceived, established ideas.

—Jim Fowler

See also: Biodiversity; Communities; Deserts; Ecological niches; Ecology; Ecosystems; Fauna: Africa; Fauna: Antarctica; Fauna: Arctic; Fauna: Asia; Fauna: Australia; Fauna: Caribbean; Fauna: Central America; Fauna: Europe; Fauna: Galápagos Islands; Fauna: Madagascar; Fauna: North America; Fauna: Pacific Islands; Fauna: South America; Forests, coniferous; Forests, deciduous; Grasslands and prairies; Lakes and rivers; Mountains; Paleoecology; Population fluctuations; Population growth; Rain forests; Savannas; Swamps and marshes; Territoriality and aggression; Tidepools and beaches; Tundra; Urban and suburban wildlife; Wildlife management; Zoos.

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HABITUATION AND SENSITIZATION

Type of animal science: Behavior
Field of study: Ethology

Habituation is learning to ignore irrelevant stimuli that previously produced a reaction. Results of habituation studies have been used to explain, predict, and control behavior of humans and other organisms.

Principal Terms

ACETYLCHOLINE: a neurotransmitter produced by a nerve cell that enables a nerve impulse to cross a synapse and reach another nerve or muscle cell

APLYSIA: a large sluglike mollusk that lives in salt water and has been used in habituation experiments; its outer covering is called the mantle

IMPULSE: a "message" traveling within a nerve cell to another nerve cell or to a muscle cell

MOTOR NEURON: a nerve cell that causes a muscle cell to respond

NEUROTRANSMITTER: a chemical substance which enables nerve impulses to cross a synapse and reach another nerve cell or muscle cell

ORIENTING REFLEX: an unspecific reflex reaction caused by a change in the quantity or quality of a stimulus; it will disappear or decrease after repeated presentations of the stimulus

SENSITIZATION: an arousal or an alerting reaction which increases the likelihood that an organism will react; also, a synonym for loss of habituation with increased intensity of response

SYNAPSE: the minute space or gap between the axon of one nerve cell and the dendron of the next; also, the gap between a nerve cell and a muscle cell

Habituation is a simple form of nonassociative learning that has been demonstrated in organisms as diverse as protozoans, insects, *Nereis* (clam worms), birds, and humans. The habituated organism learns to ignore irrelevant, repetitive stimuli which, prior to habituation, would have produced a response. With each presentation of the habituating stimulus, the responsiveness of the organism decreases toward the zero, nonresponse level. If habituation training continues after the zero-response level, the habituation period is prolonged. Habituation to a particular stimulus naturally and gradually disappears unless the training continues. If training is resumed after habituation has disappeared, habituation occurs more rapidly in the second training series than in the first. Habituation is important for survival of the individual. Many stimuli are continuously impinging upon it: Some are important, others are not. Important stimuli require an immediate response, but those which result in neither punishment nor reward may be safely ignored.

Stimulus and Response

When a new stimulus is presented (when a sudden change in the environment occurs), the organism—be it bird, beast, or human—exhibits the "startle" or "orientation" response. In essence, it stops, looks, and listens. If the stimulus is repeated and is followed by neither reward nor punishment, the organism will pay less and less attention to it. When this happens, habituation has occurred, and the organism can now respond to and deal with other stimuli. On the other hand, if, during habituation learning, a painful consequence follows a previously nonconsequential stimulus, the organism has been sensitized to that stimulus and will respond to it even more strongly than it did before the learning sessions, whether they are occurring in the laboratory or in the field.

Young birds must learn to tell the difference between and respond differently to a falling leaf and a descending predator. A young predatory bird must learn to ignore reactions of its prey which pose no danger, reactions that the predator initially feared.

A theory known as the dual-process habituation-sensitization theory was formulated in 1966 and revised in 1973. It establishes criteria for both habituation and sensitization. Criteria for habituation (similar to those proposed by E. N. Sokolov in 1960) are that habituation will develop rapidly; the frequency of stimulation determines the degree of habituation; if stimulation stops for a period of time, habituation will disappear; the stronger the stimulus, the slower the rate of habituation; the frequency of stimulation is more important than the strength of the stimulus; rest periods between habituation series increase the degree of habituation; and the organism will generalize and therefore exhibit habituation to an entire class of similar stimuli. Stimulus generalization can be measured: If a different stimulus is used in the second habituation series, habituation occurs more rapidly; it indicates generalization.

Sensitization

Sensitization, a very strong response to a very painful, injurious, or harmful stimulus, is not limited to stimulus-response circuits but involves the entire organism. After sensitization, the individual may respond more strongly to the habituating stimulus than it did prior to the start of habituation training.

There are eight assumptions about sensitization in the dual-process theory. Sensitization does not occur in stimulus-response circuits but involves the entire organism. Sensitization increases during the early stages of habituation training but later decreases. The stronger the sensitizing stimulus and the longer the exposure to it the greater the sensitization; weaker stimuli may fail to produce any sensitization. Even without any external intervention, sensitization will decrease and disappear. Increasing the frequency of sensitization stimulation causes a decrease in sensitization. Sensitization will extend to similar stimuli. Dishabituation, the loss of habituation, is an example of sensitization. Sensitization may be time-related, occurring only at certain times of the day or year.

According to the dual-process theory, the response of an organism to a stimulus will be determined by the relative strengths of habituation and sensitization. Charles Darwin, the father of evolution, observed and described habituation, although he did not use the term. He noted that the birds of the Galápagos Islands were not disturbed by the presence of the giant tortoises, *Amblyrhynchus*; they disregarded them just as the magpies in England, which Darwin called "shy" birds, disregarded cows and horses grazing nearby. Both the giant tortoises of the Galápagos Islands and the grazing horses and cows of England were stimuli which, though present, would not produce profit or loss for the birds; therefore, they could be ignored.

The Neurology of Stimulus Response

Within the bodies of vertebrates is a part of the nervous system called the reticular network or reticular activating system; it has been suggested that the reticular network is largely responsible for habituation. It extends from the medulla through the midbrain to the thalamus of the forebrain. (The thalamus functions as the relay and integration center for impulses to and from the cerebrum of the forebrain.) Because it is composed of a huge number of interconnecting neurons and links all parts of the body, the reticular network functions as an evaluating, coordinating, and alarm center. It monitors incoming message impulses. Important ones are permitted to continue to the cerebral cortex, the higher brain. Messages from the cerebral cortex are coordinated and dispatched to the appropriate areas.

During sleep, many neurons of the reticular network stop functioning. Those that remain operational may inhibit response to unimportant stimuli (habituation) or cause hyperresponsiveness (sensitization). The cat who is accustomed to the sound of kitchen cabinets opening will sleep through a human's dinner being prepared (habituation) but will charge into the kitchen when she hears the sound of the cat food container opening (sensitization).

Researcher E. N. Sokolov concluded that the "orientation response" (which can be equated with sensitization) and habituation are the result of the functioning of the reticular network. According to Sokolov, habituation results in the formation of models within the reticular activating system. Incoming messages that match the model are disregarded by the organism, but those that differ trigger alerting reactions throughout the body, thus justifying the term "alerting system" as a synonym for the reticular network. Habituation to a very strong stimulus would take a long time. Repetition of this strong stimulus would cause an even stronger defensive reflex and would require an even longer habituation period.

The Role of Neurotransmitters

Neurotransmitters are chemical messengers that enable nerve impulses to be carried across the synapse, the narrow gap between neurons. They transmit impulses from the presynaptic axon to the postsynaptic dendrite(s). E. R. Kandell, in experiments with *Aplysia* (the sea hare, a large mollusk), demonstrated that as a habituation training series continues, smaller amounts of the neurotransmitter acetylcholine are released from the axon of the presynaptic sensory neuron. On the other hand, after sensitization, this neuron released larger amounts of acetylcholine because of the presence of serotonin, a neurotransmitter secreted by a facilitory interneuron. When a sensitizing stimulus is very strong, it usually generates an impulse within the control center—a ganglion, a neuron, or the brain. The control center then transmits an impulse to a facilitory interneuron, causing the facilitory interneuron to secrete serotonin.

Increased levels of acetylcholine secretion by the sensory neuron result from two different stimuli: direct stimulation of the sensory neurons of the siphon or serotonin from the facilitory interneuron. Facilitory interneurons synapse with sensory neurons in the siphon. Serotonin discharged from facilitory interneurons causes the sensory neurons to produce and secrete more acetylcholine.

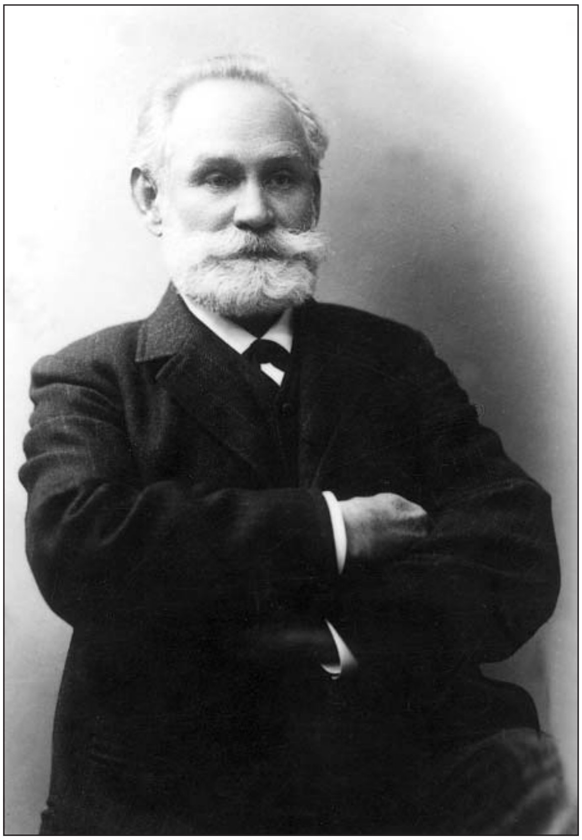
On the molecular level, the difference between habituation and adaption—the failure of the sensory neuron to respond—is very evident. The habituated sensory neuron has a neurotransmitter in its axon but is unable to secrete it and thereby enable the impulse to be transmitted across the synapse. The adapted sensory neuron, by contrast, has exhausted its current supply of neurotransmitter. Until new molecules of neurotransmitter are synthesized within the sensory neuron, none is available for release.

In 1988, Emilie A. Marcus, Thomas G. Nolen, Catherine H. Rankin, and Thomas J. Carew published the multiprocess theory to explain dishabituation and sensitization in the sea hare, *Aplysia*. On the basis of their experiments using habituated sea hares that were subjected to different stimuli, they concluded that dishabituation and sensitization do not always occur together; further, they decided, there are three factors to be considered: dishabituation, sensitization, and inhibition.

Habituation Studies

Habituation studies have utilized a wide variety of approaches, ranging from the observation of intact organisms carrying out their normal activities in their natural surroundings to the laboratory observation of individual nerve cells. With different types of studies, very different aspects of habituation and sensitization can be investigated. Surveying the animal kingdom in 1930, G. Humphrey concluded that habituation-like behavior exists at all levels of life, from the simple one-celled protozoans to the multicelled, complex mammals.

E. N. Sokolov, a compatriot of Ivan P. Pavlov, used human subjects in the laboratory. In 1960, he reported on the results of his studies, which involved sensory integration, the makeup of the orientation reflex (which he credited Pavlov with introducing in 1910), a neuronal model and its role in the orientation reflex, and the way that this neuronal model could be used to explain the conditioned reflex. Sokolov measured changes in the diameter of blood vessels in the head and finger, changes in electrical waves within the brain, and changes in electrical conductivity of the skin. By lowering the intensity of a tone to which human subjects had been habituated, Sokolov demonstrated that habituation was not the result of fatigue, because subjects responded to the lower-intensity tone with the startle or orientation reflex just as they would when a new stimulus was introduced. Sokolov concluded that the orientation response (which is related to sensitization) and habituation are the result of the functioning of the reticular network of the brain and central nervous system. Sokolov emphasized that the orientation response was produced after only the first few exposures to a particular stimulus, and it increased the discrimination ability of internal organizers. The orientation response was an alerting command. Heat, cold, electric shock, and sound were the major stimuli that he used in these studies.



Ivan Pavlov's groundbreaking work on habituation and sensitization, especially in dogs, earned him a Nobel Prize in Medicine in 1904. (Nobel Foundation)

E. R. Kandell used the sea hare, *Aplysia*, in his habituation-sensitization studies. *Aplysia* is a large sluglike mollusk, with a sheetlike, shell-producing body covering, the mantle. *Aplysia* has a relatively simple nervous system and an easily visible gill-withdrawal reflex. (The gill is withdrawn into the mantle shelf.) Early habituation-sensitization experiments dealt with withdrawal or absence of gill withdrawal. Later experiments measured electrical changes that occurred within the nerve cells that controlled gill movement. These were followed by studies which demonstrated that the gap (synapse) between the receptor nerve cell (sensory neuron) and the muscle-moving nerve cell (motor neuron) was the site where habituation and dishabituation occurred and that neurohormones such as acetylcholine and serotonin played essential roles in these processes. Kandell called the synapse the "seat of learning."

Charles Sherrington used spinal animals in which the connection between the brain and the spinal nerve cord had been severed. Sherrington demonstrated that habituation-sensitization could occur within the spinal nerve cord even without the participation of the brain. Pharmaceuticals have also been used in habituation-sensitization studies. Michael Davis and Sandra File used neurotransmitters such as serotonin and norepinephrine to study modification of the startle (orientation) response.

Habituation studies conducted in the laboratory enable researchers to control variables such as genetic makeup, previous experiences, diet, and the positioning of subject and stimulus; however, they lack many of the background stimuli present in the field. In her field studies of the chimpanzees of the Gombe, Jane Goodall used the principles of habituation to decrease the distance between herself and the wild champanzees until she was able to come close enough to touch and be accepted by them. The field-experimental approach capitalizes on the best of both laboratory and field techniques. In this approach, a representative group of organisms that are in their natural state and habitat are subjected to specific, known stimuli.

Learning to Survive

Habituation is necessary for survival. Many stimuli are constantly impinging upon all living things; since it is biologically impossible to respond simultaneously to all of them, those which are important must be dealt with immediately. It may be a matter of life or death. Those which are unimportant or irrelevant must be ignored.

Cell physiologists and neurobiologists have studied the chemical and electrical changes that occur between one nerve cell and another and between nerve and muscle cells. The results of those studies have been useful in understanding and controlling these interactions as well as in providing insights for therapies. Psychologists utilize the fruits of habituation studies to understand and predict, modify, and control the behavior of intact organisms. For example, knowing that bulls serving as sperm donors habituate to one cow or model and stop discharging sperm into it, the animal psychologist can advise the semen collector to use a different cow or model or simply to move it to another place—even as close as a few yards away.

Conservationists and wildlife protectionists can apply the principles of habituation to wild animals, which must live in increasingly closer contact with one another and with humans, so that both animal and human populations can survive and thrive. For example, black-backed gulls, when establishing their nesting sites, are very territorial. Males which enter the territory of another male gull are rapidly and viciously attacked. After territorial boundaries are established, however, the males in contiguous territories soon exhibit "friendly enemy" behavior: They are tolerant of the proximity of other males that remain within their territorial boundaries. This has been observed in other birds as well as in fighting fish.

—Walter Lener

See also: Communication; Defense mechanisms; Hearing; Instincts; Intelligence; Learning; Nervous systems of vertebrates; Reflexes; Rhythms and behavior; Sense organs; Smell; Vision.

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HADROSAURS

Types of animal science: Classification, evolution
Fields of study: Anatomy, evolutionary science, paleontology, systematics (taxonomy)

Hadrosaurs are a group of bipedal dinosaurs that were the most diverse and widespread large-bodied herbivores of the Late Cretaceous. The presence of eggs and nests provides evidence for hadrosaur social behavior.

Principal Terms

ALTRICIAL: animals that need parental care after hatching

CLADISTICS: a method of analyzing biological relationships in which advanced characters of organisms are used to indicate closeness of origin

CRETACEOUS: a period of time that lasted from about 146 to 65 million years ago, the end of which was marked by the extinction of the dinosaurs

LAMBEOSAURINES: hadrosaurs in which the skull bears a large tubular crest

ORNITHISCHIA: one of the two main dinosaur groups, characterized by a pelvis in which the pubis is swung backward

PUBIS: one of the three bones that make up the pelvis (the others are the ischium and ilium)

The hadrosaurids, or "duck-billed" dinosaurs, were large, bipedal dinosaurs, with body lengths up to fifteen meters, that lived during the Upper Cretaceous across North and Central America, South America, Europe, and Asia. It is thought that they originated in Asia, but once they arose, they spread and diversified worldwide, quickly becoming the primary constituent of herbivorous dinosaur faunas. The first hadrosaur remains to be found were represented by a few fragments from Montana and South Dakota, described by Joseph Leidy in 1856. Shortly afterward, a partial skeleton was found in New Jersey, the first nearly complete dinosaur found anywhere, and described by Leidy in 1858 as *Hadrosaurus foulkii*.

Hadrosaurs are ornithopod (bird-footed) dinosaurs, a term that refers to their three-toed feet. They are thus part of the Ornithischia, one of the two major dinosaur subdivisions, and characterized by a pubis (one of the three bones of the pelvis) that is inclined backward. In cladistic terms, they are considered to be a monophyletic group; that is, they are all derived from a common ancestor. They are particularly characterized by a toothless front to the mouth, which is flared outward to form a broad, flat "bill," prompting early re-

Hadrosaur Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Reptilia
Order: Ornithischia
Suborder: Ornithopoda (bipedal herbivores)

Geographical location: Western and eastern North America, central and southern South America, Europe, Asia

Habitat: Terrestrial habitats

Gestational period: Unknown

Life span: Estimated at twenty-five years

Special anatomy: Large, bipedal dinosaurs in which the snout was developed into a beak and a crest was often developed on the head searchers to dub them the duck-billed dinosaurs. This bill was covered by a thick, horny sheath, and the rest of the jaws bore closely packed batteries of grinding teeth, up to four hundred on each side of each jaw. The postcranial anatomy of hadrosaurs is generally very similar and the really obvious differences lie in the crests that many species bear on the top of their heads. These are formed of outgrowths of the nasal bones, are frequently hollow, and are found particularly in the hadrosaurs known as lambeosaurines.

Hadrosaurid Lifestyle

More is known about the life history of hadrosaurids than about any other group of dinosaurs, due to information from skin impressions, trackways, and eggs and nesting sites. They were originally thought to be amphibious animals, inhabiting marshy areas and swimming and diving for soft aquatic plants. This was partly based on skin impressions from mummified specimens which appeared to show webbing between the digits. It was even suggested that the crested forms used the crests as snorkels and were able to breathe through them while underwater. More recent analyses of stomach contents and the function of the tooth batteries suggest, however, that they were adapted to efficiently process fibrous vegetation of low nutritional value, such as coniferous needles and twigs. The crests are now thought to have developed for a variety of purposes, including increased sensory area for an improved sense of smell, and to act as resonators for producing distinctive calls.

Image Not Available

In 1979, juvenile hadrosaurid bones were discovered in the Two Medicine Formation in Montana by Jack Horner. Subsequently, he discovered nesting sites with eggs that provide evidence for reproductive strategies in the hadrosaur *Maiasaura*. These animals appear to have built large, circular nesting mounds with concave centers in common nesting areas. There is evidence of site fidelity, indicating that the nesting sites were used from season to season. Up to twenty eggs were laid in the nest in a circular pattern, then covered by vegetation that kept the eggs warm as it decomposed. Bones of young have been found in some of the nests and these indicate from tooth wear that the animals had already been feeding on vegetation. Also, the ends of the bones were still poorly formed, showing that they were altricial or nest-bound for some period after they had hatched. During this period they would have been fed by adults, which in turn suggests social behavior in which the eggs were protected by adults who then fed and raised the nest-bound hatchlings.

—David K. Elliott

See also: *Allosaurus*; *Apatosaurus*; *Archaeopteryx*; Dinosaurs; Evolution: Animal life; Extinction; Fossils; Ichthyosaurs; Nesting; Paleoecology; Paleontology; Prehistoric animals; Pterosaurs; Sauropods; Stegosaurs; *Triceratops*; *Tyrannosaurus*; Velociraptors.

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THE HARDY-WEINBERG LAW OF GENETIC EQUILIBRIUM

Type of animal science: Evolution
Fields of study: Ecology, evolutionary science, genetics

The Hardy-Weinberg law of genetic equilibrium is one of the foundations of mathematical population genetics. A description of the genetic makeup of a population under ideal conditions, it acts as a benchmark against which the effects of natural selection or other evolutionary forces can be measured.

Principal Terms

ALLELE: one of several alternate forms of a gene; the deoxyribonucleic acid (DNA) of a gene may exist as two or more slightly different sequences, which may result in distinct characteristics

ALLELE FREQUENCY: the relative abundance of an allele in a population

DIPLOID: having two chromosomes of each type

GENE: a section of the DNA of a chromosome, which contains the instructions that control some characteristic of an organism

GENE POOL: the array of alleles for a gene available in a population; it is usually described in terms of allele or genotype frequencies

GENOTYPE: the set of alleles an individual has for a particular gene

GENOTYPE FREQUENCY: the relative abundance of a genotype in a population

HAPLOID: having one chromosome of each type

POPULATION: the individuals of a species that live in one place and are able to interbreed

RANDOM MATING: the assumption that any two individuals in a population are equally likely to mate, independent of the genotype of either individual

Genetics began with the study of inheritance in families: Gregor Mendel's laws describe how the alleles of a pair of individuals are distributed among their offspring. Population genetics is the branch of genetics that studies the behavior of genes in populations. The population is the only biological unit that can persist for a span of time greater than the life of an individual, and the population is the only biological unit that can evolve. The two main subfields of population genetics are theoretical (or mathematical) population genetics, which uses formal analysis of the properties of ideal populations, and experimental population genetics, which examines the behavior of real genes in natural or laboratory populations.

Population genetics began as an attempt to extend Mendel's laws of inheritance to populations. In 1908, Godfrey H. Hardy, an English mathematician, and Wilhelm Weinberg, a German physician, each independently derived a description of the behavior of allele and genotype frequencies in an ideal population of sexually reproducing diploid organisms. Their results, now termed the Hardy-Weinberg principle, or Hardy-Weinberg equilibrium, showed that the pattern of allele and genotype frequencies in such a population followed simple rules. They also showed that, in the absence of external pressures for change, the genetic makeup of a population will remain the same, at an equilibrium. Since evolution is change in a population over time, such a population is not evolving. Modern evolutionary theory is an outgrowth of the "New Synthesis" of R. A. Fisher, J. B. S. Haldane, and Sewall Wright, which was done in the 1930's. They examined the significance of various factors that cause evolution by examining the degree to which they cause deviations from the predictions of the Hardy-Weinberg equilibrium.

Assumptions and Predictions

The predictions of the Hardy-Weinberg equilibrium hold if the following assumptions are true: The population is infinitely large; there is no differential movement of alleles or genotypes into or out of the population; there is no mutation (no new alleles are added to the population); there is random mating (all genotypes have an equal chance of mating with all other genotypes); and all genotypes are equally fit (have an equal chance of surviving to reproduce). Under this very restricted set of assumptions, the following two predictions are true: Allele frequencies will not change from one generation to the next, and genotype frequencies can be determined by a simple equation and will not change from one generation to the next.

The predictions of the Hardy-Weinberg equilibrium represent the working through of a simple set of algebraic equations and can be easily extended to more than two alleles of a gene. In fact, the results were so self-evident to the mathematician Hardy that he at first did not think the work was worth publishing.

If there are two alleles (A, a) for a gene present in the gene pool, let p = the frequency of the A allele and q = the frequency of the a allele. As an example, if $p = 0.4$ (40 percent) and $q = 0.6$ (60 percent), then $p + q = 1$, since the two alleles are the only ones present and the sum of the frequencies (or proportions) of all the alleles in a gene pool must equal 1 (or 100 percent). The Hardy-Weinberg principle states that at equilibrium the frequency of AA individuals will be p^2 (equal to 0.16 in this example), the frequency of Aa individuals will be $2pq$, or 0.48, and the frequency of aa individuals will be q^2, or 0.36.

The basis of this equilibrium is that the individuals of one generation give rise to the next generation. Each diploid individual produces haploid gametes. An individual of genotype AA can make only a single type of gamete, carrying the A allele. Similarly, an individual of genotype aa can make only a gametes. An Aa individual, however, can make two types of gametes, A and a, with equal probability. Each individual makes an equal contribution of gametes, since all individuals are equally fit and there is random mating. Each AA individual will contribute twice as many A gametes as each Aa individual. Thus, to calculate the frequency of A gametes, add twice the number of AA individuals and the number of Aa individuals, then divide by twice the total number of individuals in the population (note that this is the same as the method to calculate allele frequencies). That means that the frequency of A gametes is equal to the frequency of A alleles in the gene pool of the parents.

The next generation is formed by gametes pairing at random (independent of the allele they carry). The likelihood of an egg joining with a sperm is the frequency of one multiplied by the frequency of the other. AA individuals are formed when an A sperm joins an A egg; the likelihood of this occurrence is $p \times p = p^2$ (that is, $0.4 \times 0.4 = 0.16$ in the first example). In the same fashion, the likelihood of forming an aa individual is $q^2 = 0.36$. The likelihood of an A egg joining an a sperm is pq, as is the likelihood of an a egg joining an A sperm; therefore, the total likelihood of forming an Aa individual is $2pq = 0.48$. If one now calculates the allele frequencies (and hence the frequencies of the gamete types) for this generation, they are the same as before: The frequency of the A allele is $p = (2p^2 + 2pq)/2$ (in the example, $(0.32 + 0.48)/2 = 0.4$), and the frequency of the a allele is $q = (1 - p) = 0.6$. The population remains at equilibrium, and neither allele nor genotype frequencies change from one generation to the next.

Ideal Versus Real Conditions

The Hardy-Weinberg equilibrium is a mathematical model of the behavior of ideal organisms in an ideal world. The real world, however, does not approximate these conditions very well. It is important to examine each of the five assumptions made in the model to understand their consequences and how closely they approximate the real world.

The first assumption is infinitely large population size, which can never be true in the real world, as all real populations are finite. In a small population, chance effects on mating success over many generations can alter allele frequencies. This effect is called genetic drift. If the number of breeding adults is small enough, some genotypes will not get a chance to mate with one another, even if mate choice does not depend on genotype. As a result, the genotype ratios of the offspring would be different from the parents'. In this case, however, the gene pool of the next generation is determined by those genotypes, and the change in allele frequencies is perpetuated. If it goes on long enough, it is likely that some alleles will be lost from the population, since a rare allele has a greater chance of not being included. Once an allele is lost, it cannot be regained. How long this process takes is a function of population size. In general, the number of generations it would take to lose an allele by drift is about equal to the number of individuals in the population. Many natural populations are quite large (thousands of individuals), so that the effects of drift are not significant. Some populations, however, especially of endangered species, are very small: The total population of California condors is less than twenty-five, all in captivity.

The second assumption is that there is no differential migration, or movement of genotypes into or out of the population. Individuals that leave a population do not contribute to the next generation. If one genotype leaves more frequently than another, the allele frequencies will not equal those of the previous generation. If incoming individuals come from a population with different allele frequencies, they also alter the allele frequencies of the gene pool.

The third assumption concerns mutations. A mutation is a change in the DNA sequence of a gene—that is, the creation of a new allele. This process occurs in all natural populations, but new mutations for a particular gene occur in about one of 10,000 to 100,000 individuals per generation. Therefore, mutations do not, in themselves, play much part in determining allele or genotype frequencies. Yet, mutation is the ultimate source of all alleles and provides the variability on which evolution depends.

The fourth assumption is that there is random mating among all genotypes. This condition may be true for some genes and not for others in the same population. Another common limitation on random mating is inbreeding, the tendency to mate with a relative. Many organisms, especially those with limited ability to move, mate with nearby individuals, which are often relatives. Such individuals tend to share alleles more often than the population at large.

The final assumption is that all genotypes are equally fit. Considerable debate has focused on the question of whether two alleles or genotypes are ever equally fit. Many alleles do confer differences in fitness; it is through these variations in fitness that natural selection operates. Yet, newer techniques of molecular biology have revealed many differences in DNA sequences that appear to have no discernible effects on fitness.

Theoretical and Experimental Genetic Studies

The field of population genetics uses the Hardy-Weinberg equations as a starting place, to investigate the genetic basis of evolutionary change. These studies have taken two major pathways: theoretical studies, using ever more sophisticated mathematical expressions of the behavior of model genes in model populations, and experimental investigations, in which the pattern of allele and genotype frequencies in real or laboratory populations is compared to the predictions of the mathematical models.

Theoretical population genetics studies have systematically explored the significance of each of the assumptions of the Hardy-Weinberg equilibrium. Mathematical models allow one to work out with precision the behavior of a simple, well-characterized system. In this way, it has been possible to estimate the effects of population size or genetic drift, various patterns of migration, differing mutation rates, inbreeding or other patterns of nonrandom mating, and many different patterns of natural selection on allele or genotype frequencies. As the models become more complex, and more closely approximate reality, the mathematics becomes more and more difficult. This field has been greatly influenced by ideas and tools originally devised for the study of theoretical physics, notably statistical mechanics. Some of the most influential workers in this field were trained as mathematicians and view the field as a branch of applied mathematics, rather than biology. As a consequence, many of the results are not easily understood by the average biologist.

Experimental population genetics tests predictions from theory and uses the results to explain patterns observed in nature. The major advances in this field have been determined, in part, by some critical advances in methodology. In order to study the behavior of genes in populations, one must be able to determine the genotype of each individual. The pattern of bands on the giant chromosomes found in the salivary glands of flies such as *Drosophila* form easily observed markers for groups of genes. Since these animals can be easily manipulated in the laboratory, as well as collected in the field, they have been the subjects of much experimental work. Using population cages, one can artificially control the population size, amount of migration, mating system, and even the selection of genotypes, and then observe how the population responds over many generations. More recently, the techniques of allozyme or isozyme electrophoresis and various methods of examining DNA sequences directly have made it possible to determine the genotype of nearly any organism for a wide variety of different genes. Armed with these tools, scientists can address directly many of the predictions from mathematical models. In any study of the genetics of a population, one of the first questions addressed is whether the population is at Hardy-Weinberg equilibrium. The nature and degree of deviation often offer a clue to the evolutionary forces that may be acting on it.

Understanding Genotypes

As the cornerstone of population genetics, the Hardy-Weinberg principle pervades evolutionary thinking. The advent of techniques to examine genetic variation in natural populations has been responsible for a great resurgence of interest in evolutionary questions. One can now test directly many of the central aspects of evolutionary theory. In some cases, notably the discovery of the large amount of genetic variation in most natural populations, evolutionary biologists have been forced to reassess the significance of natural selection compared with other forces for evolutionary change.

In addition to the great theoretical significance of this mathematical model and its extensions, there are several areas in which it has been of practical use. An area in which a knowledge of population genetics is important is agriculture, in which a relatively small number of individuals are used for breeding. In fact, much of the early interest in the study of population genetics came from the need to understand the effects of inbreeding on agricultural organisms. A related example, and one of increasing concern, is the genetic status of endangered species. Such species have small populations and often exhibit a significant loss of the genetic variation that they need to adapt to a changing environment. Efforts to rescue such species, especially by breeding programs in zoos, are often hampered by an incomplete consideration of the population genetics of small populations. A third example of a practical application of population genetics is in the management of natural resources such as fisheries. Decisions about fishing limits depend on a knowledge of the extent of local populations. Patterns of allele frequencies are often the best indicator of population structure. Population genetics, by combining Mendel's laws with the concepts of population biology, gives an appreciation of the various forces that shape the evolution of the earth's inhabitants.

—Richard Beckwitt

See also: Cloning of extinct or endangered species; Evolution: Animal life; Gene flow; Genetics;

Natural selection; Neutral mutations and evolutionary clocks; Nonrandom mating, genetic drift, and mutation; Population analysis; Population fluctuation; Population genetics; Punctuated equilibrium and continuous evolution; Reproduction; Wildlife management; Zoos.

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HAWKS

Type of animal science: Classification
Fields of study: Anatomy, ornithology

Hawks are a diverse group of birds adapted to exploit a wide variety of habitats, prey, and climatic conditions. All hawks are distinguished by sharp, strongly hooked bills, a fleshy cere, and strong legs with sharp talons. Most are active and efficient hunters that use their keen vision to target and track suitable prey.

Principal Terms

CERE: the covering of the nostrils, typical of all hawklike birds of prey.

CREPUSCULAR: active in the twilight periods of dawn and dusk

FLEDGING: time period when young hawks and owls develop the ability to fly

FOVEA: specific area with an exceptionally dense concentration of light-sensitive cells in eyes of animals

FRATRICIDE: deliberate killing of one sibling by another sibling

HABITAT SELECTION: process of choosing a home range, territory, nesting site, or feeding site on the basis of specific features of the habitat that the raptor is best adapted to exploit

HOME RANGE: geographic area used by an individual, pair, or group for their daily, seasonal, and sometimes their yearly activities; the defended portion of the home range is called a territory

TALONS: the long, curved, sharply pointed claws of a bird of prey, used for slashing and killing, holding, and carrying prey, and for defense

TERRITORIALITY: all behaviors involved with the establishment, proclamation, and defense of a specific area

WING LOADING: ratio of weight to lifting area of wing

Hawks are a diverse group of birds adapted to exploit a wide variety of habitats, prey, and climatic conditions. Although varying in size from the 75-gram male tiny hawk (*Accipiter superciliosus*) and pearl kite to the 6.5-kilogram female harpy eagle (*Harpia* spp.), all hawks are distinguished by sharp, strongly hooked bills, a fleshy cere, and strong legs with sharp talons or claws. Most are active and efficient hunters that use their keen vision to target and track suitable prey.

The 237 species of hawks are placed in the avian order Falconiformes. Families within this order include the booted eagles, harpy eagles, buteo hawks, subbuteos, chanting goshawks, accipiters, harriers, and kites. Only the fifty-four species of accipiters are strictly considered true hawks, but most raptor biologists and hawk enthusiasts also include the buteo hawks, called buzzards in Europe, within the category of hawks, while the most liberal definition incorporates the kites, harriers, and eagles as well.

Habitats and Lifestyles

Hawks are a widespread and successful group that occurs on all continents and the larger islands. They are absent only from Antarctica, the ice-covered mountaintops, and the most remote oceanic islands. Hawks are primarily birds of woodland and woodland-edge habitats, and reach their greatest diversity in the rain forests of the tropics. They are components of all temperate woodlands of varying density and diversity, but some species occur in a wide variety of more open habitats, including chaparral, grasslands, desert, and tundra. Many species take readily to conifer plantations and ornamental conifer stands, provided that sufficient food is nearby. Black kites (*Milvus migrans*), Cooper's (*Accipiter cooperi*), red-tailed (*Buteo jamaicensis*), and Swainson's hawks (*Buteo swainsoni*) exemplify species that tolerate human-modified habitats, especially farmlands, pastures, and orchards. Given their need for large territories and abundant prey, few species have either the tolerance or ability to exploit urban landscapes, although wooded suburbs and city open-space habitats do attract an occasional furtive nesting or roosting pair of red-tailed hawks or brahminy kites (*Hiliastur indus*).

The daily lives of hawks center around finding food and avoiding enemies. To ensure an adequate food base, most hawks maintain large home ranges for at least part of the year, and some remain on territory throughout the year. If prey populations suffice, hawks are sedentary, but if they decline, hawks must move elsewhere. Some species are nomadic, often wandering widely in search of food, but most northern species move southward in spectacular migrations along traditional flyways each fall. Red-tailed hawks migrate only a few hundred miles but others, such as the lesser spotted eagle (*Aquila pomarina*) and Eurasian buzzard *(Buteo buteo*), fly thousands of miles to their wintering grounds. Their return migration in spring is timed to ensure arrival on the breeding grounds when weather conditions and prey populations are optimal.

Most hawks are entirely carnivorous, or nearly so, and use their remarkable eyesight and intimate knowledge of their territory to locate, pursue, and capture food. Their large eyes are set forward in the head with overlapping fields of vision. Each eye has a long focal length from lens to retina, which produces a telescopic vision that enables hawks to spot prey at great distances. Hawk eyes also have two concentrations of visual cells, called fovea, instead of one, as in other birds and mammals. The central fovea and lateral fovea apparently permit the simultaneous estimate of both distance to and movement of prey, thereby increasing hunting efficiency when pursuing agile, fast-moving animals.

Most hawks are larger—some considerably larger—than the prey that they take. Many species exhibit pronounced sexual dimorphism, with the female being larger than the male. Bigger females can better incubate eggs and protect young, but the sexual size difference enables exploitation of a much wider prey range. Sexual dimorphism is best illustrated in the bird-eating accipiter hawks, in which the larger female takes grouse and duck-sized prey while the smaller male pursues the smaller and more agile birds. Conversely, insectivorous and scavenger hawks show little or no sexual dimorphism.

Almost all hawks that hunt live animals have comparatively light bodies on large wings for a low wing loading, which facilitates extended periods of soaring in search of prey and also for carrying prey. Many species show subtle differences in overall size and wing shape that reveal differences in hunting techniques or diet. For example, the long, narrow wings and light bodies of swallow-tailed (*Elanoides forficatus*) and plumbeous (*Ictinia plumbea*) kites enhance their aerial maneuverability for catching insects just above the rain forest canopy. In contrast, the long, broad wings of hawks and eagles maximize lift needed to soar for hours or to carry medium-sized mammals and birds, along with an occasional reptile or amphibian. The larger hawks and eagles take correspondingly bigger prey up to the size of rabbits, hares, hyraxes, sloths, small antelope, foxes, and young deer.

The long tails and rounded wings of bird hawks such as goshawks, sparrow hawks, hawk-eagles (*Spizaetus* spp.) and bat hawks (*Macheirhamphus alcinus*) provide just the right combination of speed and agility to pursue birds through the often cluttered microhabitat just beneath the woodland canopy.

The long, dihedral wings of harriers (*Circus* spp.) provide a stable flying platform for slow quartering flight over open grasslands and marshes. Harriers use both eyes and ears to hunt small mammals in the tall grasses and, like owls, have a distinctive facial ruff that helps gather sounds to pinpoint prey in the tall grasses.

Hunting and dietary specializations abound in this group. At least twelve species of kites are insectivorous or nearly so, but many other hawks and eagles feed opportunistically on abundant locusts, and grasshoppers, ants, termites, and locust swarms invariably attract a variety of hawks and other birds. Reptile specialists include the snake eagles (*Circateus* spp) and serpent eagles (*Spilornatus* spp.), which sit quietly for hours, patiently watching for the slow and stealthy movements of snakes. Possibly the most extreme dietary specialist is the rufous crab-hawk (*Buteogallus aequinoctialis*), which picks through aerial roots of mangroves in search of crabs, but snail kites (*Rostrhamus sociabilis*) and slender-billed kites (*Rostrhamus hamatus*) focus almost exclusively for pulmonate snails, which they extract with their long, hooked bills.

Hawk Facts

Classification:
Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Class: Aves
Order: Falconiformes
Families: Accipitridae
Subfamilies: Elaninae (white-tailed kites, five genera, eight species); Milvinae (kites, eight genera, fifteen species); Accipitrinae (hawks, five genera, twenty-two species); Circinae (harriers, three genera, eight species); Pandioninae (ospreys, one genus, seven species)
Geographical location: All continents except Antarctica
Habitat: Woods and woodland edges, rain forests; may also inhabit chaparral, grasslands, deserts, and tundra
Gestational period: One to two months, depending on species
Life span: Eighteen to fifty years, depending on species
Special anatomy: Talons; exceptionally keen eyesight; nostril coverings (cere); sharp, hooked bills

Courtship and Nesting

Most hawks breed each year, but some of the larger tropical eagles and snake eagles may breed once every several years. All phases of the breeding cycle of hawks are dependent on prey abundance: In low prey years pairs often do not nest and may not even establish a territory, while in high prey years nesting success, measured by the number of eggs produced, hatched, and young fledged, is highest. Tropical hawks may nest at any time of year, but usually do so during the dry season. Temperate species are more strictly tied to a spring and early summer nesting cycle when prey abundance is maximal and longer days permit extended hunting periods.

The breeding cycle of temperate species begins when males or mated pairs claim and advertise territories by often extravagant displays that may include sky dancing, dives and swoops, perches, calling, and posturing. Unmated males court females with aerial displays such as circling, following flights, sky dancing, and food transfers from males to females. As courtship proceeds, the pair bond is cemented by synchronized flights, following flights, mutual preening, food begging by the female, and courtship feeding.

Territory size depends on food needs and prey density. Smaller tropical hawks may limit their breeding activities to a hundred acres or so, while the larger eagles that inhabit open habitats, such as the Scottish golden eagles, sometimes establish home ranges of thousands of acres on the moors and grasslands. Most hawk territories are cone-shaped, with little or no overlap permitted near the base of the cone, which is typically centered near the nest site or feeding site.

Hawks build stick nests in trees (for example, Cooper's hawks, sharp-shinned hawks), on cliffs (ferruginous hawks, *Buteo regalis*), bluffs and outcrops (Swainson's hawks, *Buteo swainsoni*), on structures (ospreys, red-tailed hawks), or directly on the ground (harriers). Depending on habitat, some species are flexible in choice of substrate;

Hawks, such as this red-tailed hawk, spend most of their day flying over fields, using their keen eyesight to search for the small animals that are their prey. (PhotoDisc)

thus, red-tailed hawks may build their nests in trees, on ledges, less frequently on structures, or directly on the ground. Many hawks (ferruginous hawks, Swainson's hawks) readily accept artificial platforms such as bridge abutments, piers, telephone poles, and towers.

Both members of a pair bring sticks to the nest site, but the female does the actual work of nest building, arranging the materials into a compact nesting platform with a shallow bowl. Many species refurbish one or more nests year after year, sometimes resulting in massive nesting platforms of sticks and branches after many years of use. Nests are generally lined with dried grasses or mosses and many may decorate them with sprigs of greenery.

Depending on species, from one to ten eggs are laid at two- to four-day intervals, and incubation begins immediately. In most species, the female incubates the eggs while the male supplies her with food, which he may deliver to her or to a nearby site. In some species the male may replace her for brief periods of time to allow her to rest, roost, or forage.

The female is often highly secretive during this nesting phase as she hunkers down to incubate the eggs. The young hatch in about one month in the smaller accipiters and kites, and up to two months in the larger eagles. Eggs hatch asynchronously, producing a nest of uneven-aged young. The female keeps constant company with the newly hatched young, brooding them and feeding them with food supplied by the male. As the young grow, their food demands increase and both male and female spend most of their time hunting food to feed the young.

Adults become increasingly aggressive with young in the nest. Generally, both adults participate in nest defense, although the female is almost invariably the most aggressive. Warning cries (most hawks), power dives (many buteos), and determined slashing attacks (goshawks) can drive all but the most determined intruders away, but unfortunately have little effect on humans intent on destruction of the nest and young. Otherwise, the only natural predators of eggs and young are nest-robbing birds, chiefly corvus species, mammals, other larger diurnal raptors, and the larger owls, especially the *Bubo* species, which take young during the night.

Survival of the young depends entirely on the ability of the adults to find sufficient food. If prey is sufficient, all of the young successfully fledge, but if prey populations decline, one or all of the smallest and weakest young of a nest die of starvation. Nestling fratricide has been observed in many species and may help ensure survival of the strongest young at the expense of their younger or weaker nestlings.

After leaving the nest, the young usually stay with the adults for several weeks or longer—a year or more in some tropical eagles—learning how to perfect their hunting skills and avoid enemies. Many retain a streaked or spotted juvenile plumage for several years that may help conceal them from potential enemies. This plumage is replaced at sexual maturity by adult coloring that probably promotes sexual advertisement and territorial displays.

Conservation and Economic Importance of Hawks

Humans are the most consistent and potent threat to hawks. Historically, huge numbers of hawks were slaughtered by farmers, hunters, gamekeepers, and trappers for sport and as control measures designed to increase game and poultry populations. Many hawks still fall victim to illegal shooting by hunters and sportsman who prefer live target practice, while accipiter hawks are sometimes shot by pigeon fanciers or grouse managers to protect their interests. Generally, the larger buteo hawks and eagles are at greater risk because of their size and habit of selecting open, conspicuous perches for territorial posturing and while hunting. Globally, some hawks are still slaughtered for the taxidermy market, some are taken for falconry, and some are captured as part of the lucrative international trade in zoo specimens, despite the fact that they are all federally protected in most countries of the world.

Hawks also fall victim to pesticides and industrial wastes, which accumulate within their tissues and eventually reach harmful levels that result either in death of the bird or reduction of its productivity. Toxic levels of chemicals have been documented in almost every hawk species on every continent and have particularly affected populations and productivity of fish-eating hawks, such as the osprey and bald eagle.

While all of these forms of deliberate and inadvertent human persecutions take an annual toll, the most persistent threat to hawk populations results from habitat destruction or fragmentation and deforestation. Habitat losses are especially critical for hawks, which require large areas of undisturbed habitat for home range to provide a food base for themselves and their young.

Although no species have become extinct in the last several hundred years, twenty-nine species are on the current list of endangered or threatened species, and it took concerted efforts by state and federal programs on many levels to save several species, such as the bald eagle and osprey. Bans on dichloro-diphenyl-trichloroethane (DDT) and other environmental poisons, along with extensive programs of captive breeding, nesting platforms, and reintroduction programs have helped reestablish bald eagles (*Haliaetus leucocephalus*) in North America and red kites and white-tailed sea eagles (*Haliaetus albicilla*) in Scotland. Conservation programs continue to target the protection and recovery of many species throughout the world, including the harpy eagle in Latin America and the Philippine eagle (*Pithecophaga jefferyi*) of the Philippine Islands.

—Dwight G. Smith

See also: Beaks and bills; Birds; Eagles; Feathers; Flight; Molting and shedding; Nesting; Respiration in birds; Wildlife management; Wings.

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HEARING

Types of animal science: Anatomy, physiology
Fields of study: Anatomy, biophysics, neurobiology, physiology

One of the five major senses, hearing is utilized by animals to detect sound in the environment through the transduction of sound waves to the universal language of the nervous system, the nerve impulse.

Principal Terms

AUDITORY NERVE: the cranial nerve that conducts sensory impulses from the inner ear to the brain

PITCH: the frequency of sound—the higher the frequency, the greater its pitch

SOUND FREQUENCY: the distances between crests of sound waves measured in hertz

SOUND INTENSITY: the loudness of a sound directly related to the amplitude of the sound waves measured in decibels

SYNAPSE: the functional connection between nerve cells or an effector cell, such as a sensory receptor and a nerve cell

TETRAPODS: vertebrates with four limbs

Sensory perception provides the only means of communication between the external world and the nervous system. The process of sensory perception begins in the sense organs, where specially designed receptor cells are stimulated by various types of energy. These receptor cells are highly selective for specific forms of stimulus energy. For example, the photoreceptors in the eye are specific for light energy and largely ignore other forms of stimuli. Each receptor cell transduces (changes) the stimulus into an electrical charge (nerve impulse) which travels through nerve fibers to the brain, where the electrical impulse is translated into a particular sensation. The major types of sensory receptor cells are the chemoreceptors (sense chemical energy), mechanoreceptors (sense mechanical energy), photoreceptors (sense light energy), thermoreceptors (sense thermal energy), and electroreceptors (sense electrical energy). The sensory receptors for the organs of hearing are called hair cells, which are extraordinarily sensitive mechanoreceptors. Tiny filaments (like hair follicles, only much smaller) called cilia project from the ends of the receptor cell. This filament bends in response to mechanical pressure, and the bending generates the nerve impulse.

Through the course of evolution, the sensory systems developed from single, independent receptor units into complex sense organs, such as the vertebrate ear, in which receptor cells are organized into a tissue associated with accessory structures. The organization of the receptor cells and the architecture of the accessory structures allow far more intricate and accurate sampling of the environment than is possible by independent, isolated receptor cells. While invertebrates possess receptor cells that sense vibrational (mechanical) energy, the true sense of hearing originated with the vertebrates.

The Vertebrate Ear

All vertebrates possess a pair of membranous labyrinths (cavities lined by a membrane) embedded in the cranium, lateral to the hindbrain. This region is often referred to as the inner ear. Each labyrinth consists of three semicircular canals, a utriculus, and a sacculus, which, during development, become filled with a fluid called endolymph. The semicircular canals and utriculus are primarily associated with equilibrium, but the sacculus has evolved into an organ of hearing. In fishes, the lagena, a depression in the floor of the sacculus, has its own maculae (patches of hair cells) which respond to vibratory stimuli of relatively high frequency (sound waves). In tetrapods, the lagena has evolved into an additional fluid-filled duct of the labyrinth called the spiral duct or cochlea. With the evolution of the cochlea, the sensory region enlarged into the organ of Corti. The hair cells are located in the organ of Corti. Most of the structures of the ear assist in the transformation of sound waves (airborne vibrations) into movements of the organ of Corti, which stimulate the hair cells. These hair cells then excite the sensory neurons (nerve cells) of the auditory nerve.

Mammals are the only vertebrates to possess a true cochlea, but birds and crocodilians have a nearly straight cochlear duct that contains some of the same features, including an organ of Corti. Detection of sound in the lower vertebrates that have no cochlear ducts is carried out by hair cells associated with the utriculus and lagena. The cochlea is coiled somewhat like the shell of a snail and is divided into three longitudinal compartments. The two outer compartments, the scala tympani and the scala vestibuli, are filled with a fluid called perilymph and are connected to one another by a structure called the helicotrema. The scala media, filled with endolymph, is located between the two outer compartments and is bound by the basilar membrane and Reissner's membrane. The organ of Corti lies within the scala media and sits upon the basilar membrane. Four rows of hair cells are present in adult mammals—one inner and three outer rows. The cilia of the inner row are thought to be sensitive primarily to the velocity (speed) at which they are displaced by sound waves. The cilia of the outer rows are more sensitive and can detect the degree of deflection as well as the speed.

Sound waves are transported to the inner ear via the outer ear and middle ear. The outer ear consists of the tympanic membrane (ear drum), which is situated on the surface of the head in frogs and toads. In reptiles, birds, and mammals, the tympanic membrane is located deeper in the head at the dead end of an air-filled passageway called the outer ear canal or external auditory

Comparison of Hearing Organs

Jawless fishes: These primitive vertebrates have only two semicircular canals within the inner ear. In jawless fishes, the structures of the inner ear are more associated with equilibrium than hearing.

Gnathostome fishes: All fishes possess membranous labyrinths embedded in the auditory region of the skull. The labyrinths consist of the utriculus and sacculus and three semicircular canals. The inner ear serves primarily as an organ of equilibrium in fishes, but a few species have developed an accessory function of detecting sound transmissions.

Amphibians: The hearing organ of amphibians is considerably advanced over that of the fishes. In frogs and toads, the outer ear consists of a tympanic membrane in the adults that lies flat on the head. The middle ear is an air-filled chamber with a small movable bone. The inner ear consists of a utriculus, a sacculus, a lagena, and three semicircular canals filled with endolymph and perilymph. The hair cells are located at the base of each canal.

Reptiles and birds: Hearing is well developed in reptiles and especially birds. There is a tympanic membrane, a well-developed middle ear, and a straight-tubed cochlea and spiral organ. Some birds can hear ultralow frequencies that may be important in navigating.

Mammals: The membranous labyrinth and the sense of hearing are highly developed in mammals. Mammal ears consist of all of the components discussed in the text. Mammals are keenly adapted to hearing. Humans can hear in a range of sixteen to twenty thousand hertz, but bats can detect frequencies up to one hundred thousand hertz.

meatus. In mammals, there is also an outer appendage, the pinna, which collects sound waves and directs them into the outer ear canal. The tympanic membrane makes contact with the bones (ossicles) of the air-filled inner ear. In amphibians, birds, and reptiles, there is a single bone called the columella (or stapes). In mammals, there is a series of three bones. The malleus (hammer) is in contact with the tympanic membrane at one end and articulates with a second bone, the incus (anvil). The incus then articulates with a third bone, the stapes (stirrup), which connects to a structure called the oval window of the cochlea.

Mammals have a mobile outer ear appendage, called a pinna, which catches and funnels sound waves into the interior ear to increase hearing acuity. (Digital Stock)

Detection of Sound

Sound waves striking the tympanic membrane cause it to vibrate. These vibrations are transmitted through the auditory ossicles of the middle ear and through the oval window to the perilymph. The bones of the middle ear amplify the pressure of the vibrations set up in the eardrum by airborne vibrations. Vibrations reaching the oval window pass through the cochlear fluids and the Reisner's and basilar membranes separating the cochlear compartments before dissipating their energy through the membrane-covered round window of the cochlea. The distribution of pertubations (disturbances) within the cochlea depends on the frequencies of the vibrations entering the oval window. Very long, low frequencies travel through the perilymph of the scala vestibuli, across the helicotrema to the scala tympani, and finally toward the round window. Short wave frequencies take a shortcut from the scala vestibuli through the Reissner's membrane and the basilar membrane to the perilymph of the scala tympani. Movement of perilymph from the scala vestibuli to the scala tympani produces displacement of both Reissner's membrane and the basilar membrane. Movement of Reissner's membrane does not directly contribute to hearing, but displacement of the basilar membrane is required for pitch discrimination. Displacement of the basilar membrane into the scala tympani produces vibrations of the basilar membrane. Each region of the basilar membrane vibrates with maximum amplitude to a different sound frequency. Sounds of higher frequency (pitch) cause maximum vibrations of the basilar membrane at the apical region (closest to the stapes), while sounds of low frequency produce maximum vibrations at the distal region of the basilar membrane.

The sensory hair cells are situated on the basilar membrane with the cilia projecting into the endolymph of the cochlear duct. The cilia of the outer hair cells are embedded with the tectorial membrane located above the hair cells within the cochlear duct. Displacement of the cochlear duct by pressure waves of perilymph produces a shearing force between the basilar membrane and the tectorial membrane. This causes the cilia to bend, and the bending of the cilia produces a nerve impulse in the sensory nerve endings that synapse with the hair cells. The higher the intensity of the sound, the greater the displacement of the basilar membrane, which results in greater bending of the cilia of the hair cells. Increased bending of the cilia produces a higher frequency of nerve impulses in the fibers of the cochlear nerve that synapse with hair cells. Since a specific region of the basilar membrane is maximally displaced by a sound of a particular frequency, those nerve cells that originate in this region will be stimulated more than nerve cells which originate in other regions of the basilar membrane. This mechanism results in a neural code for pitch discrimination. Within the brain, sensory neurons of the eighth cranial (auditory) nerve synapse with neurons in the medulla which project to the inferior colliculus of the brain. Neurons from this region of the brain project into the thalamus, which in turn sends nerve fibers to the auditory cortex of the temporal lobe of the brain. Through this pathway, neurons in different regions of the basilar membrane stimulate neurons in corresponding areas of the auditory cortex. Hence, each area of this cortex represents a different part of the basilar membrane and a different pitch.

—D. R. Gossett

See also: Antennae; Brain; Communication; Ears; Eyes; Nervous systems of vertebrates; Noses; Physiology; Sense organs; Smell; Vision; Vocalizations.

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HEART

Types of animal science: Anatomy, physiology
Fields of study: Anatomy, biochemistry, cell biology, genetics, histology, pathology, physiology, zoology

The heart is a muscular pump that moves blood throughout the body to deliver oxygen and nutrients to the tissues, remove metabolic waste products, and warm the animal by distributing metabolic heat.

Principal Terms

ATRIUM (AURICLE): a thin-walled muscular heart chamber that receives blood returning to the heart

CLOSED CIRCULATION: a circulation system made of arteries, capillaries, and veins that returns blood flow back to the heart

DIASTOLE: period of heart muscle relaxation and declining pressure

HEART: general term for a muscular vessel segment or organ that contracts and provides for unidirectional movement of blood or hemolymph

OPEN CIRCULATION: an open-ended sinus or arterial vessel system in which the circulation system does not return blood or hemolymph directly back to the heart

SYSTOLE: period of heart muscle contraction and peak pressure

VENTRICLE: a thick-walled muscular heart chamber that receives blood from the atrium and pumps blood into the circulation

The heart beats with a lifelong, continual rhythm to supply a constant flow of oxygen and nutrients, as well as to remove metabolic waste products from every cell in the body. The interstitial fluid that surrounds each cell keeps a constant supply of these factors and prevents a buildup of waste products by communicating with the blood. However, the blood can only keep the interstitial fluid in balance by remaining in motion. If the blood flow stops, the oxygen and nutrients are quickly depleted and harmful waste products accumulate. In adult humans, the heart beats about seventy times per minute, or one hundred thousand times per day. Each heartbeat moves about seventy milliliters of blood, which equals over seven thousand liters of blood per day, or enough blood to fill 7,400 quart-sized milk cartons.

Heart Structure

Hearts vary in their complexity, from simple pulsing vessel segments in insects to the complex four-chambered heart in birds and mammals. Hearts typically have a rhythmic contraction rate determined by specialized muscle cells and can even beat outside the body. A strong, saclike structure called the pericardium encloses, supports, and aids the heart in refilling during diastole by creating negative pressures in the atria and ventricles. Fluid is secreted into the space between the outside wall of the heart and the pericardium. This fluid lubricates and reduces friction during contraction and relaxation. When the heart contracts and ventricular pressure develops, pressure valves made from strong, thin, fibrous tissue are arranged to open and close in such a manner that blood or hemolymph flows in one direction out of the heart (unidirectional flow). When the heart relaxes and ventricular pressure decreases, the valves close to prevent flow reversal from the arteries, and other valves open to allow flow into the heart from the tissues.

Heart chambers fill with blood during diastole and pump blood during systole. One complete heart cycle involves one phase of relaxation and one phase of contraction. The highest pressure developed in the ventricle during contraction is called the systolic pressure, and the lowest pressure in the arteries just before the next contraction is called the diastolic pressure.

The fluid pumped by the heart can be divided into two categories: blood and hemolymph. Blood has two major components: the liquid plasma and cells. The red cells contain hemoglobin for oxygen transport, while the white cells defend against invading germs and viruses. Hemolymph, on the other hand, lacks red blood cells and has hemoglobin freely dissolved in the circulating fluid. In addition, hemolymph flows directly around each cell, whereas blood exchanges nutrients and oxygen across the capillary wall to the interstitial fluid that surrounds cells.

Heart Rate

A heart will rhythmically contract even when removed from the animal. This property is called automaticity and results from a specialized collection of cells in the upper part of the right atrium called the sinoatrial node. The sinoatrial nodal cells spontaneously generate an electrical impulse or action potential that travels throughout the heart by specialized heart muscle cells called conduction fibers. The conduction fibers provide for a uniform and effective heart contraction. Intercalated disks connect each heart muscle cell together and conduct the electrical impulse. Intercalated disks assure all of the heart muscle cells will contract together and effectively pump the blood.

Heart rate varies by animal size. Elephants have a slow, thirty-five beats per minute rate, while the smallest mammal, the shrew, has a heart rate of over six hundred beats per minute. The tiny hummingbird's heart beats at over 1,200 beats per minute while in flight.

The rate at which the sinoatrial node generates impulses can be modified by the autonomic nervous system. The sympathetic branch of the autonomic nervous system increases the heart rate, for example, during exercise or when frightened, while the parasympathetic branch slows the heart down, for example, during sleep.

Different Beats for Different Beasts

One of the simplest hearts is a rhythmically contracting muscular section in the dorsal vessel of the annelid worm, grasshopper and other arthropods. This "heart" contracts and pumps hemolymph into open-ended sinuses that distribute the hemolymph throughout the body. The hemolymph fluid does not directly return to the heart, but is drawn in through ostia or pores in the heart during the relaxation phase (open circulation).

Mollusks and octopuses have a greater diversity of heart structure, with many having two chambers. The thin-walled chamber that collects blood from venous vessels is called an auricle or atrium. The thick-walled muscular chamber that receives blood from the atrium and propels blood to the body is called a ventricle. The open circulation system in these animals delivers blood flow through several main arteries to important regions such as the kidney, head, and digestive tract.

The two-chambered fish heart has one atrium and one ventricle and represents a slight increase in complexity compared to mollusks and crustaceans. The sinus venosus collects blood at the convergence point of great veins and empties into the atrium. The bulbus arteriosus in teleosts (bony fishes), or the conus arteriosus in elasmobranchs (cartilaginous fishes), stores pressure energy from the ventricular ejection and helps to maintain a steady blood flow through the circulation during diastole.

The fish atrium receives deoxygenated blood and the ventricle pumps blood to gills, where the blood releases carbon dioxide and picks up oxygen from the water. The oxygenated blood then leaves the gills and circulates through the rest of the body. A significant amount of pressure is lost as the blood travels through the small capillaries in the gills. So, movements of the fish's body are important to help move the blood through the body and back to the heart.

Fish have a single path of circulation, from the ventricle through the gills and then to other body organs and tissues. In contrast, air-breathing animals have two separate circulations, one through the lungs (pulmonary circulation) and another to the rest of the body (systemic circulation). Lungfish (dipnoan lungfish) have the first indications of two separate circulations where oxygenated and deoxygenated blood are separated by a ridge of tissue in the ventricle. This diverts deoxygenated blood to the lungs and oxygenated blood to the rest of the body or systemic circulation.

Amphibians, Reptiles, Birds, and Mammals
Amphibians have an increased distinction between systemic and pulmonary circulations, with two separate atria. The right atrium receives deoxygenated blood from the systemic circulation, and the left atrium receives oxygenated blood from the lung or pulmonary circulation. The ventricle is partially divided into a right and left side by a muscular wall called a septum. The septum keeps the oxygenated blood coming in from the lungs separate from the deoxygenated blood returning from systemic circulation. Differential flow timings also help to separate deoxygenated and oxygenated blood. The ventricle delivers blood into a divided artery, with the pulmonary circuit leading to the lungs and skin (frogs receive some oxygen from the skin circulation on their backs), and the systemic circuit leading to all organs except the lungs. The amphibian heart is relatively weak, with spongy, poorly muscularized ventricles compared to mammals.

Most reptiles also have two separate atria, similar to amphibians; however, the sinus venosus is no longer a distinct structure and is incorporated into the right atrium. In contrast, adult crocodiles have a completely divided ventricle, thus having

Heart Valves

The heart valves provide for unidirectional blood flow and separate the atria from the ventricles and the heart from the arterial blood vessels. The valves are made of thin, strong, fibrous tissue, and each flap is called a leaflet or cusp. The valve cusps close by pressure differences across their opening. The valves that separate the atria from the ventricles are called the atrioventricular valves. In the four-chambered mammalian heart, the right atrioventricular valve is called the tricuspid valve, and the left atrioventricular valve is called the mitral or bicuspid valve. As indicated by their names, the tricuspid valve has three cusps, while the bicuspid or mitral valve has two. Another characteristic of the atrioventricular valves is their support structures, the chordae tendinae and the papillary muscles. The chordae tendinae attach to the valve cusps and, during the high pressures created by ventricular contraction, prevent the valve cusps from being forced open into the atrium. The papillary muscles are specialized heart muscles that arise from the inside of the heart and attach to the chordae tendinae. These muscles contract with each heartbeat and pull down the leaflets to keep the valve closed, and further prevent their opening into the atria.

The valves that separate the heart from the pulmonary artery and the aorta are called the semilunar valves. These valves prevent blood that has been ejected into the arteries from flowing backward into the ventricles during diastole, when the ventricular muscle is relaxed. The semilunar valves, in contrast to the atrioventricular valves, lack additional supportive structures such as the chordae tendinae and papillary muscles. Instead, their three cusps meet together and form a tight seal between the artery and ventricle.

The rhythmic "lub-dub" sounds associated with the heartbeat result from the vibration of the valve cusps and rapid blood flow through the valve just as it narrows and then closes. The first heart sound, or the "lub," is associated with the closing of the atrioventricular valves. The second heart sound, or the "dub," is associated with the closing of the semilunar valves. The term "heart murmur" refers to the hissing sound of blood squirting through a defective valve.

completely separate pulmonary and systemic circulations, similar to birds and mammals.

Birds and mammals are characterized by two completely separate atria and ventricles. The right atrium receives deoxygenated venous blood from the systemic veins, and the right ventricle pumps blood through the pulmonary circulation to pick up oxygen. The left atrium receives the oxygenated blood from the pulmonary veins, and the left ventricle pumps this blood throughout the systemic circulation (all organs except the lungs).

With the complete separation of the right and left ventricles, the pressures between the two can be different. The ventricles are highly muscularized, with the left ventricle being approximately six times thicker than the right ventricle, and this reflects the greater pressures needed to circulate blood through the systemic and pulmonary circulations. However, the volume of blood pumped by each ventricle needs to be the same, because each ventricle returns blood to the other. For example, the right ventricle pumps blood through the pulmonary circulation that returns to the left ventricle. If the right ventricle pumps a larger volume of blood than the left, blood will accumulate in the pulmonary circulation. In humans, a heart attack involving the left ventricle weakens the muscle, which decreases the volume of blood pumped. The right ventricle pumps normally and blood accumulates in the pulmonary circulation, causing breathing problems.

During flight, birds can have an increase in oxygen demand of ten- to fifteen-fold to power their flight muscles. Birds have very powerful hearts that can deliver five to seven times more blood to active muscles compared to similarly sized mammals.

—Robert C. Tyler

See also: Anatomy; Beaks and bills; Bone and cartilage; Brain; Circulatory systems of invertebrates; Circulatory systems of vertebrates; Claws, nails, and hooves; Digestive tract; Ears; Endoskeletons; Exoskeletons; Eyes; Fins and flippers; Immune system; Kidneys and other excretory structures; Lungs, gills, and tracheas; Muscles in invertebrates; Muscles in vertebrates; Nervous systems of vertebrates; Noses; Physiology; Reproductive system of female mammals; Reproductive system of male mammals; Respiratory system; Sense organs; Skin; Tails; Teeth, fangs, and tusks; Tentacles; Wings.

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HERBIVORES

Types of animal science: Anatomy, classification, ecology, reproduction
Fields of study: Anatomy, ecology, zoology

Herbivores, animals which eat only plants, include insects and other arthropods, fish, birds, and mammals. They keep plants from overgrowing and are food for carnivores or omnivores.

Principal Terms

CARNIVORE: any animal that eats only the flesh of other animals

GESTATION: the term of pregnancy

METAMORPHOSIS: insect development into adults, passing through two or more dissimilar growth forms

RUMINANT: a herbivore that chews and swallows plants, which enter its stomach for partial digestion, are regurgitated, chewed again, and reenter the stomach for more digestion

Herbivores are animals whose diets consist entirely of plants. They have two ecological functions. First, they eat plants and keep them from overgrowing. Second, they are food for carnivores, which subsist almost entirely upon their flesh, and omnivores, which eat both plants and animals. Herbivores live on land or in oceans, lakes, and rivers. They can be insects, other arthropods, fish, birds, or mammals.

Wild Herbivores

Insects are the largest animal class, with approximately one million species. Fossils show their emergence 400 million years ago. Insects occur worldwide, from pole to pole, on land and in fresh or salt water. They are the best developed invertebrates, except for some mollusks. They mature by metamorphosis, passing through at least two dissimilar stages before adulthood. Metamorphosis can take up to twenty years or may be complete a week after an egg is laid.

Many insects are herbivores. Some feed on many different plants; others depend on one plant variety or a specific plant portion, such as leaves or stems. Relationships between insects and the plants they eat are frequently necessary for plant growth and reproduction. Among the insect herbivores are grasshoppers and social insects such as bees.

Artiodactyls are hoofed mammals, including cattle, pigs, goats, giraffes, deer, antelope, and hippopotamuses. Most are native to Africa, but many also live in the Americas, Europe, and Asia. Artiodactyls walk on two toes. Their ancestors had five, but evolution removed the first toe and the second and fifth toes are vestigial. Each support toe—the third and fourth—ends in a hoof. The hippopotamus, unique among artiodactyls, stands on four toes of equal size and width.

Artiodactyls are herbivores, lacking upper incisor and canine teeth, but pads in upper jaws help the lower teeth grind food. Many are ruminants, such as antelope, cattle, deer, goats, and giraffes. They chew and swallow vegetation, which enters the stomach for partial digestion, is regurgitated, chewed again, and reenters the stomach for more digestion. This maximizes nutrient intake from food.

Deer are hoofed ruminants whose males have solid, bony, branching antlers that are shed and regrown yearly. The deer family, approximately 40 species, occurs in Asia, Europe, the Americas, and North Africa. Deer live in woods, prairies, swamps, mountains, and tundra. Their size ranges from the seven-foot-tall moose to the one-

Buffalo, like all herbivores, spend much of their time grazing. The low nutrient content of grass requires most herbivores to opt for quantity over quality in their digestive strategy. (PhotoDisc)

foot-tall pudu. Deer first appear in the fossil record ten million years ago. Deer eat the twigs, leaves, bark, and buds of bushes and saplings, and grasses. Females have one or two offspring after ten-month pregnancies. Common species are the white-tailed and mule deer in the United States; wapiti in the United States, Canada, Europe, and Asia; moose in North America and Europe; and reindeer in Russia, Finland, and Alaska.

Antelope, a group of approximately 150 ruminant species, have permanent, hollow horns in both sexes. Most are African, although some are European or Asian. They eat grass, twigs, buds, leaves, and bark. There are no true antelope in the United States, where their closest relatives are pronghorns and Rocky Mountain goats (goat-antelope with both goat and antelope anatomic features). The smallest antelope, the dik-dik, is rabbit-sized. Elands, the largest antelope, are ox-sized. Unlike deer horns, antelope horns are unbranched. Most antelope run rather than fighting, and are all swift. Antelope live on plains, marshes, deserts, and forests. Females birth one or two offspring per pregnancy. Impala and gazelles, such as the springbok, are found in Africa. In Asia, Siberian saigas and goat antelope (takin) inhabit mountain ranges. Chamois goat antelope live in Europe's Alps.

Giraffes and hippos are unusual artiodactyls. Giraffes inhabit dry, tree-scattered land south of the Sahara. Their unusual features are their very long legs and necks. Males are over sixteen feet tall, including the neck. Both sexes have short, skin-covered horns. Long necks, flexible tongues, and upper lips pull leaves—their main food—from trees. Giraffes have brown blotches on buff coats and blend with tree shadows. They live for up to twenty years. They have keen senses of smell, hearing, and sight, and can run thirty-five miles per hour. Due to their two-ton weights, they live on hard ground. Giraffes rarely graze, and go for months without drinking, getting most of their water from the leaves they eat, because it is difficult for them to reach the ground or the surface of a river with their mouths. Females have one offspring after a fifteen-month gestation.

The unusual feature of hippos is that they walk on all four toes of each foot. Perhaps this is because they weigh three to four tons. Hippos are short-legged, with large heads, small eyes, small ears, and nostrils that close underwater. Huge hippo mouths hold long, sharp incisors and canines in both jaws. Hippos once lived throughout Africa. Now they are rarer, due to poaching for ivory. A hippo can be fifteen feet long and five feet high at the shoulder. Semiaquatic, hippos spend most daylight hours nearly submerged, eating aquatic plants. At night they eat land plants. Females bear one offspring at a time.

Elephants

Herbivorous elephants, the largest land animals, eat three hundred pounds per day of grass, fruits, leaves, flowers, roots, twigs, branches, and bark. Elephants are African or Asian. African males reach twenty-five feet long, eleven feet tall, and weigh seven tons. Females are shorter and half the weight of males. Asian elephants exhibit anatomic differences, including smaller ears, tusks, and overall size.

Elephants lift trees with their trunks and have long been domesticated to carry things. Elephants also grab food from the ground and trees via the ends of their trunks, with nostrils and grasping lips. They also suck water into their trunks and squirt it into their mouths or on their bodies. The showers keep them cool. Their ivory tusks, several feet long, are used to dig roots, peel edible tree bark, and fight enemies and male competitors. The use of tusk ivory in jewelry leads poachers to kill males. Elephant ears have keen hearing and act as cooling fans.

Adult males live alone. Females and young form herds, led by a sagacious female. Herd members breed with visiting males, protect each other, and raise young. Gestation, two years, produces one offspring, which nurses for three years. Elephants can live for sixty years in the wild and eighty years in captivity, but only 10 percent of wild elephants reach age forty.

Aquatic Herbivores

Fish are aquatic vertebrates, having gills, scales and fins. They include rays, lampreys, sharks, lungfish, and bony fishes. The earliest vertebrates, 500 million years ago, were fishes. They comprise over 50 percent of all vertebrates and have several propulsive fins: dorsal fins along the central back; caudal fins at tail ends; and paired pectoral and pelvic fins on sides and belly. Fish inhabit lakes, oceans, and rivers, even in Arctic and Antarctic areas. Most marine fish are tropical. The greatest diversity of freshwater species is found in African and rain-forest streams.

Fish vary in length from half an inch to fifty feet, and some weigh seventy-five tons. Many, including giant whale sharks, are herbivores. Fish respiration uses gills, through which blood circulates. When water is taken in and expelled, oxygen enters the blood via the gills and carbon dioxide leaves. Fishes reproduce by laying eggs that are fertilized outside the body, or by internal fertilization and development with the birth of well-developed young.

Domesticated Artiodactyls

Bovids are domesticated artiodactyls. Most have horns and hooves. Bovid horns are spiraled, straight, tall, or L-shaped from the sides of the head. All have hooves to help them grip the ground. Most are ruminants. Their breeding habits are similar. Males fight over females and the strongest wins. Gestation, four to eleven months, yields two to three young. The young nurse for several months and then join the herd. Young males leave female herds to live with other bachelors.

Cattle are domesticated bovids, raised for meat, milk, and leather. Modern cattle come from European, African, and Asian imports. Breeding modern cattle began in Europe in the mid-1800's.

Today, three hundred breeds exist. Dairy cattle, such as Holsteins, make copious milk. Beef cattle, such as Angus, were bred to yield meat. As of 1990, about 1.3 billion cattle were found worldwide.

Sheep are also artiodactyls. Wild sheep occur in some places, such as the North American bighorn and Mediterranean mouflon. Sheep were domesticated eleven thousand years ago from mouflon. Today, domesticated sheep have a world population of approximately 1.3 billion and inhabit most countries, being more widely distributed than any other domesticated animal. These ruminants have paired, hollow, permanent horns. Male horns are massive spirals; those of females are smaller. Adult body length is five feet and weights are 250 to 450 pounds. Females birth two or three young after five-month gestations. Sheep can live for up to twenty years.

Sheep provide wool, meat, and milk. About eight hundred domesticated breeds exist, in environments from deserts to the tropics. Those bred for wool, half the world's sheep, live in semiarid areas, are medium sized, and produce fine wool. Most are in Australia, New Zealand, and South America. Mutton-type sheep, 15 percent of the world sheep population, produce meat. Fat-tailed sheep, 25 percent of the sheep population, produce milk. In 1990, the five leading sheep countries were Australia, China, New Zealand, India, and Turkey. The United States raised less than 1 percent of the world total.

Goats are ruminants, closely related to sheep, but have shorter tails, different horn shape, and bearded males. They eat grass, branches, and leaves and breed from October to December. A five-month gestation yields two offspring. Numerous goat breeds are domesticated worldwide for meat and milk, and as pets and burden carriers. Domesticated Angora goats yield silky mohair. Goat milk is as nutritious as cow milk and used in cheese-making.

It is clear that wild herbivores are ecologically important to food chains. This is because they eat plants, preventing their overgrowth, and they are eaten by carnivores and omnivores. Domesticated herbivores—cattle, sheep and goats, used for human sustenance—account for three to four billion living creatures. Future production of better strains of domesticated herbivores via recombinant deoxyribonucleic acid (DNA) research may cut the numbers of such animals killed to meet human needs. Appropriate species conservation should maintain the present balance of nature and sustain the number of wild herbivore species living on earth.

—Sanford S. Singer

Horses, Donkeys, and Zebras

The horse, donkey, and zebra (HDZ) family lives in habitats from grasslands to deserts. Wild specimens inhabit East Africa and the Near East to Mongolia. Domesticated horses and donkeys are used for food, meat, leather, drayage, and racing worldwide. Zebras are too savage to domesticate. All HDZ have long heads and necks, slender legs, and manes on their necks, as well as long tails to swat insects. They have good wide-angle day and night vision. Their sense of smell is also excellent. The smallest family members are African wild donkeys, 4.0 feet tall, 6.5 feet long, with 1.5-foot tails, weighing five hundred pounds. The largest are Grevy's zebras, 5 feet tall at the shoulder, 9 feet long, with 1.5-foot tails, and weights up to nine hundred pounds.

Zebras have black or brown and white vertically striped coats. All HDZ family members are herbivores. Donkeys eat bark, leaves, buds, fruits, and roots. Horses and zebras mostly eat grasses, and some bark, leaves, buds, and fruits. Wild HDZ spend their waking hours foraging for and eating food. When attacked, they bite, kick, or run off at speeds up to forty miles per hour.

Wild donkeys and horses live in herds with a male leader and female mates. Young stay in a herd until two years old for females or four years old for males. Males join bachelor groups until winning a herd. Females join another herd. Donkeys usually live alone. Most HDZ mate in spring and summer. A twelve-month gestation yields one offspring, which nurses for a year.

See also: American pronghorns; Antelope; *Apatosaurus*; Beavers; *Brachiosaurus*; Camels; Carnivores; Cattle, buffalo, and bison; Coevolution; Deer; Digestion; Digestive tract; Donkeys and mules; Ecosystems; Elephants; Elk; Food chains and food webs; Giraffes; Goats; Gophers; Hadrosaurs; Herds; Hippopotamuses; Horns and antlers; Horses and zebras; Hyraxes; Ingestion; Kangaroos; Koalas; Mammoths; Manatees; Metabolic rates; Mice and rats; Moles; Moose; Nutrient requirements; Omnivores; Pandas; Pigs and hogs; Plant and animal interactions; Platypuses; Porcupines; Predation; Rabbits, hares, and pikas; Reindeer; Rhinoceroses; Rodents; Ruminants; Sauropods; Sheep; Squirrels; Stegosaurs; Teeth, fangs, and tusks; *Triceratops*; Ungulates.

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HERDS

Types of animal science: Behavior, ecology
Fields of study: Ecology, ethology, population biology, wildlife ecology, zoology

Herds are associations of animals, usually the same species, that keep, feed, or move together. Generally, the use of the word "herd" is reserved for large, terrestrial animals.

Principal Terms

CARNIVORES: animals that eat the flesh of other animals

DILUTION EFFECTS: the reduction in per capita probability of death from a predator due to the presence of other group members

HERBIVORES: animals that eat plants and show specializations of teeth and digestive tracts to do so

PHALANGES: the free toes of the foot; some can be modified to bear claws, hoofs, or nails

SUBUNGULATES: nonhoofed mammals that support their weight on more than the terminal phalanges; some, such as elephants and hyraxes, have pads under their metatarsals, and others, such as the sirenians, have forelimbs modified into flippers

UNGULATES: hoofed mammals that support their weight only on the hoof-clad terminal phalanges and have teeth specialized for clipping vegetation

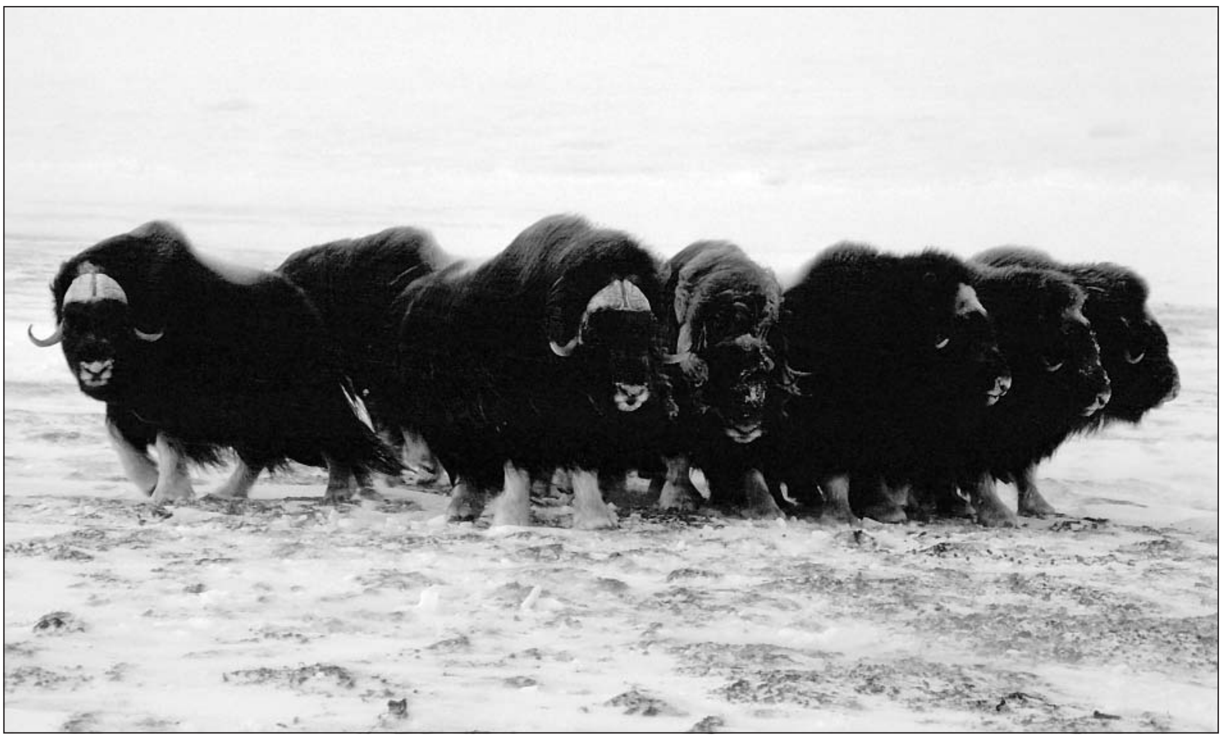
Herding in animals serves several purposes, most commonly exploitation of food resources and reduction of the probability of predation via dilution effects. When food is spaced irregularly into patches and cannot be easily defended, individuals of a particular species will form a herd, simply as a result of coming together to feed on the same resource in the same location. Sizable grazing mammals are well known for forming some of the largest and most dense herds seen. The most familiar of these include African ungulates (wildebeests, zebra, gazelle, wild horses, rhinos, hippopotami) and subungulates (elephants, sirenians, the extinct mastadons); bison, buffalo, caribou, elk, moose, and deer in North America; kangaroo in Australia; and deer, elk, moose, antelope, wild horses, sheep, goats, pigs, boars, and peccaries in Eurasia. In addition to large mammalian herbivores, small grazers that exploit vegetation in herds include marine and freshwater snails, tortoises and turtles, geese, and hyrax.

Those grazers that feed indiscriminately tend to form herds that vary in density with season and density of foliage. Furthermore, these herds tend to vary their densities and vegetation utilization patterns with the type of vegetation exploited and its productivity potential. In seasons or areas where rainfall is common, herds tend to congregate together and exploit small patches of grass, which they clip into grazing lawns. Maintaining grazing lawns increases the productivity of the plants via increased nitrogen content and increased digestibility in freshwater, marine, and terrestrial environments. When rainfall is scarce, the herds disperse over vast areas, which allows some grasses to grow into tall meadows. The benefits to individuals in a herd from grazing a larger area and creating a grazed lawn are greater than those to a lone individual that would only be able to graze a small patch of grass and that would, presumably, be at greater risk of predation than one individual surrounded by many others. Furthermore, if the lone individual were subject to a greater risk of predation, there would be less likelihood of it being able to return to the same patch over and over again to keep it as a grazed lawn. Thus, by grouping, an individual benefits twice: once by the gain in nutrition from a grazed lawn and again from the dilution effect, where the risk of predation is diluted by the number of members forming the group.

Herding to Avoid Predation

The large herbivores that most commonly form herds are clearly visible to predators. Predation risk reduction via the dilution effect or the selfish herd effect is the other main benefit of herding. In the dilution effect, the probability of a particular individual being killed or injured is reduced by the presence of other group members that might be attacked first. In other words, there is safety in numbers. Individuals in a group may also benefit by putting other animals between themselves and the predator (the selfish herd effect). Grouping thus provides the opportunity to decrease the area of danger around each individual. If individuals within the group are acting in a selfish herd manner, the groups formed tend to be tightly clumped, as all individuals attempt to put other individuals on all sides around them and move into a central location. Finally, formation of a herd can make it more difficult for a predator to select one specific individual from the crowd for attack, or once an attack is initiated and herd members scatter during flight, can make it difficult for the predator to decide who it should chase.

Herd members also benefit by a reduction in the time necessary to scan for predators while foraging. An individual foraging has to split its time between consuming as much food as possible and avoiding becoming another animal's meal. Thus, a solitary individual has to be much more vigilant than does a member of a group who can rely on many other eyes and thus reduce its own scan



Musk oxen form a tightly packed clump characteristic of the selfish herd effect, where animals try to put as many others as possible between themselves and potential predators. (Corbis)

Dinosaur Herds

Dinosaur fossils have been known for over a century and yet little is known about their daily life when they were alive. Paleontologists, however, argue that discoveries made since the late 1970's indicate that some, if not many, dinosaurs might have been social organisms. Fossil beds of duck-billed dinosaurs not only revealed scooped-out, mud-filled nests with as many as fifteen offspring, but also showed that the nests were closely spaced, strongly suggesting communal nesting grounds, as are seen in birds. Within the nests were offspring of varying ages, suggestive of parental care.

Dinosaur footprints are also used to infer that many species grouped together in herds, some of which may have migrated long distances in what are known as trackways. Trackways preserve the footprints of a number of individuals in mud, which was later fossilized. These trackways show dozens of animals traveling in the same direction at roughly the same speed. Such trackways have been found for *Eubontes* (a Jurassic dinosaur), *Triceratops*, *Iguanodon*, and others.

The final piece of evidence that paleontologists use to infer herding in dinosaurs is the presence of horns and superfluous appendages. Observations of extant herding species indicate that males most often display horns, tusks, or other features that are used in male dominance fights over sexually receptive females within the herd. Paleontologists use these modern-day rituals to hypothesize that dinosaurs may have used their horns in a similar fashion.

rate. Because of this advantage and the advantage in the reduction of the rate of per capita predation, even herds that simply congregate around a resource benefit greatly.

Migratory and Social Herds

Many large herbivores migrate in response to food availability in different seasons. Red deer, caribou, wildebeest, mountain goats, northern fur seals, and humpback whales are examples of animals that all migrate in response to seasonal changes in rainfall or food abundance. Some of these migrations are over incredible distances: Wildebeests travel about six hundred miles; northern fur seals and humpbacks can travel three to four thousand miles. During these migrations, small herds unite with bigger herds to form even larger herds. While terrestrial herbivores migrate to follow food, some marine mammals, such as gray whales and humpbacks, migrate south to calf and breed (but do not feed, living off food reserves instead) and migrate north to abundant feeding grounds.

Some herding species display social organization beyond that expected by mere association. This social organization tends to break a herd into smaller units (matrilineal groups, harems, or small territories controlled by one or several males) that are clustered within the entire herd. These species include the horses, zebras, pronghorn sheep, walruses, sea lions, seals, and elephants. Horse and zebra herds are composed of a number of small groups of females and their foals. These individual groups are overseen by a single stallion; young males leave these groups to form bachelor herds. Group members distinguish each other via a "corporate smell." Stallions generally control a group of females and will fight with challenging stallions in elaborate rearing displays. If a stallion is challenged and loses after inseminating the females in his group, the challenger will mount the females and rape them to induce them to abort. They will then come into estrus quickly and he will remate them. Stallions will groom females to cement their relationship with them; likewise, mares will groom their foals for the same purpose. Male impalas and gazelle maintain harems during the breeding season; male wildebeest do the same, but if the herd is large, the defense of the harem may be accomplished by several males, rather than one. Male elk are divided into four main categories: Primary bulls are the first to establish harems, but as they become exhausted from challenges and herding and mating females, all the while not eating, the harems are taken over by secondary bulls. Once the secondary bulls become exhausted, tertiary bulls take over. The fourth category, opportunistic bulls, only mate with females by chance.

Pinniped herds (sea lions, seals, and walruses) form breeding herds, where males establish territories. In some groups, females are herded together in harems to remain in the male's territory; in other groups, females are free to move from territory to territory. Males vigorously defend their territories against intruding males.

Sirenians, the dugong and manatee, have proved difficult to study, but dugongs often form large herds for unknown reasons. During mating, a series of males follows a receptive female to form a cluster of up to twenty animals. Males then initiate fighting to determine who will mount the female. Following mating, the main social unit is the female and her calf. A similar situation exists in the manatee, with females and their calves being the main social unit and females in estrus becoming the focus of a mating herd of males.

Herding serves important purposes for animals: utilization of a common resource (usually food) and predator reduction via a safety-in-numbers principle. Herds can also be formed during migrations or for breeding purposes. While many herds are simply loose associations of animals, some are more highly organized into a number of social units such as harems or matrilineal groups.

—Kari L. Lavalli

See also: Communities; Competition; Defense mechanisms; Ecological niches; Groups; Hierarchies; Mammalian social systems; Migration; Offspring care; Population analysis; Predation; Reproductive strategies.

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HERMAPHRODITES

Types of animal science: Anatomy, development, physiology, reproduction
Fields of study: Developmental biology, ethology, invertebrate biology, marine biology, neurobiology, reproduction science, zoology

Hermaphrodites are individuals having both male and female reproductive organs. Depending on the species, individuals may be simultaneously both male and female, or may change from one sex to the other.

Principal Terms

GONAD: the organ that produces reproductive cells (sperm or eggs)
PROTANDRY: the condition of starting out male with the potential to become female
PROTOGYNY: the condition of starting out female with the potential to become male
SEQUENTIAL HERMAPHRODITE: species or individual with the potential to change from one sex to the other
SEX-LIMITED TRAITS: features that are only expressed in one sex
SEXUAL DIMORPHISM: the existence of anatomical, physiological, and behavioral differences between the two sexes of a species
SIMULTANEOUS HERMAPHRODITISM: the condition of being simultaneously male and female

In most species, reproduction involves sex—that is, the joining of genetic material from two individuals to create new, genetically unique offspring. In sexually reproducing species, females are those individuals which produce relatively large sex cells that are full of nutrients (eggs), and males are those individuals which produce relatively small sex cells that have little or no nutrients, but which can be produced in much greater numbers (sperm). Generally there are other differences between the sexes as well—differences in hormones, anatomy, body shape, size, color, and behavior. Such distinguishing features are referred to as sex-limited traits because they appear in only one sex; collectively, they result in sexual dimorphism—literally the two sexual forms of a single species.

Whether an individual animal develops into a male or a female depends on which genes get turned on early in development. In mammals, genes for maleness get turned on in individuals with an X and a Y chromosome, while genes for femaleness get turned on in individuals with two X chromosomes. In other animals, sex determination may depend on other factors. For example, in many reptiles, development into a male or a female depends upon the temperature of the embryo as it develops in its egg.

Hermaphrodites are individuals that have both male and female reproductive organs—that is, they have both ovaries to produce eggs and testes to produce sperm. In most animals, hermaphroditism is a result of abnormal development and is extremely rare. In some species, however, hermaphroditism is normal.

Simultaneous Versus Sequential Hermaphroditism

Depending on the species, hermaphroditism can be found in either simultaneous or sequential form. In species with simultaneous hermaphroditism, individuals are simultaneously both male and female; each adult has the ability to produce both sperm and eggs. Depending on the species, a single reproductive encounter between simultaneous hermaphrodites may involve both partners exchanging sperm and eggs (for example, earthworms) or may involve the partners taking turns as male and female (for example, some coral reef fishes).

On the other hand, individuals of species with sequential hermaphroditism start life as either male or female, but have the ability to change sex at some later point. In protandrous species, individuals start out as male and have the potential to later change to female. These are typically species which require large body bulk before they can produce eggs, so individuals start out as male and change to female only if they get old enough and large enough to make eggs. In protogynous species, individuals start out as female and have the potential to later change to male. These are typically species in which males must defend a harem or a territory in order to mate, so individuals start out as female and change to male only if they get large enough to fight and win.

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Triggers for Sex Change

In both protandrous and protogynous species, the trigger for sex change may relate not only to body size but also to the social structure of the individual's community. For example, a large female of a protogynous species may not change to male if there is an even bigger male present who would clearly win every fight. On the other hand, a relatively small female might change to male if she is the biggest female around and the larger local males suddenly died or disappeared. Thus, body size is a relative, not an absolute trigger for sex change, and in a very few species individuals can revert back to their original sex if social circumstances change again.

When a sequential hermaphrodite changes sex, it changes not only its reproductive organ or gonad, but also all the other sexually dimorphic aspects of its anatomy, physiology, and behavior. Hormones and behavior are the first things to change; then, over a period of time, the hormonal changes induce changes in the gonad and other tissues, including the brain. As a hermaphroditic fish, for example, switches from one sex to another, it may change the size and shape of its fins, its color, its aggression level, and its sexual preferences and rituals. These miraculous changes provide visible proof of the (generally silent) presence in both sexes of sex-limited genes for both male and female attributes.

—*Linda Mealey*

See also: Asexual reproduction; Breeding programs; Cleavage, gastrulation, and neurulation; Cloning of extinct or endangered species; Copulation; Courtship; Determination and differentiation; Development: Evolutionary perspective; Estrus; Fertilization; Gametogenesis; Hydrostatic skeletons; Mating; Parthenogenesis; Pregnancy and prenatal development; Reproduction; Reproductive strategies; Reproductive system of female mammals; Reproductive system of male mammals; Sexual development.

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HETEROCHRONY

Type of animal science: Evolution
Fields of study: Development, evolutionary science, physiology

Neoteny is a heterochronic effect in which descendants grow more slowly than their ancestors and thus appear to be juveniles relative to their ancestors. It is one of several different heterochronic phenomena that can involve differential rates and duration of growth for ancestral and descendant species.

Principal Terms

ACCELERATION: a faster rate of growth during ontogeny that causes a particular characteristic to appear earlier in a descendant ontogeny than it did in the ancestral ontogeny

HETEROCHRONY: any phenomenon in which there is a difference between the ancestral and descendant rate or timing of development

HYPERMORPHOSIS: a phenomenon in which the rate and initiation of growth in the descendant are the same as in the ancestor but the cessation of development takes place later

ONTOGENY: the life history of an individual, including both its embryonic and postnatal development

PHYLOGENY: the history of a lineage of organisms, often illustrated by analogy to the branches of a tree

POSTDISPLACEMENT: a form of paedomorphosis in which the initiation of growth in a descendant occurs later than in the ancestor, ensues at the ancestral rate, and ceases at the ancestral point

PREDISPLACEMENT: a form of peramorphosis in which the initiation of growth in a descendant occurs earlier than in the ancestor, ensues at the ancestral rate, and ceases at the ancestral point

Heterochronic phenomena are processes by which changes in the timing, rate, and duration of an ancestral pattern of growth and development result in changes in descendants. One of the six types of heterochrony is neoteny, in which a descendant's slower rate of development causes it to be an immature or truncated expression of its ancestor.

Paedomorphosis and Peramorphosis

The six types of heterochrony fall into two general patterns: paedomorphosis and peramorphosis. In these patterns, ancestral and descendant ontogenetic trajectories are compared. If the descendant morphology exceeds or surpasses the ancestral morphology, this is called peramorphosis. There are three types of peramorphosis: acceleration, hypermorphosis, and predisplacement. In acceleration, the beginning and end of development occurs at the same time in both the ancestral and descendant ontogenetic trajectories. The rate of development is faster in the descendant, however, so its morphology transcends that of the ancestor. In hypermorphosis, development begins at the same time and ensues at the same rate in both the ancestor and descendant; however, the descendant continues development for a longer interval—that is, it stops growing later. In predisplacement, the descendant begins development earlier than the ancestor, and the rate of development and the time at which growth ceases remain the same. The result of both predisplacement and hypermorphosis is a longer interval of growth. In acceleration, however, the interval of growth is the same in both the ancestor and its descendant; only the rate of growth has changed.

If a descendant morphology is a truncated or an abbreviated version of ancestral morphology, this is called paedomorphosis. There are also three types of paedomorphosis: neoteny, progenesis, and postdisplacement. In progenesis, descendant development begins and proceeds at the ancestral rate but stops sooner. In postdisplacement, the ancestral rate of development and the time of cessation are the same in the descendant; however, development begins later. Thus, for postdisplacement and progenesis, the time interval over which the descendant morphology develops is truncated when compared to the ancestral ontogenetic trajectory. In contrast, neoteny is characterized by a slower descendant rate of development but an unchanged time interval for growth and development.

The Contributions of Von Baer and Haeckel

Two scientists of the nineteenth century were especially important contributors to the early ideas concerning development and its impact on evolutionary change. Karl Ernst von Baer suggested that the features that appear early in ontogeny are those that are shared by the most organisms, whereas the features that appear later in ontogeny are those that are shared by successively smaller groups of organisms. This maxim has been called von Baer's law. Ernst Heinrich Haeckel held a different, more restricted, concept of ontogeny. He popularized the phrase "ontogeny recapitulates phylogeny." By this he meant that the ontogenetic or developmental phases through which an organism passes can be interpreted as being equal to the sequence of events that occurred during the evolutionary history of that particular organism. Haeckel's narrower concept of the relationship between ontogeny and phylogeny has been rejected by modern biologists in favor of von Baer's law.

Von Baer and Haeckel laid the foundation for ideas of heterochrony, but it was not until the later twentieth century that the subject of heterochrony was once again an area of active research. An important book by Stephen Jay Gould entitled *Ontogeny and Phylogeny* (1977) was instrumental in reopening the discussion initiated a century earlier. One of the most important things accomplished in Gould's book was the distinction that was made between different types of paedomorphosis. Frequently, in earlier works dealing with species with a juvenile appearance, no distinction was made among neoteny, postdisplacement, and progenesis: All three were discussed as neoteny. This confusion prevented generalization.

Organisms for which neoteny is used as an explanation for their origins include some salamanders of the family Ambystomatidae and the primates of the family Hominidae (the family that includes humans). In the latter case, *Homo sapiens* is considered a juvenilized anthropoid; the reduction in the amount of hair and the longer period of infancy can be used as evidence for this supposition.

Studying Heterochronic Change

Two kinds of information are necessary for documenting heterochronic processes of change. Because frequent reference must be made to ancestral and descendant ontogenetic trajectories, it is of crucial importance to have available, for the organisms under study, an estimate of their phylogenetic, or evolutionary, history. This is not an easily obtained body of evidence, and much scientific debate has occurred over the procedures that should be followed in seeking to unravel phylogenetic history. Some researchers even doubted that it would ever be possible to obtain evidence sufficient for the task. Nevertheless, some small consensus has emerged. This is especially gratifying for students of heterochrony, who depend so much upon the phylogenies that anchor their conclusions.

It is also necessary to document ontogeny, development, and/or growth in either a quantitative or qualitative sense. The quantitative measurement of growth is relatively straightforward. Measurements are taken from specimens of known ages. It is most desirable that measurements be taken from the same individual specimens throughout their ontogenies. This is not always possible, nor is it always possible to obtain accurate ages for the available specimens. Another problem is that the ages of the specimens of different species might not be directly comparable. These are among the factors that complicate the otherwise simple process of measuring the sizes and shapes of specimens over time—that is, measuring in various places along an ontogenetic trajectory. Assuming that appropriate measurements have been gathered, a variety of statistical procedures can then be applied to the accumulated data. These procedures include some rather sophisticated multivariate statistics that have only become feasible with the advent of computers.

The qualitative documentation of an ontogenetic trajectory suffers from many of the same sources of complication. In this approach, ontogenies are conceptualized as a series of discrete stages, phases, events, or appearances. These sequences are determined for the organisms under examination, and the stages that bear close resemblance are sometimes considered identical. The problem with this view is that it conceives of ontogeny as being composed of static sequences; this is a largely Haeckelian view. In fact, ontogenies are best viewed as dynamic, which makes it conceptually difficult to compare isolated parts of an indivisible ontogeny.

An unanswered question of evolutionary biology concerns the processes by which new morphologies and new organisms originate. Although many promising inroads have been made, none has been more hopeful than the idea of heterochrony. The conjecture is that small shifts in the timing, rate, and duration of ontogeny contribute to the appearance of new structures or perhaps even new organisms. This approach has so far proved both effective and promising, but it has not yet been applied to a sufficient range of organisms. Thus, it is not yet possible to tell whether heterochrony will prove to be a universally applicable approach to the study of the origin of new structures and species.

—Charles R. Crumly

See also: Convergent and divergent evolution; Development: Evolutionary perspective; Evolution: Animal life; Gene flow; Growth; Metamorphosis; Morphogenesis; Phylogeny; Population genetics.

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HIBERNATION

Type of animal science: Behavior
Fields of study: Biochemistry, genetics, zoology

Hibernation is a dormancy into which some animals enter as winter approaches, remaining in a state of suspended animation until the weather moderates.

Principal Terms

ANESTHESIOLOGIST: a physician who administers anesthetics during surgical procedures

CELSIUS: a scale for measuring temperature in which freezing is zero degrees and boiling is one hundred degrees, abbreviated C

FAHRENHEIT: a scale for measuring temperature in which freezing is 32 degrees and boiling is 212 degrees, abbreviated F

HIBERNACULA: the winter habitats of brown bats

SYNCHRONIZATION: causing events to occur simultaneously

VERTEBRATES: animals with brains and spinal cords

As winter approaches, some animals enter a barely living state. Whereas the body temperature of warm-blooded animals is generally about 37 degrees Celsius (98.6 degrees Fahrenheit), some of the larger vertebrates, such as bears, enter a restful state for several of the colder months, during which body temperatures sink to about 30 degrees Celsius (88 degrees Fahrenheit).

In another class of smaller animals, notably the brown bat, the body temperature hovers just above freezing, usually between 1 and 3 degrees Celsius (34 to 38 degrees Fahrenheit). At these levels, the animal is barely alive. It does not bleed when cut. It breathes infrequently. Its heartbeat drops dramatically.

Groundhogs and chipmunks are found in areas where there may be sporadic periods of warm weather during the winter, at which times these animals awaken from their torpor temporarily. Their body temperatures, which will have sunk to about 10 degrees Celsius (50 degrees Fahrenheit), increase as the temperature outside their underground lairs rises. When the temperature sinks again, these animals resume their sleep.

Animals such as bears, brown bats, some rodents, hummingbirds, whippoorwills, chipmunks, ground squirrels, skunks, and marmots have built-in mechanisms that prevent their temperatures from sinking below the levels their systems can withstand. When their temperatures approach life-threatening levels, they begin to shiver, thereby maintaining or raising their temperatures without wakening them from their slumbers.

The Why and How of Hibernation

During hibernation the body shuts down and requires little energy. All of its systems, including endocrine, circulation, respiration, and elimination, are reduced to the barest essentials necessary to maintain life. Animals living in this state require almost no nutrition. They draw what nourishment they need from stores of fat that they accumulate by eating a great deal immediately before hibernating. They conserve their body heat by rolling themselves into balls.

The mechanisms that trigger hibernation mystify scientists. Some sort of internal clock, probably responding to light and temperature, clicks in at given times, determining the beginning of hibernation and its extent. This mechanism is far from precise. Some animals that have been maintained from year to year under consistent conditions may lose their synchronization, entering hibernation possibly in spring or summer.

The Light Sleepers

On hearing the word "hibernation," people think immediately of bears, who enter periods of dormancy as winter approaches. By the time they enter their lair for their winter's sleep, they have gained considerable weight and have added to their bodies layers of fat to provide them with the nutritional reserves they will require to survive the next three or four months.

During this period of dormancy, the bear's temperature drops less than 10 degrees Fahrenheit. Some scientists resist designating as hibernation the period during which such animals as bears, chipmunks, raccoons, and skunks sleep beneath ground. This period is sometimes called "winter lethargy."

The Hibernation Inducement Trigger

Scientists studying hibernation note that the hibernation inducement trigger (HIT) springs into action in three specific circumstances, occurring singly or in combination: when the days grow shorter in autumn, restricting the amount of light to which organisms are subjected; when temperatures drop, which often happens when the days grow shorter; and when food becomes scarce.

Questions about how HIT works have increased rather than decreased in recent years. Blood extracted from squirrels during hibernation that is preserved and injected into other squirrels in the spring, when hibernation would normally be ending, triggers an offseason onset of hibernation in the second group of squirrels. This experiment points to the existence of some sort of biochemical basis for hibernation, although its precise workings are little understood. Although the results are known, the causes remain shrouded in mystery.

Animals whose body temperatures do not drop dramatically during their dormant period may waken from their sleep several times during the winter. When the weather moderates, they often leave their lairs and scurry about seeking food. When cold weather resumes, they return to their lairs to continue their slumbers.

The eastern chipmunk is among the light sleepers. Unlike bears, it does not accumulate excess body fat to see it through its three or four dormant months. Rather, it stores food in its burrow as winter approaches, building its nest on top of the food it has gathered. It wakens frequently in winter to eat and to defecate in a section of the burrow away from the food supply.

The male chipmunk usually ends its sleep late in February. Leaving the burrow, it first seeks food and water, then looks for a mate, who produces from two to five babies one month after mating.

Skunks are also among the light sleepers. When the outside temperature approaches 10 degrees Celsius (50 degrees Fahrenheit), skunks retreat to their dens for the winter. They may take over an abandoned woodchuck's nest, but often they build their own dens below the frost line, at depths of between six and twelve feet. They line the den with dried leaves and grasses, creating a cozy nest. Although skunks are solitary in summer, they often live in groups during the winter, huddling together to keep warm.

Raccoons enter a dormant state in cold climates but are active throughout the year in milder ones, undergoing fewer body changes in winter than other true hibernators. Their body temperature drops minimally. Their heartbeat, while decreasing slightly, remains close to normal. Raccoons sleep as long as cold weather persists. They stir during warm spells but sleep again when the temperature drops.

In winter, raccoons, usually solitary dwellers, change that pattern and share their dens with other raccoons for their body warmth. Regardless of the weather, male raccoons become active late in January, which is mating season. After mating, they return to their dens for more sleep before spring.

During hibernation, the body temperature of ground squirrels drops approximately 50 degrees Fahrenheit, to a point only a few degrees above freezing. (Corbis)

The Heavy Sleepers

Some species undergo significant changes during dormancy that qualify them as true hibernators. In these animals, heartbeat, temperature, and respiration drop so dramatically during winter that life is barely sustained. These heavy sleepers do not respond to temporary increases in outside temperature, rather sleeping soundly through the months of their hibernation.

The most renowned of the heavy sleepers is the woodchuck, also known as the groundhog. People watch groundhogs' burrows every February 2 to determine whether the groundhog will see his shadow. If he does, legend has it, he will return to his den and there will be six more months of winter. The groundhog actually leaves its burrow in February seeking a mate.

Woodchucks accumulate as much body fat as possible before hibernation, sometimes achieving a weight of ten pounds. During their deep sleep, they take nourishment from their layers of fat, although they may waken at times to nibble seeds stored in their dens. By the time they emerge from hibernation, most have lost between 35 to 50 percent of their weight.

The den into which woodchucks retreat when winter arrives may have a forty-foot tunnel, camouflaged at its entry, that leads into the den. The winter den is below the frost line, usually about five feet deep. The winter rooms are high in the tunnel so that they cannot flood.

When the woodchuck enters its den for hibernation, it seals off the tunnel leading into it. The outer tunnel may become the winter dwelling of skunks or rabbits. During hibernation, the woodchuck, which normally breathes about thirty-five times a minute, breathes about once in five minutes. Its body temperature drops from about 36.7 degrees Celsius (98 degrees Fahrenheit) to 3.3 degrees Celsius (38 degrees Fahrenheit), only slightly above freezing. Its heart, beating in warm weather at about eighty times a minute, now beats four times a minute.

Woodchucks have a layer of brown fat that builds up around their vital organs. When it is time for hibernation to end, the animal receives an instant jolt of energy from this brown fat. It begins to shiver, which gradually warms it up. Its supply of oxygen increases steadily, resulting in increased blood flow, which warms the woodchuck. It takes a few hours for it to move from its dormant state to its spring time state.

In mild climates, ground squirrels are active all year. The bodies of those that do hibernate change slowly from their summer to their winter phase. Their body temperature, around 32.2 degrees Celsius (90 degrees Fahrenheit) in summer, drops a couple of degrees every day until it approaches 4.4 degrees Celsius (40 degrees Fahrenheit). An internal mechanism keeps the squirrel's body temperature from dropping below that number. Brown bats enter hibernation when the air temperature stabilizes around 10 degrees Celsius (50 degrees Fahrenheit), entering their win-

Humans and Hibernation

Considerable research related to hibernation and its implications for humans is ongoing. Noting that when animals' bodies approach the freezing point, they feel little pain and bleed little, if at all, when they are cut, anesthesiologists and other physicians have begun to simulate some conditions of hibernation in the operating room.

Only in the last third of the twentieth century was it possible to perform some kinds of delicate, lifesaving surgery by packing the body in ice and chilling it to the point that most vital signs are significantly reduced. Open-heart and transplant surgery have advanced considerably by using such techniques. The loss of blood accompanying such surgery in earlier eras has been substantially reduced by operating on chilled bodies, then gradually warming them to normal temperatures. The need for anesthetics also has been greatly reduced, thereby eliminating much of the risk that anesthetization frequently carries.

Hibernation among humans would be useful in space travel, where reducing their vital functions for extended periods would curtail the need for oxygen and food among space venturers.

ter quarters, or hibernacula, in swarms. In these caves, the temperature remains constant and is above freezing, which is crucial to the bats' survival, because bats subjected to lower temperatures develop fatal ice crystals in their blood.

Brown bats hang upside down in their caves in winter. Their bodies become stiff and appear to be dead. Their heartbeats drop from over five hundred beats a minute to between seven and ten beats a minute. They hibernate for three to four months, waking occasionally for water and any insects they can find to devour. In dormancy, brown bats' bodies assume the temperature of the atmosphere surrounding them.

The jumping mouse is another true hibernator. Late in October, it seals itself into its den, having gorged on all the food it can find in the weeks prior to hibernation. It curls up into a ball, placing its head between its hind legs. During hibernation, it breathes just once every fifteen minutes.

—R. Baird Shuman

See also: Estivation; Metabolic rates; Metamorphosis; Rhythms and behavior; Sleep; Thermoregulation; Warm-blooded animals.

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HIERARCHIES

Type of animal science: Behavior
Fields of study: Anthropology, evolutionary science, population biology

Hierarchies, systems of establishing dominance and subordination, are important in maintaining social order in many species of animals.

Principal Terms

ADAPTION: in evolutionary biology, any structure, physiological process, or behavior that gives an organism an advantage in survival or reproduction in comparison with other members of the same species

AGGRESSION: a physical act or threat of action by one individual that reduces the freedom or genetic fitness of another

COMPETITION: the active demand by two or more organisms for a common resource

DOMINANCE: the physical control of some members of a group by other members, initiated and sustained by hostile behavior of a direct, subtle, or indirect nature

FITNESS: in the genetic sense, the contribution to the next generation of one genotype in a population relative to the contributions of other genotypes

SOCIOBIOLOGY: the study of the biological basis of the social behavior of animals

All animal species strive for their share of fitness. In this struggle for reproductive success, there is often competition among the individuals that make up the population. This competition is generally for some essential resource such as food, mates, or nesting sites. In many species, the competition over resources may lead to actual fighting among the individuals. Fighting, however, can be costly to the individuals involved. The loser may suffer real injury or even death, and the winner has to expend energy and still may suffer an injury. In order to prevent constant fighting over resources, many animal species have adapted a system of dominance, or what students of sociobiology call a dominance hierarchy or social hierarchy. The dominance hierarchy is a set of aggression-submission relationships among the animals of a population. With an established system of dominance, the subordinate individuals will acquiesce rather than compete with the dominant individuals for resources.

General Characteristics of Hierarchies

The simplest possible type of hierarchy is a despotism where one individual rules over all other members of the group and no rank distinctions are made among the subordinates. Hierarchies more frequently contain multiple ranks in a more or less linear fashion. An alpha individual dominates all others, a beta individual is subordinate to the alpha but dominates all others, and so on down to the omega individual at the bottom, who is dominated by all of the others. Sometimes, the network is complicated by triangular or other circular relationships where two or three individuals might be at the same dominance level. Such relationships appear to be less stable than despotisms or linear orders.

Hierarchies are formed during the initial encounters between animals through repeated threats and fighting, but once the issue of dominance has been determined, each individual gives way to its superiors with little or no hostile exchange. Life in the group may eventually become so peaceful that the existence of ranking is hidden from the observer until some crisis occurs to force a confrontation. For example, a troop of baboons can go for hours without engaging in sufficient hostile exchanges to reveal their ranking, but in a moment of crisis such as a quarrel over food the hierarchy will suddenly be evident. Some species are organized in absolute dominance hierarchies in which the rank orders remain constant regardless of the circumstances. Status within an absolute dominance hierarchy changes only when individuals move up or down in rank through additional interaction with their rivals. Other animal societies are arranged in relative dominance hierarchies. In these arrangements, such as with crowded domestic house cats, even the highest-ranking individuals acquiesce to subordinates when the latter approach a point that would normally be too close to their personal sleeping space.

The stable, peaceful hierarchy is often supported by status signs. In other words, the mere actions of the dominant individual advertise his dominance to the other individuals. The leading male in a wolf pack can control his subordinates without a display of excessive hostility in the great majority of cases. He advertises his dominance by the way he holds his head, ears, and tail, and the confident face-forward manner in which he approaches other members of his pack. In a similar manner, the dominant rhesus monkey advertises his status by an elaborate posture which includes elevated head and tail, lowered testicles, and slow, deliberate body movements accompanied by an unhesitating but measured scrutiny of other monkeys he encounters. Animals not only utilize visual signals to advertise dominance, but they also use acoustic and chemical signals. For example, dominant European rabbits use a mandibular secretion to mark their territory.

Special Properties of Dominance Hierarchies

A stable dominance hierarchy presents a potentially effective united front against strangers. Since a stranger represents a threat to the status of each individual in the group, he is treated as an outsider. When expelling an intruder, cooperation among individuals within the group reaches a maximum. Chicken producers have long been aware of this phenomenon. If a new bird is introduced to the flock, it will be subjected to attacks for many days and be forced down to the lowest status unless it is exceptionally vigorous. Most often, it will simply die with very little show of fighting back. An intruder among a flock of Can-

Pecking Orders in Domestic Fowl

Among common barnyard chickens, social behavior is a relatively simple system based on the dominance hierarchy. A power struggle begins soon after a new flock is established. The chickens quickly form a hierarchy that is quite literally a pecking order. The chickens establish their status by pecking or by threatening actions toward an opponent with the obvious intention of attacking in this manner. Superior genetic fitness is attained by the high-ranking birds. They enjoy more freedom of movement, and they have priority of access to food, better nesting sites, and favored roosting places. While the dominant males mate far more frequently than the subordinates, the dominant females actually mate less, because the subordinate females more readily display submissive and receptive postures to the males. The fitness of the dominant females is still enhanced due to the advantages gained in access to food and nesting sites. Males establish a separate hierarchy above that of the females. The adaptive advantage to this behavior lies in the fact that males who are subordinate to females will not be able to mate. It has been well documented that fighting ability among fowl is an inherited trait, and significant genetic variation in this trait can be observed both between and within the various species of fowl. It is advantageous for chickens to live in a stable hierarchy. If the hierarchy of the flock is intentionally disrupted, the chickens will eat less food, lose more weight, and lay fewer eggs.

ada geese will be met with the full range of threat displays and repeated mass approaches and retreats.

In some primate societies, the dominant animals use their status to stop fighting among subordinates. This behavior has been observed in rhesus and pig-tailed macaques and in spider monkeys. This behavior has been observed even in animal societies, such as squirrel monkeys, that do not exhibit dominance behavior. Because of the power of the dominant individual, relative peace is observed in animal societies organized by despotisms, such as hornets, paper wasps, bumblebees, and crowded territorial fish and lizards. Fighting increases significantly among the equally ranked subordinates as they vie for the dominant position when the dominant animal is removed.

Young males are routinely excluded from the group in a wide range of aggressively organized mammalian societies such as baboons, langur monkeys, macaques, elephant seals, and harem-keeping ungulates. At best, these young males are tolerated around the fringes of the group, but many are forced out of the group and either join bachelor herds or wander as solitary nomads. As would be expected, these young males are the most aggressive and troublesome members of the society. They compete with one another for dominance within their group and often unite into separate bands that work together to reduce the power of the dominant males. Males in the two groups show different behaviors. Among the Japanese macaques, the dominant males stay calm and aloof when introduced to a new object so as to not risk loss of their status, but the females and young males will explore new areas and examine new objects.

Nested hierarchies are often observed in some animal species. Societies that are divided into groups can display dominance both within and between the various components. For example, white-fronted geese establish a rank order of several subgroups including parents, mated pairs without young, and free juveniles. These hierarchies are superimposed over the hierarchy within each of the subgroups. In wild turkeys, brothers establish a rank order among their brotherhood, but each brotherhood competes for dominance with other brotherhoods on the display grounds prior to mating.

Dominants and Subordinates

To be dominant is to have the priority of access to the essential resources of life and reproduction. In almost all cases, the superior dominant animals will displace the subordinates from food, mates, and nest sites. In the matter of obtaining food, for example, wood pigeons are flock feeders. The dominant pigeons are always found near the center of the flock when feeding and feed more quickly than the subordinate birds at the edge of the flock. The birds at the edge of the flock accumulate less food and often obtain just enough to sustain them through the night. Among sheep and reindeer, the lowest-ranking females are also the worst-fed animals and among the poorest of mothers. Baby pigs compete for teat position on the mother and once established will maintain that position until weaning. Those piglets that gain access to the most anterior teats will weigh more at weaning than those who have to settle for posterior teat positions. In gaining access to mates, one study with laboratory mice has shown that while the dominant males constituted only one third of the male population, they sired 92 percent of the offspring.

Life is still not all that hopeless for the subordinates. Oftentimes the loser in the battle for dominance is given a second chance, and in some of the more social species, the subordinate only has to await its turn to rise in the hierarchy. In some species, cooperation among subordinate groups, especially kin groups, can lead to the formation of a new colony and a new opportunity to establish dominance. In other species, it may well be advantageous for the subordinate to stay with the group. For example, individual baboons and macaques will not survive very long if they are away from the group's sleeping area, and they will have no opportunity to reproduce. It has been shown that even a low-ranking male eats well if he is part of a troop, and he may occasionally have the opportunity to mate. In addition, the dominant male will eventually lose prowess, and the subordinate will have a chance to move up in the dominance hierarchy.

—D. R. Gossett

See also: Communication; Communities; Competition; Courtship; Defense mechanisms; Ethology; Groups; Herds; Insect societies; Mammalian social systems; Nesting; Offspring care; Pair-bonding; Population analysis; Predation; Symbiosis; Territoriality and aggression; Zoos.

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HIPPOPOTAMUSES

Type of animal science: Classification
Fields of study: Anatomy, wildlife ecology, zoology

The Hippopotamidae family has two genera, each with a single species. The two genera differ greatly in size, but both are characterized by a round tubular body, short stocky legs, broad snout, and a very large mouth.

Principal Terms

BLOOD SWEAT: oily secretion from mucous glands serving a protective function
CALF CRÈCHE: group of newborn calves in a place of protection
DUNG SHOWERING: behavior by bulls to show dominance over other males
NONRUMINATING: digesting grasses without chewing cud

The name hippopotamus means "river horse," and these mammals spend most of their time in the water. They have inflated-looking bodies that resemble barrels, supported on short, pillarlike legs with four toes ending in hooflike nails. The tail is short and bristled, with flattened sides. The belly is carried only a few inches above the ground. The eyes are raised on top of a flat head, the ears are small, and the nostrils are slits high up on the muzzle and can be closed when the animal is submerged. The two species, *H. amphibius* and *C. liberiensis* (pygmy hippopotamus) differ greatly in size, with the former up to 5.5 feet high and weighing seven thousand to ten thousand pounds. The pygmy hippopotamus is much smaller, with an average height of 2.5 to 3 feet, and weighing 350 to 600 pounds.

Hippopotamus Life

Hippopotamuses must submerge frequently because their naked skin is vulnerable to overheating and dehydration. They can stay submerged up to thirty minutes. Their skin has a brown to gray-purple coloration with pinkish creases. The pygmy hippopotamus is black-brown to purple in color with the cheeks often tinted pink. Unlike the pygmy hippopotamus, which is a solitary mammal dwelling in rivers and forests, *H. amphibius* is a huge animal that can be found in herds of up to eighty members.

Seeking food, *H. amphibius* travels at night from the rivers for grazing, but will return before dawn to spend the day digesting and socializing in the riverbeds. During the forays from the water,

Hippopotamuses spend most of their day in the water because their bare skin makes them prone to dehydration in the hot African sun. (Corbis)

Hippopotamus Facts

Classification:
Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertabrata
Class: Mammalia
Order: Ariodactyla
Suborder: Suiformes
Family: Hippopotamidae
Genus and species: Hippopotamus amphibius (hippopotamus), *Choeropsis liberiensis* (pygmy hippopotamus)

Geographical location: Although once numerous in the rivers throughout Africa, *H. amphibius* can now be found only south of Khartoum and north of the Zambezi River; the pygmy hippopotamus is found in West African lowland rain forests

Habitat: Hippopotamuses live in short grasslands, rivers, and lakes; pygmy hippopotamuses live in lowland forests and swamps

Gestational period: Eight months for hippopotamuses, seven months for pygmy hippopotamuses

Life span: Up to forty-two years in the wild, past fifty in captivity

Special anatomy: The genera differ greatly in size, but both have a broad snout, a very large mouth, a short round body, and short stocky legs; the smooth, hairless skin is covered with special pores that secrete a pinkish substance known as blood sweat, which is protective when in the water or dry land; large canine teeth enlarge into tusks that grow continually; the stomach is three-chambered but is nonruminating; hippopotamuses appear to have good eyesight, hearing, and smell

the animals typically travel two to three miles. *H. amphibius* eats up to ninety pounds of grass on a nightly basis, often mowing twenty-inch-wide swaths with its muscular lips and mouth. The pygmy hippopotamus prefers to seek food on high, dry ground and is most active between 6 P.M. and midnight. They have home ranges that may cover between one hundred and four hundred acres. Most movements are along established paths in their home range, and rarely do they cross paths with others of their own species. During these forays, they seek water plants, grasses, fallen fruits and leaves.

For *H. amphibius*, their watery homelands are partitioned into individual mating territories by mature bulls that defend defined sections. These territories can remain fixed for years. Dung showering is used to mark territories and express dominance. Other behaviors that signal threats can include water scooping, head shaking, grunting, roaring, explosive exhaling, and charging. Submission is signaled by turning tail, approaching in a crouched position, lying prone on the land, or diving and swimming away from the dominant male.

Reproduction

Herds usually breed between ten to fifteen hippopotamuses. Nonbreeding males are tolerated in the territories if they do not bother the cows. Cows and calves associate in nursery herds and establish calf crèches, which serve as protection against predation from crocodiles, lions, and hyenas. Mating takes place during the dry season while the animals are in the water. After the birth of a calf, either on land or in the water, the cow remains with the calf for about a month before returning to the herd. Baby hippopotamuses are able to nurse underwater until they are weaned, at around eight months of age.

During mating season, the solitary pygmy hippopotamus seeks out a receptive female who tolerates the male's presence when in heat. One to four copulations may take place over a period of two days on both land and in the water. The young are born on land or in the water and remain concealed for three to four weeks. The main predator for the pygmy hippopotamus is the leopard. The pygmy hippopotamuses are considered to be in jeopardy for survival because of hunting and destruction of habitat by logging.

—Frank J. Prerost

See also: Fauna: Africa; Herds; Lakes and rivers.

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HOME BUILDING

Type of animal science: Behavior
Fields of study: Entomology, marine biology, ornithology, zoology

A home is the place or physical structure in which an animal lives, eats, finds a safe haven, and raises its family. The nature of animal homes varies greatly.

Principal terms

ARTIODACTYL: a hoofed mammal with an even number of toes
CARNIVORE: an animal that eats only animal flesh
HERBIVORE: an animal that eats only plants
MOLE HILL: an earth mound a mole dug up in search of food.
OMNIVORE: an animal that eats plant and animal matter
SOLITARY: living alone

The term "home" designates the area, place, or physical structure in which an animal lives, finds a safe haven, and raises its family. The nature of animal homes varies greatly. The very simplest example might be a spot on an ocean bottom where a marine sponge attaches to the sand and grows. Other sea animals, such as gastropods (snails) live in their shells and take their homes wherever they go. Crustaceans, such as lobsters, or land arthropods, such as scorpions, live in simple burrows in the oceans or in the earth. However, a large number of lake, ocean, and river dwelling species, such as fish and whales, have no fixed homes.

Land animals often live in more complex homes. For example, social insects such as bees, termites, and wasps inhabit nests or hives. Birds also build nests. They nest in trees, on the ground, or on rocky mountain terrain. In contrast, grazing animals such as deer and antelope live on the ground, wherever their search for food takes them on a given day. In the case of small mammals, individuals or groups often live in complex underground burrows such as mole holes. Larger carnivores and omnivores often inhabit dens that are underground burrows, as do members of the weasel family, or in caves and other natural formations, as do bears and big cats.

Insect and Bird Homes

Social insects such as bees, ants, and some wasps live in nests of differing sizes which are made of wax, paper, or dried mud. Social wasps, for example, live in spherical paper nests that are a foot in diameter. These nests are seen in trees or under the porch roofs of human habitations. A wasp colony lasts only one year because wasps do not store food as do ants and bees. Only a few fertilized females, queens-to-be, survive the winter to begin new colonies in spring. Many solitary wasps live alone, except for breeding. Then, females build small brood nests of materials other than paper. For example, potter wasps use mud and saliva, and stone-working wasps mix small pebbles, mud, and saliva.

Termites, also social insects, are known for damaging wood homes. Most species are tropical, but some inhabit the Americas and Europe. They live in huge, long-lasting colonies that may hold millions of inhabitants. These colonies (called nests or termitaries) vary greatly. Tropical species build huge mounds with walls of soil particles and dried saliva. Inside the mounds are many chambers, passages, and good ventilation and drainage systems. Termites are often subterranean, burrowing up into logs and wood structures.

Image Not Available

Many birds, such as the commonly seen crows, robins, sparrows, doves, and other small to medium birds, nest in trees or warm places around human homes. For instance, doves may nest atop porch lights. Nests of such birds are most often made of intertwined pieces of grass, twigs, and human trash. The nests are often abandoned yearly and in some cases are reused by other species. Also of interest are the nests of woodpeckers, which are located in tree holes.

Flamingos nest along shores of shallow, saltwater lagoons and lakes. The nest is a foot-tall mound of mud with a depression at its top. Flamingos are monogamous, and couples use the same nest over and over. In contrast, vultures usually live on bare ground under mountain overhangs or in caves, building no nests, and laying eggs on bare rock of these spartan home sites. Vultures are also monogamous and will live in a home site for up to forty years. An exception to the "bare rock" rule occurs with lammergeiers of Europe, Asia, and Africa. These bearded vultures build several nests per pair. They are conical in shape, located on rock ledges or in caves, and are used many times, in cycles, as home sites and to raise families.

Mammal Homes

Mammals have a wide variety of home sites. In many cases, such sites are temporary and are simply the last place the mammal found itself each day. Creatures living in this way are usually herbivores, ranging from hippopotamuses to deer and other artiodactyls. This is because every day, these animals range over areas of several square miles or more seeking food. The other end of the home site range is seen with many omnivores and carnivores. These creatures have specific home sites or dens, which may be burrows in the ground, caves, logs, and natural crevices. Small mammals that live like this include gophers and moles. They dig burrows or tunnels with the sharp claws of their front feet. Gophers store food in chambers in the burrows. They are solitary and territorial, coming together only to breed. Females use their burrows to live in and raise young.

The homes of moles are more complex. Moles are voracious and solitary, continually burrowing in the ground for food, which includes insects, worms, slugs, snails, and spiders. They defend their homes when other moles—even of their own species—intrude. Moles only socialize when entering tunnels of females to mate.

Mole burrows or holes are close to the ground surface and may be recognized by large, central earth mounds. These "mole hills" are the earth that has been dug up in search of food. The burrows are very elaborate, holding warmly lined central nest chambers, connected galleries, bolt holes that allow escape from enemies, and many passageways.

Wolves and spotted hyenas are somewhat similar, related species. These carnivores tend to live in dens and claim large hunting territories. Wolf and hyena homes and living habits are different. Wolves live in dens or lairs that may be caves, hollow tree trunks, crevices under large fallen logs, or holes they dug in the ground. Few improvements are made in the natural dens wolves inhabit. They are shelters used for safety, protection from the elements, and for raising offspring.

Spotted (laughing) hyenas, in contrast, are much more communal. They live in clans of up to one hundred individuals and inhabit shared communities comprising many dens. In the dens they sleep, mate, and socialize. Dens may be caves on rocky ground or holes dug by individuals, as a clan grows. The individual cave or tunnel dens are most often inhabited by one individual or a female with cubs. This is because extended pairing is unusual in spotted hyenas.

Lions and tigers, the largest predatory land carnivores, often roam through large territories in search of game and inhabit dens of varying permanence. The dens are dense thickets, groups of rocks surrounded by thick underbrush, or caves whose entrances are screened by thorn bushes or dense underbrush. Very often, dens are used to birth offspring and protect the big cats from the elements.

Primate Homes

Monkeys, which live in Africa, Asia, and South and Central America, live in bands which most often inhabit trees, sheltering in the forks between branches. African baboons are large, more highly organized, ground-living primate species. They live in groups called troops, which are often found living in rocky terrain or on cliffs. In many cases, group members inhabit convenient caves.

Gorillas, the largest, strongest, rarest apes, look almost human. They inhabit West African forests from lowlands to altitudes of ten thousand feet. Gorillas live in bands of up to twenty individuals. Each band claims a territory, which may be viewed as the band's neighborhood. A band forages over several square miles each day and lacks permanent dwellings. Instead, its members build temporary shelters each night after a day of foraging for the honey, eggs, plants, berries, bark, and leaves that are their diet. When terrain and time permit, females and young sleep on temporary tree platforms made of branches and leaves. Mature males nest at the bases of these trees, to protect them.

Beavers: Engineers of the Animal World

An example of animal engineering at its best is the beaver home. These herbivores live in streams, ponds, or lakes near woods. Beaver home building starts with making dams where water flows steadily but slowly. Dams create deep water pools used for food storage. Beavers work in groups—usually extended families—to build their dams. Their sharp incisor teeth are used to cut down nearby softwoods such as aspens and willows. The trees are interwoven with mud, stones, and sticks to form and seal the dam.

Inside or near the dam, the beavers build lodge chambers and tunnels to live in. Nearby they store piles of tree branches underwater to use as winter food. A lodge may be on an island, a pond bank, or the shore of a lake. An island lodge holds a central chamber, with its floor a little above water level. A pond lodge, built partly on the bank, has a front wall rising up from the pond bottom. A lake lodge is built on the lake shore. Beaver lodges are made of sticks, grass, and moss, interwoven and plastered with mud. Their interiors are often nine feet square and over three feet tall.

Homes, Lifestyles, and Forms

The homes of animals depend upon their lifestyles, habitats, and forms. Many herbivores and omnivores range widely to find sustenance. Hence, they often lay themselves down to sleep wherever the search for food takes them. Animals that live in hot, relatively dry climates often sleep out of doors. However, similar species inhabiting cool to cold climates very often build or find burrows or dens to live in. Some animals have forms and eating habits that cause them to live outdoors regardless of world location. This is typical of animals, such as zebras and reindeer, that graze daily over large areas and cannot restrict themselves to homes where they return each evening. In contrast, animals that hunt often prefer to have a safe haven where they can bring their catch home to devour in peace, while animals that live in cold climates use their homes to store food for the long winter.

—*Sanford S. Singer*

See also: Biogeography; Communities; Domestication; Ecological niches; Ethology; Groups; Habitats and biomes; Herds; Insect societies; Mammalian social systems; Mark, release, and recapture methods; Nesting; Offspring care; Packs; Population analysis; Reefs; Territoriality and aggression; Urban and suburban wildlife; Zoos

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HOMEOSIS

Type of animal science: Development
Fields of study: Developmental biology, embryology, genetics, physiology, reproduction science

Homeotic genes determine the identity of different body segments early in development. Research on these genes provides insight into how complex body patterns are established during development and how these patterns have evolved.

Principal Terms

EMBRYO POLARITY GENES: genes whose expression in maternal cells results in products being stored in the egg that establish polarity, such as the anterior-posterior axis, after fertilization

GAP RULE GENES: expressed in the zygote, these genes divide the anterior-posterior axis of fruit flies into several regions

HOMEOBOX: one of 180 nucleotide pairs that code for a protein called the homeodomain, found in such diverse organisms as insects, frogs, and humans; they are known to influence body plan formation in fruit flies

HOMEOSIS: a process that results in the formation of structures in the wrong place in an organism, such as a leg developing in place of a fly's antenna

HOMEOTIC SELECTOR GENES: genes that determine the identity and developmental fate of segments established in fruit flies by a hierarchy of genes

IMAGINAL DISK: a small group of cells that differentiate adult fruit fly structures after the last larval molt

PAIR-RULE GENES: segmentation genes of fruit flies that divide the anterior-posterior axis into two-segment units

SEGMENTATION GENES: these include the gap rule, pair-rule, and segment polarity genes

The body plans of advanced animals and plants can be viewed as a series of segments with unique identities. This is especially obvious in the annelids (segmented worms), but even in vertebrates the muscular regions and the backbone are segmented. Occasionally, a segment takes on the identity of another segment of the organism. This is called homeosis, and it was first described in 1984. Numerous examples of homeosis have been cited, including the Antennapedia mutant of the fruit fly, which has a leg developing in the antennal socket of the head. Much has been learned about developmental patterns in organisms, and about the evolution of these patterns, from the study of homeotic mutants.

The Genetic Control of Body Plans

The role of homeosis in elucidating genetic control of overall body plans is best illustrated in the development of the fruit fly. Early in its embryogenesis, the basic plan for the adult fly form is established, and this information is stored in imaginal disks (an adult fly is called an imago) through three larval stages and associated molts. Imaginal disks are small groups of cells that differentiate adult structures after the last larval molt. The early determination of these imaginal disks for specific developmental fates is controlled by a hierarchy of genes. This hierarchy of gene regulation has been carefully documented for the establishment of the anterior-posterior axis (a line running from the head to the abdomen) of larval and adult fruit flies. Three levels of genetic control—egg polarity genes, segmentation genes, and homeotic selector genes—result in an adult fly with anterior head segments, three thoracic segments, and eight abdominal segments.

Egg polarity genes are responsible for establishing the anterior-posterior axis. Mutations of these genes result in bizarre flies that lack head and thoracic structures or lack abdominal structures. Maternal egg polarity genes are transcribed, and the resulting ribonucleic acid (RNA) is translocated into the egg and localized at one end. This RNA is not translated into protein until after fertilization. Following translation, the proteins are dispersed unequally in the embryo, forming an anterior-posterior gradient that regulates the expression of the segmentation genes.

Segmentation genes represent the second tier of the genes that establish the body plan of the fly. Within the segmentation genes, there are three levels of control—gap genes, pair-rule genes, and segment polarity genes—resulting in progressively finer subdivisions of the anterior-posterior axis. While there is hierarchical control within the segmentation genes, genes in a given level also interact with one another. Gap genes of the embryo respond to the positional information of the gradient established by the maternal egg polarity genes. Gap genes form boundaries that specify regional domains, and several gap genes with distinct regions of influence have been identified.

Pair-rule genes follow next in the sequence; they appear to function at the level of two-segment units. Mutant pair-rule genes are responsible for flies that have half the normal number of segments. Ultimately, the larval fly body is divided into visible segments, but while the patterns are forming, genes appear to exert their influence on parasegments. A parasegment is half a segment that is "out of phase" with the visible adult segments. Parasegments include the posterior of one segment and the anterior of the adjacent segment. Developmental programming of parasegments ultimately gives rise to visibly distinct segments. The final level of control of the segmentation genes focuses on individual segments and is controlled by the segment polarity genes. In response to the pair-rule genes, the segment polarity genes subdivide each segment into anterior and posterior compartments. Thus, the segmentation genes create a series of finely tuned boundaries.

Homeotic Selector Genes

It is the third tier of genes, however, the homeotic selector genes, that actually specify segment identity. Segmentation gene mutations result in missing body parts, whereas mutations of the homeotic selector genes result in a normal number of segments, but segments with abnormal identities. Homeotic selector genes are found in two gene clusters, the *Antennapedia* complex and the bithorax complex, both of which were identified based on mutant phenotypes. Genes associated with the *Antennapedia* complex appear to determine the fate of segments associated with the anterior body segments, whereas the bithorax complex is responsible for the more posterior segments, such as the abdominal segments. The pattern that arises is modulated both by interactions among the homeotic selector genes and by interactions with the segment polarity genes.

The genes found within the *Antennapedia* and bithorax complexes have been identified based on mutations that have arisen. These genes function within smaller regions of the anterior or posterior axis, much as pair-rule genes subdivide regions established by the gap genes. It is intriguing that the genes within the two complexes appear to be lined up in the same order that they function spatially. That is, the position of an *Antennapedia* complex gene on the chromosome relative to other *Antennapedia* complex genes correlates with the actual position of the segments controlled by the gene. Recent analyses of homeotic mutants in beetles indicate that the homeotic genes are also physically organized in a left-to-right sequence corresponding to the location of the segments they control on the anterior-posterior axis. Unlike the fruit fly, however, the beetle has a single homeotic gene complex controlling the entire anterior-posterior axis.

The interactions between homeotic selector genes and other genes in the hierarchy may, in part, be controlled by the homeodomain protein coded for by the "homeobox" associated with many of these genes. The homeobox is a 180-nucleotide-pair sequence that is included in many of the homeotic selector genes as well as in some segmentation genes (including the pair-rule gene). The homeodomain protein has a unique structure that may bind the deoxyribonucleic acid (DNA) and affect its transcription. It is possible that this allows genes to regulate expression of themselves and other related genes. For example, a pair-rule gene known as *fushi tarazu* (meaning "not enough segments" in Japanese) is found in the *Antennapedia* complex and has a homeobox, although *fushi tarazu* is not a homeotic selector gene. Its homeodomain can bind to the *Antennapedia* gene and thus can regulate when this gene is turned on and off. *Antennapedia*, a homeotic selector gene, was first identified when a mutation of it resulted in the replacement of an antenna with a leg. Thus, the ability of the homeodomain to bind to DNA provides a way for the hierarchical control of homeotic selector genes by segmentation genes to occur.

The homeotic selector genes are ultimately linked with gene expression that leads to the development of specific structures associated with different segments. It is not known exactly how homeotic selector genes regulate segment differentiation. Although the homeotic selector genes are active early in development, they appear to be involved in programming cells for fates that are not expressed until much later.

Studying Homeosis Through Mutations

Most of what is known about homeosis has been learned from studying mutations. Sometimes these mutations have arisen spontaneously; sometimes they have been induced by exposing organisms to mutagenic substances, such as chemicals or X ray or ultraviolet radiation. The large number of mutations identified in fruit flies accounts for the wealth of information on homeosis in this organism, in sharp contrast to the limited information on humans, for whom ethical considerations prohibit mutagenesis. Mutations affecting segmentation and determination of segment identity represent defective developmental switches and provide insight into the normal developmental sequence.

Classical genetic approaches have been used with homeotic mutants to map genes to chromosomes and to identify interactions between genes. For example, it can be determined whether two genes are on the same chromosome by making a series of specific matings between flies with mutations in these genes and wild-type ("normal") flies. If the genes are not on the same chromosome, offspring with one mutation will not necessarily have the other mutation. If the mutations are both on the same chromosome, they will be inherited together, except in rare situations where there is recombination between chromosomes. Geneticists use the frequency of recombination to assess how close together two genes are on a chromosome. This approach helped geneticists determine the order of genes within the *Antennapedia* and bithorax complexes. Matings between different mutants have also established the hierarchy of genetic control among egg polarity, segmentation, and homeotic selector genes. For example, a pair-rule mutant will have no effect on gap genes, but a gap gene mutant will affect pair-rule genes.

To visualize the results of these crosses of hierarchical mutants, researchers employed a second technique: in situ hybridization. To investigate the effect of gap genes on pair-rule genes, a wild-type fly embryo and one with a gap mutation affecting the middle section were exposed to radioactively labeled DNA that was a copy of the pair-rule gene *fushi tarazu*. The DNA hybridized (bound) to *fushi tarazu* RNA, and it thus labeled tissues where the *fushi tarazu* gene was turned on and was making RNA copies of itself. Excess radioactive DNA was washed away, and a photographic emulsion that was then placed over the tissue was exposed by the bound radioactive DNA. This permitted researchers to see that the *fushi tarazu* gene was being expressed in the middle of the wild-type embryo, but not in the gap mutant embryo. When this experiment was repeated using radioactive gap gene DNA in a pair-rule mutant, no effect on gap gene expression was observed.

In situ hybridization has also provided information on how egg polarity genes provide segmentation genes with positional information. The egg polarity gene bicoid was identified by mutations resulting in a fly with abdominal structures but no head or thoracic structures. When radioactive DNA copies of the bicoid gene were hybridized to eggs, it was found that all the RNA was located at the anterior tip after being transferred from the mother. When this RNA was translated into protein, the protein was tagged with an antibody specific for the bicoid protein. Tagging the protein with an antibody is similar to tagging RNA with a radioactive DNA segment; both techniques allow researchers to see how the RNA or protein is distributed in tissues. In this case, the bicoid protein formed an anterior to posterior gradient after the egg was fertilized, with more protein being found at the anterior end.

Homeotic genes have been isolated and used for in situ hybridization studies. In addition, the sequence of nucleotides in the DNA in these genes has been established. A variety of techniques is available for DNA sequencing. Generally the DNA is broken into smaller segments that can be more readily identified. Cutting the DNA yields overlapping segments, and the overall sequence can be established by piecing these overlapping fragments back together. The presence of the homeobox was established by comparing DNA sequences from different genes in flies and other organisms. It was evident, based on these types of data, that the homeobox sequence differs by only a small number of nucleotides even between very distantly related organisms.

The role of the homeobox was investigated by inserting DNA containing a homeobox from the *fushi tarazu* gene into a bacteria in such a way that the bacteria then produced large amounts of the homeodomain protein. This protein was then tested for its ability to bind the DNA and was found to bind to specific fragments of DNA that were involved in homeosis, such as the *Antennapedia* gene. Homeodomain protein from a mutant *fushi tarazu* gene was defective in its DNA binding ability. This provided evidence that the homeobox may regulate gene expression via the direct binding of the homeodomain to DNA. This is only one of numerous examples illustrating how researchers have utilized genetic mutants and molecular biology to investigate the role of homeotic genes in the development of segmented organisms.

Implications of Homeotic Research

Research on homeosis and homeoboxes has made significant contributions to the fields of developmental biology and evolution. Since all higher animals and plants exhibit some form of segmented development, the common link of the homeobox has intrigued scientists interested in how body plans are established. Questions concerning the evolution of segmentation patterns in animals have also arisen as more is understood about the genes affecting segmentation and how they are regulated.

Significant similarities both among the homeoboxes identified in fruit flies and among the homeoboxes of distantly related species have been found. In fruit flies, homeoboxes have been identified in homeotic selector genes, segmentation genes, and egg polarity genes. Whether homeoboxes affect gene regulation and segmentation in other organisms is an exciting, and open, question. Segmented worms, leeches, earthworms, sea urchins, frogs, mice, and humans all have homeoboxes. Different mouse homeobox genes have been shown to be expressed in specific regions during embryogenesis. Relatively little is known about the process of segmentation in vertebrates, so it is more difficult to interpret the results of such experiments. Also, it appears that segmentation in vertebrates and in fruit flies (and other invertebrates) evolved separately. Thus, the presence of a homeobox may or may not indicate a common developmental process for segmentation among animals.

There is an intriguing possibility that addition and modification of homeotic selector genes were responsible for the evolution of insects from segmented worms. The presence of two homeotic gene complexes in fruit flies, contrasted with one in beetles, suggests that duplication of the gene complex, followed by subsequent specialization, may have allowed for greater fine-tuning of segmental identity. Evolutionary alterations of the initial homeotic gene complex may have been responsible for the addition of legs to a wormlike creature composed of similar segments, giving rise to a millipede-like creature. The reduction of all legs except for the walking legs in the thoracic region and, ultimately, the addition of wings to the thoracic region could also reflect changes in homeotic selector genes. Parts of this evolutionary journey can be reconstructed with homeotic fruit fly mutants that bear similarities to their ancestors. This is exemplified by the deletion of the *Antennapedia* gene, which results in a wingless fly; winged insects presumably arose from nonwinged insects. It is impossible, however, to create a millipede from a fly via mutations of the homeotic selector genes, so caution must be taken in speculating on the role of homeotic selector genes in insect evolution.

—*Susan R. Singer*

See also: Anatomy; Cell types; Determination and differentiation; Development: Evolutionary perspective; Embryology; Genetics; Metamorphosis; Morphogenesis; Mutations; Physiology; Pregnancy and prenatal development; Regeneration; Reproduction.

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HOMINIDS

Type of animal science: Anthropology
Fields of study: Anatomy, anthropology, evolutionary science, human origins, systematics (taxonomy)

Though understanding of human ancestry is rudimentary at best, an astonishing series of discoveries since the nineteenth century has created a lively field of knowledge where there was none before.

Principal Terms

APES: large, tailless, semierect anthropoid primates, including chimpanzees, gorillas, gibbons, and orangutans, and their direct ancestors—but excluding man and his ancestors

AUSTRALOPITHECINES: nonhuman hominids, commonly regarded as ancestral to present-day humans

DRYOPITHECINES: extinct Miocene-Pliocene apes (sometimes including *Proconsul*, from Africa) found in Europe and Asia; their evolutionary significance is unclear

HUMANS: hominids of the genus *Homo*, whether *Homo sapiens sapiens* (to which all varieties of modern man belong), earlier forms of *Homo sapiens*, or such presumably related types as *Homo erectus* and the still earlier (and more problematic) *Homo habilis*

PRIMATES: placental mammals, primarily arboreal, whether anthropoid (humans, apes, and monkeys) or prosimian (lemurs, lorises, and tarsiers)

The idea that humankind might be significantly older than the six thousand years previously allotted by biblical scholars, who tried to calculate the generations of man since Adam, was not widely maintained until 1859, when human stone tools and the bones of extinct animals were found lying close to each other in France. Charles Darwin's *On the Origin of Species* appeared on November 1 of the same year, but it suggested only that "light will be thrown on the origin of man and his history" by the theory of evolution he had just proposed.

A series of important and widely noticed books then followed, including J. Boucher de Perthes' *De l'homme antédiluvien et de ses œuvres* (1860; of antediluvian man and his works); Thomas Henry Huxley's *Evidence as to Man's Place in Nature* (1863); and Charles Lyell's *Antiquity of Man* (1863), with others later by John Lubbock, James Geikie, and W. Boyd Dawkins. In *The Descent of Man* (1871), Darwin sagely hypothesized that the human line evolved in Africa (not Asia, as had previously been assumed) from a long-tailed, probably arboreal, ancestor. Yet, in Darwin's time only two fossil apes were known at all, together with some controversial bones of a creature known as Neanderthal man. Extinct species such as the australopithecines and *Homo erectus* had not been discovered.

Humans and Other Primates

The scientific name for mankind is *Homo sapiens sapiens* (wise man); the taxonomic family is the Hominidae, which also includes chimpanzees and gorillas. This classification is reasonable because, bone for bone, their skeletons are almost identical to human skeletons. On other evidence as well, man and his cousins appear to be remarkably alike. The protein sequences in chimpanzee and human hemoglobin, for example, are identical; there are only two chemical differences between gorilla and human hemoglobin. Between humans and all other animals, there are more than two. Strands of deoxyribonucleic acid (DNA) from chimpanzees and humans, moreover, are 99 percent identical. Chimpanzees, finally, are second only to humans in intelligence; their brains closely resemble those of humans. These remarkable similarities attest a common ancestry for all the Hominidae, as the classification itself would imply, and a fairly recent differentiation among its members. Some biochemists have argued that man, the chimpanzee, and the gorilla shared a common ancestor no more than six or eight million years ago.

Whatever the timing may have been, it is almost universally accepted that the link between humans and their protosimian ancestors was a now extinct genus of ape-men, the australopithecines (southern apes). The first of these, called, originally, the Taung child, was discovered in South Africa by Robert Dart in 1924. Its identity and significance remained controversial until 1936, when further discoveries by Robert Bloom convinced skeptical professionals and the public. Today, *Australopithecus* and *Homo* (man) are often grouped together as Hominini, as opposed to the Pongidae (apes), to which the chimpanzee and gorilla belong.

The Australophithecines

The australopithecines arose at least 4 million years ago, probably from dryopithecine ancestors. They lasted until two million years ago, evolving into a series of species. Of these, *Australopithecus afarensis* (found in the Afar region of Ethiopia) was the oldest and smallest. Males stood no taller than four feet, and the females were smaller. Most significantly, however, *afarensis* was fully bipedal; unlike the apes, it walked upright, with increasingly specialized hands, and with legs a bit longer than arms. Chimpanzee-like hips, together with curved toe and finger bones, suggest that it was essentially a tree-dweller living on fruits and seeds. A remarkably complete skeleton of *afarensis*, familiarly called Lucy, was found in 1974; it is about three million years old and is the oldest hominine skeleton yet found. *Afarensis* died out around 2.5 million years ago; it is thought to be ancestral to the later australopithecines and to modern humans.

Australopithecus africanus, deriving from Africa some three to one million years ago, probably evolved from *afarensis*. Most specimens come from Sterkfontein in South Africa, though others have been found in Ethiopia, Kenya, and Tanzania. This species was about the same size as *afarensis*, but it had a less apelike face. The arms were proportionately longer than a modern human's, yet shorter than those of *afarensis*; hands and teeth show similar "modernization." Dart's Taung child was the first (and is still the most famous) example of this species.

Australopithecus robustus (robust southern ape), found only in South African caves thus far, was once thought identical to *Australopithecus boisei*; in older literature, it was also known as *Paranthropus* (past man). Larger and more strongly built than *africanus*, *robustus* was more than a foot taller and had a larger brain. His teeth indicate that *robustus* was a plant eater. There is also a remarkable specimen (discovered by C. K. Brain at Swartkrans) of a child's skullcap in which the imprint of a leopard's lower canines can be seen. Since an exact-fit leopard's jaw was found nearby, it is assumed that the leopard killed the child and was then itself killed by an adult *robustus* armed with some kind of weapon. (A diorama at the Transvaal Museum, Pretoria, reconstructs this hypothetical incident.) *Australopithecus boisei*—a famous discovery by Mary Leakey, named for the Leakeys' sponsor, Charles Boise—called *Zinjanthropus*, was even bigger than *robustus* and lived at the same time, though in East Africa. A *boisei* skull discovered in 1985 in Kenya proved not only to be particularly massive but also considerably older (2.5 to 2.6 million years) than any known *robustus* specimen. *Australopithecus boisei* must therefore have been a separate and earlier species probably not descended from *africanus*. If so, then there was more than one australopithecine lineage, and the previously held idea that the australopithecines became increasingly robust through time must be reversed. As a result of this one find, there no longer are widely accepted ideas as to who gave rise to whom.

Throughout their history, the australopithecines manifest a regular progression from apelike characteristics to human ones. All the australopithecines walked upright, a fact that evidently encouraged increasing height, hand specialization, and brain development. Gradual changes in australopithecine dentition, moreover, suggest not only changing diet but revised habits as well. With advanced hands and evolving arms and shoulders, *Australopithecus* probably carried loads and used weapons, regardless of whether he was capable of making them. Though australopithecines may have done some hunting, they probably depended primarily upon foraging and scavenging—filching from leopard kills, for example.

The Evolution into *Homo*

At what point *Australopithecus* evolved into *Homo* is unclear, in part because the distinction between them is rather arbitrary. Though still regarded by some researchers as an advanced form of *Australopithecus* (that is, as more than one species) *Homo habilis* (handy man), another Leakey family discovery, is otherwise usually accepted as the earliest member of a distinctly human line. He was still only about five feet high (perhaps an optimum height for the environmental conditions), but had a larger brain, a rounder head, a less projecting face, advanced dentition, reduced jaws, and essentially modern feet. Stone artifacts have been found in close association with his remains; *habilis*, who lived between 2 and 1.5 million years ago, almost certainly made tools, hunted, built shelters, gathered plants, and scavenged. He is assumed to be ancestral to *Homo erectus*, and may have exterminated *Australopithecus*.

In 1859, when the prehistory of humankind was first broadly acknowledged, the only remains then known belonged to Neanderthal man (now called *Homo sapiens neanderthalensis*). Until 1924, when *Australopithecus* was discovered, all the intervening finds (excluding "Piltdown man," a deliberately planted fake) have since been classified as varieties of *Homo erectus* (erect man—a designation assuming that its predecessors stooped). Of these, the two best-known are Java man, discovered in 1891 by Eugène Dubois in Java, and Peking man, found in China by Davison Black in 1926. Only after a number of specimens had accumulated was it realized that Java man and Peking man were examples of the same species. An exceptionally complete *Homo erectus* skeleton was discovered in Kenya in 1984 and dated at 1.6 million years old. Overall, *Homo erectus* lived from some time before 1.6 million years ago to as recently as two hundred thousand years ago. He probably evolved in Africa but migrated from there (as no previous hominid had) to Europe and the Pacific shores of Asia. This species was as tall as modern humans, but more robust overall, with a noticeably thicker, somewhat "old-fashioned" skull that still included prominent brow ridges and a sloping forehead. He had large, projecting jaws, no chin, teeth that were larger than ours; he also had a bigger brain. *Homo erectus* was not only widespread in distribution, but also showed considerable regional variation. His success as a colonizer was attributable in large part to his intelligence, which was manifested in standardized but increasingly sophisticated toolkits, big-game hunting (almost certainly cooperative), the use of fire, and advanced housing. He lived during the Pleistocene, or glacial, epoch, and was probably stimulated to use his creative abilities by the deteriorating environments he sometimes encountered. Very late examples of *Homo erectus* are sometimes alternatively classified as *Homo sapiens*. Despite some continuing opposition, it is now usually accepted that *Homo erectus* gave rise to *Homo sapiens*.

Searching for the Fossil Remains

Considering the efforts that have been made to find them, hominid fossils are remarkably few. This is the case for three main reasons: First, the early hominids (unlike modern humans) did not exist in huge numbers; second, the majority of their bones were not preserved as fossils; and third, it is certain that only a small proportion of the hominid fossils that do exist have been found.

The hominid line evolved in Africa, and its earlier members (including the australopithecines and *Homo habilis*) have been found only there. *Homo erectus* was both more widespread and more numerous, but none of these types practiced ritual burials (Neanderthals were the first to do that), so the most usual agent of presentation was some sort of nonhuman carnivore. Predators, such as the large cats, might actually have hunted the early hominids; in any case, they certainly scavenged hominid carcasses. Hyenas and other cleanup animals then grabbed what they could, taking the leftover pieces to their dens in limestone caves. (There must be some truth to this scenario, because leopards and hyenas have left their toothmarks on australopithecine bones.) The gnawed bones, now thoroughly disarticulated, were scattered about the cave—and eventually solidified by limy deposits into a bone breccia.

When twentieth century investigators find such embedded hominid bones, or suspect their presence, they collect chunks of the breccia and dissolve the limy matrix with acetic acid, a procedure that does no harm to fossil bones. It is unlikely that any of the latter will be whole. Once the fragmented bones have been freed from the matrix, they are cleaned, preserved, sorted by type, and tallied. Whether big or small, routine or not, each must be identified. By far the great majority of the bones will belong to antelope of various kinds; less than one in a thousand, normally, proves to be hominid.

Such procedures are standard when dealing with cave deposits at the famous South African australopithecine sites of Sterkfontein, Kromdraai, and Swartkrans, all of which are adjacent to each other and to Pretoria. At Olduvai Gorge in Tanzania, where the Leakeys and others have found both australopithecine and *Homo habilis* remains, the geology is entirely different. Here, the

Image Not Available

erosive power of a now-defunct river has exposed primarily volcanic sediments that once bordered a shifting saline lake. The disadvantage of this site is that it lacked any obvious place for the location of bones; years of determined effort were required to locate productive sites. The advantages of the site were that the presence of early humans was virtually assured because stone tools were scattered about plentifully (whole campsites were eventually found); the bones involved had not been dragged about and disarticulated by animals; and the involved stratigraphy made fairly precise dating at least theoretically possible. In general, a specimen from Olduvai Gorge brings with it more useful information than does one found in the South African caves. Still other sites have provided additional unique information.

The collection, preservation, and interpretation of hominid fossil bones is very much a multidisciplinary effort. In particular, detailed geological understanding of the site is essential. Only through stratigraphical analysis, usually, can the age and situation of the discovered fossil be understood. Stratigraphy aside, certain rocks can also be dated according to the radioactive elements they contain. More often, bones can be dated approximately because they occur in association with a particular assemblage of animal bones, the animal species themselves being of reliable short-term ages. In some cases, pollen samples have been of use. All this additional information, together with comparative anatomical analysis, helps to give hominid fossils a defensible identity.

Homo sapiens Facts

Classification:
Kingdom: Animalia
Subkingdom: Metazoa
Phylum: Chordata
Subphylum: Vertebrata
Superclass: Tetrapoda
Class: Mammalia
Subclass: Theria
Infraclass: Eutheria
Order: Primates
Suborder: Anthropoidea
Superfamily: Hominoidea
Family: Hominidae
Genus and species: Homo sapiens
Geographical location: Originally Africa, now spread to all continents
Habitat: Originally savannas, now spread to all habitats
Gestational period: Nine months
Life span: Originally a maximum of twenty-five years; now over one hundred years, with averages from forty to eighty years, depending on habitat
Special anatomy: Large, well-developed brain; upright, bipedal posture; opposable thumbs; larynx, vocal chords, and tongue adapted to produce a wide variety of sounds for language

The Search for Ancestors and Origins

Thinking human beings have always been fascinated with the concept of origins, and of all origins, none has been of more interest than that of humans. Human groups have asserted deeply meaningful identities by attributing their present being to a particular origin. Most of these psychologically necessary genealogies relied upon some divine agency to explain human existence. From a surprisingly early time, however, civilized humans (such as the Greeks) recognized that there had been a time when humankind did not know the use of metals. Subsequently, many thinkers took the concept of cultural evolution for granted.

By the seventeenth century C.E., anatomy had become a popular field of study. Comparisons soon established how like human anatomy that of the higher primates was. By the mid-eighteenth century, Carolus Linnaeus, the originator of modern biological classification, even ventured to place man and the apes within the same family. Yet this classification did not imply any necessary common ancestry. Linneaus and others of his time created the notion that individual species arose through a special, divine plan. The idea of special creation lost credibility when the fact of extinction became established at the end of the eighteenth century and as the diversity of species and varieties came increasingly to be appreciated. Nature, moreover, was no longer seen to be a benign reflection of its creator. As opinions of a distinctly human nature likewise declined, the realization that humans are animals encountered lessening resistance.

Before human evolution was generally accepted during the twentieth century, the evolution of cultures, language, law, institutions, and at least some animals had already been established. Though the idea was there, reliable evidence for the biological evolution of humans remained elusive. Before 1891, the only known prehistoric human bones belonged to Neanderthals; they were quickly and effectively dismissed as pathological freaks. Since Raymond Dart's Taung child of 1924 was likewise dismissed with ridicule, only a few specimens of what would later be recognized as *Homo erectus* (Java man and Peking man) survived to satisfy the now fashionable quest for a "missing link." (There are still innumerable missing links, but the essential connection between ancestral apes and man was confirmed by the discovery of australopithecines.) It was Robert Broom who, during the 1930's, established the reality of the australopithecines and, by implication, of human evolution.

Though the evolution of the hominid line is certainly a worthwhile scientific topic, it has always been regarded as much more than that, because the claims to ancestry define humanity. Yet the formal constraints of science are limited. In a remarkable series of thirty-nine papers (published between 1949 and 1965), for example, Raymond Dart promulgated an interpretation of the australopithecines as aggressive, predatory, and cannibalistic hunters. Because of the recurrent wars in which civilization had engaged during this period and shortly before, this image of human (or almost human) nature appealed to the popular imagination—so much so that less technical restatements of the same views by Robert Ardrey were not only commercially successful but also politically influential. Interpretations of australopithecine and early hominid behavior have subsequently changed, however—many now see these species as abject scavengers disputing the possession of already picked-over animal corpses with hyenas. It is arguable whether such changing interpretations are attributable to scientific advances or are the result of changing philosophical views of humanity.

—Dennis R. Dean

See also: Apes to hominids; Convergent and divergent evolution; Evolution: Animal life; Evolution: Historical perspective; Extinction; Fossils; Genetics; Homo sapiens and human diversification; Human evolution analysis; Neanderthals; Primates.

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HOMO SAPIENS AND HUMAN DIVERSIFICATION

Type of animal science: Anthropology
Fields of study: Anthropology, evolutionary science, ecology, genetics, human origins, systematics (taxonomy)

By studying fossil, cultural, and genetic evidence, scholars have attempted to trace the evolutionary development of the human species. It is believed that the earliest form of Homo sapiens *appeared about 350,000 years ago and that the first modern humans (*Homo sapiens sapiens*) appeared somewhat before 100,000 years ago, with racial diversification following thereafter.*

Principal Terms

GENE POOL: the total collection of genes available to a species

GENERALIZED: not specifically adapted to any given environment; used to describe one group of Neanderthal humans

HOMINID: any living or fossil member of the taxonomic family Hominidae ("of man") possessing a human form

HOMINOID: referring to members of the family Hominidae and Pongidae (apes) and to the taxonomic superfamily of Hominoidae

MORPHOLOGY: the scientific study of body shape, form, and composition

NATURAL SELECTION: any environmental force that promotes reproduction of particular members of the population that carry certain genes at the expense of other members

PLEISTOCENE EPOCH: the sixth of the geologic epochs of the Cenozoic era; it began about three million years ago and ended about ten thousand years ago

WÜRM GLACIATION: the fourth and last European glacial period, extending from about seventy-five thousand years ago to twenty-five thousand years ago

All human beings on the earth today are highly adaptive animals of the genus and species *Homo sapiens sapiens* (Latin for "wise, wise human"). In terms of physical structure and physiological function, *Homo sapiens sapiens*—modern humans—are classified taxonomically as members of the order Primates, which is part of the class Mammalia. Since humans and other members of Primates (monkeys and apes) are biologically related, scientists presume both groups to be the products of an evolutionary process similar to that which affected other divergent categories of animals. The evolutionary process that produced *Homo sapiens sapiens* from previously existing species is also believed to account for diversifications within the modern human population such as racial differentiation.

Modern humans and modern apes (the two most closely related of modern primate species) are believed to possess a common biological ancestry, or line, that diverged perhaps five or six million years ago. The scanty fossil record of this early period, in conjunction with modern genetic studies, seems to indicate that the branch of hominoid evolution which eventually led to *Homo sapiens sapiens* first gave rise to the earliest hominid type, called *Ramapithecus*.

Next to appear, several million years ago, during the late Pliocene epoch, were the early forms of *Australopithecus*, which existed in Africa. They share certain characteristics with both humans and apes. Their brains are larger than those of apes but smaller than those of humans. There have been four species of *Australopithecus* identified.

The Emergence of the Genus *Homo*

Examples of the first undisputed members of the genus *Homo*—true human (though not *sapiens*)—appear in the fossil record about 1.5 million years ago. Samples of *Homo erectus* ("upright human") have been found in China, Africa, Java, and Europe. This creature habitually walked upright, made shelters, and used sophisticated tools. *Homo erectus* is also very important, since it is the first hominid to have used fire purposefully. It was suggested by John E. Pfeiffer, in a 1971 article entitled "When *Homo erectus* Tamed Fire, He Tamed Himself," that this first domestication of a natural force was a tremendous evolutionary step, changing the fundamental rhythms of life and human adaptability to environments. Most scholars accept the premise that *Homo erectus* was the hominid grade intermediate between the australopithecines and *Homo sapiens*.

Exactly when, where, and how advanced members of the species *Homo erectus* evolved into *Homo sapiens* are key questions in the study of human evolution, and they are questions that resist resolution. It might be thought that the closer one comes, in terms of time, to modern man, the easier it would be to find the answers. In actuality, such is not the case. The ancestral line or lines leading to modern man become hazy beginning approximately 500,000 years ago. Direct fossil evidence of the earliest members of the species *Homo sapiens* is scarce; moreover, finds of modern human fossils in the Middle East have intensified the debate about the immediate ancestry of *Homo sapiens sapiens*. All the evidence indicates, however, that the middle to upper Pleistocene epoch (beginning about 350,000 years ago), known as the Paleolithic or old stone age in archaeological terms, witnessed the emergence of early *Homo sapiens*.

The Earliest *Homo Sapiens*

In 1965, hominid fossil remains were found at a site named Vértesszöllös, near Budapest. They consisted of some teeth and an occipital bone (a bone at the back of the skull). The site also yielded stone tools and signs of the use of fire. Several features of the find recall *Homo erectus*, but the estimated cranial capacity of 1,400 cubic centimeters is well into the normal range for *Homo sapiens*. The age of the site was established at 350,000 years B.P. (before the present). These remains have been attributed to a *sapiens-erectus* intermediate type on the grounds that the remains, and the site, show a mixture of elements reflective of the transitional hominid evolutionary process. Such an assessment places Vértesszöllös man at the root of the *Homo sapiens* evolutionary line, some 100,000 years earlier than other specimens.

A better-known example of early *Homo sapiens* comes from a gravel deposit at Swanscombe near London, England. In 1935, 1936, and 1955, three related skull pieces were unearthed that fit together perfectly to form the back of a cranial vault with an advanced (over *Homo erectus*) cranial capacity of about 1,300 cubic centimeters. This has been dated to around 275,000 to 250,000 years B.P. A more complete skull of approximately the same age (dated to the Mindel-Riss interglacial period about 250,000 years B.P.) was found at Steinheim, in southern Germany, in 1933. Swanscombe's and Steinheim's advanced morphological characteristics, in combination with relatively primitive ones, such as low braincase heights, suggest that they are primitive members of the species *sapiens* and are representatives of a population intermediate between *Homo erectus* and *Homo sapiens*.

The finds at Swanscombe and Steinheim have been augmented by others from France and Italy, and especially from the Omo River region in southern Ethiopia. One Omo skull displays more mixed features (between *erectus* and *sapiens*) including flattened frontal and occipital areas, a thick but rounded vault, large mastoid processes (pointed bony processes, or projections, at the base of the skull behind the ears), and a high cranial capacity. Another skull is more fully *sapiens*, or modern in appearance. Some paleoanthropologists assert that the Omo group of fossils also helps bridge the gap between advanced *Homo erectus* and *Homo sapiens*.

Neanderthal Man

The best-known examples of early *Homo sapiens* come from a group of fossils known collectively as Neanderthal man. Their name derives from the place where the first fossil type was discovered in 1865, the Neander Valley near Düsseldorf, Germany. Similar Neanderthal fossil types have been found at more than forty sites in France, Italy, Belgium, Greece, the Czech Republic Slovakia, the former Soviet Union, North Africa, and the Middle East.

Neanderthal fossils tend to show an aggregate of distinctive characteristics that at one time led to their being regarded as a separate human species, *Homo neanderthalensis*. They are generally regarded as a subspecies of humans, with the designation *Homo sapiens neanderthalensis*. The characteristic features of their morphology include large heads with prominent supraorbital tori (thick brow ridges), receding jaws, stout and often curved bones, and large joints.

Most important Neanderthal fossils disclose large brain capacities (1,500 cubic centimeters) and are found in sites revealing complex and sophisticated cultures. These two facts clearly separate Neanderthal humans from more primitive "presapiens" species that exhibit some of the same morphological features. Neanderthalers generally stood fully erect between 1.5 and 1.6 meters in height; they were not the stoop-shouldered brutes of early characterizations. They lived during the last glaciation (the Würm glacial stage) in Eurasia. The sites from which most examples of the Neanderthalers have been recovered have commonly yielded tools of the Mousterian complex, a stone-tool industry named for the kind found at Le Moustier, France, and dating from about 90,000 to about 40,000 years B.P.

In fact two groups of Neanderthal humans seem to have existed. The first are referred to as classic Neanderthalers from such sites as Germany, France, Italy, Iraq (Shanidar man), and the former Soviet Union. The second group, known as either generalized or progressive Neanderthalers, lived contemporaneously with, as well as later than, classic Neanderthal humans. They display a combination of modern *sapiens* features and typical Neanderthal characteristics (especially the prominent supraorbital torus, the forehead ridge). Included in this category for the sake of simplification are those specimens termed neanderthaloid. Examples include Rhodesian man (from Zambia, formerly Northern Rhodesia) and Solo man (from Java), both unearthed at upper Pleistocene deposits (100,000 to 10,000 B.P.). Neanderthalers were cave dwellers and were well adapted to cold conditions (especially the classic Neanderthal variety). They used fire, manufactured stone flake tools, and buried their dead with care. They also seem to have practiced fairly complex religious rituals.

Cro-Magnon Man

Neanderthals were a successful group for many thousands of years, flourishing from about 127,000 B.P. to 37,000 B.P., with a wide distribution geographically. Neanderthal traces suddenly and mysteriously disappear from the fossil record, however, and they seem to have been superseded around 37,000 B.P. by other *Homo sapiens* with a more advanced culture and different morphology. In Europe, these are known as the Cro-Magnon peoples, so named for the Cro-Magnon cave near Les Eyzies in southwestern France, where the first skeletons were found in 1868 and where more than one hundred skeletons have since been discovered. Indeed, Cro-Magnon skeletal anatomy is virtually the same as that of modern European and North African populations. The skull is relatively elongated, with a large cranial capacity of about 1,600 cubic centimeters; the brow ridges are only slightly projecting. The average height of Cro-Magnon man was between 1.75 and 1.8 meters.

Cro-Magnon humans produced a culture that, in variety and elegance, far exceeded anything created by their predecessors. They made weapons and tools of bone and stone, stitched hides for clothing, and lived in freestanding shelters as well as caves. Some Cro-Magnon people produced beautiful cave paintings (they have been found in southwestern France and northern Spain) and bone carvings, and they modeled in clay. Though Cro-Magnon samples are the best-known examples of early *Homo sapiens sapiens*, mounting fossil evidence from sites outside Europe as well as genetic research performed in the 1980's suggests a much older date of origin for the emergence of modern man.

At Qafzeh, a cave near Nazareth, Israel, anatomically modern fossils classified as *Homo sapiens sapiens* were discovered in 1988 and reliably dated to 92,000 years B.P. In addition, newer fossil finds of progressive Neanderthalers from Kebara Cave in Israel, taken together with earlier Neanderthal finds from the caves of et-Tabun and es-Skhul, also in Israel, make it certain that progressive Neanderthalers and modern humans coexisted for many thousands of years.

Anthropologists have puzzled over the disappearance of the Neanderthals and, more important, over where they fit in the human family tree. It appears unlikely that classic Neanderthal humans were in the direct ancestral line of modern *Homo sapiens sapiens*. Reasons for their sudden disappearance are believed to include a combination of factors: extinction because of disease, lack of adaptation to the warmer climate following glaciation, and annihilation by the more advanced sapient groups.

Many scholars have considered the classic Neanderthals to be a cold-adapted, specialized side branch from the modern human line that became extinct as the climate became warmer. The generalized or progressive Neanderthals are considered by some to have avoided this specialization, perhaps continuing to exist through adaptation and ultimately being absorbed by flourishing modern human populations during the late Pleistocene epoch.

The Emergence of Modern Humans

Although the exact time place, and mode of the origin of the modern human species cannot yet be determined, genetic studies point to a date before 100,000 years B.P. Examination of mitochondrial DNA (mtDNA) from a sampling of present-day humans representing five broad geographic regions has allowed researchers to propose a genetic family tree and calculate roughly (assuming a fairly constant mutation rate) a temporal origin for the modern human population. Further studies seem to indicate that the modern human ancestral line emerged between 280,000 years and 140,000 years B.P. Genetic evidence, in concert with fossil finds, makes it plausible that a common ancestral population for *Homo sapiens sapiens* appeared in sub-Saharan Africa or the Levant (in the eastern Mediterranean region). Regional differentiation occurred, followed by radiation outward to other areas. The range of genetic and anatomical variability exhibited by fossil remains of modern humans is no greater than that known for the extant races of modern times.

During the late Pleistocene epoch (approximately 40,000 to 11,000 years B.P.) five different racial groups seem to have developed on the Eurasian and African landmasses. The last glaciation, approximately 30,000 to 10,000 years B.P., absorbed enough water to lower the oceans ninety meters below present levels. Emerging land bridges allowed people to move from Asia into North America, Australia, and elsewhere. In time the major racial groups became subdivided into smaller ones that resulted in the major races seen in modern times.

This view of racial diversification emphasizes the effectiveness both of geographic barriers in reducing free gene flow among varied groups of *Homo sapiens* and of environmental pressure in selecting different adaptive responses from the gene pool. These are also key factors in the entire evolutionary process by which modern humans developed over epochs into their present taxonomic position in the animal kingdom.

The Study of Paleoanthroplogy and Physical Anthropology

The study of human evolution is primarily the concern of the physical anthropologist and the paleoanthropologist. Evolution may be defined as change in the genetic composition of a population through time. Because evolution is thought to operate according to several principles and factors, modern human evolutionary theory is studied in the light of ideas and practices taken from different disciplines, including archaeology, biochemistry, biology, cultural anthropology, ecology, genetics, paleontology, and physics.

Early investigations into human evolution sought to establish the sequence of the human ancestral line through chronological and morphological analyses of hominid fossil remains (bones and teeth), thus placing them in their proper phylogenetic context (their natural evolutionary ordering). This remains the principal method of study, but it has been augmented by sophisticated techniques in fossil dating and new avenues of exploration into the evolutionary process, such as genetic research.

Image Not Available

Determination of the accurate age of a fossil is most important, since it sets the fossil in a correct stratigraphic context that allows comparison with remains from the same geologic layer or level a great distance away. Accurate dating also has helped determine the order of succession for fossils that could not be established on morphological grounds alone.

The most valuable absolute dating methods are the radioactive carbon technique, which can effectively date specimens between 60,000 years B.P. and the present; the potassium-argon technique, which most easily dates material older than 350,000 years B.P.; and the fission-track method, which helps bridge the gaps between other methods. These methods are based on the constant or absolute rates at which radioactive isotopes of carbon, potassium, and argon decay. When absolute dating is impossible, investigators have ascribed a relative age to fossil remains by noting the contents of the layer of rock or the deposit in which the remains were found. A layer containing remains of extinct animals is likely to be older than one containing remains of present forms.

In conjunction with dating, anatomical studies of fossil remains and comparisons with the morphological features of known hominid types, as well as comparisons to primate skeletal structures, have been primary approaches to the study of the evolutionary path of *Homo sapiens*. The species *Homo sapiens* (of which the modern human races compose a number of geographical varieties) may be defined in terms of the anatomical characteristics shared by its members. In general, these include a mean cranial capacity of about 1,400 cubic centimeters, an approximately vertical forehead, a rounded occipital (back) part of the skull, jaws and teeth of reduced size, and limb bones adapted to fully erect posture and bipedalism. Scientists assume that any skeletal remains which conform to this pattern and cannot be classified in other groups of higher primates must belong to *Homo sapiens*.

It is striking that the anatomical differences observed between *Homo erectus* and *Homo sapiens* have been confined to the skull and teeth. The limb bones thus far discovered for both are similar (though *erectus* appears more robust). Cranial capacity and morphology continue to be the dominant determining boundary separating sapient and presapient human species.

The Contribution of Other Sciences and Social Sciences

Human adaptability studies, using techniques from physiology, demographics, and population genetics, investigate all the biological characteristics of a population that are caused by such environmental stresses as altitude, temperature, and nutrition. It is believed that these normal stresses acted as genetic selectors in prehistoric times and continue to do so. Such racial variants as skin color and body hair are observable products of these stresses. The investigation of climatic changes during prehistoric epochs as revealed in the geologic record is important for understanding those pressures affecting the evolutionary history of man.

Genetic studies have become indispensable to the study of human evolution. Four forces have been identified as fundamental in the evolutionary process: mutation, natural selection, gene flow, and genetic drift. Since mtDNA is inherited through the female, it is possible to calculate how much time has elapsed since the mutations that gave rise to present variations originated in prehistoric populations.

Also important to the study of the evolution of *Homo sapiens* is the examination and classification of cultural remains preserved at hominid fossil sites. Not only can the relative date of a fossil be supported, but sometimes it is also possible to reconstruct the environmental situation that may have influenced the evolutionary process operating in a population. Cultural response is an integral part of hominid adaptation, and it in turn influences natural selection. Technology changes the physical and economic environment, and economic changes alter the demographic situation. Humans continue to promote or influence their own evolution by willingly or unwillingly altering the environment to which they must adapt.

The modern methods useful for investigating the evolutionary history of *Homo sapiens* are multidisciplinary. While each of them reveals an aspect of the emergence of modern man and complements the other methods of study, emphasis is placed on careful fieldwork, accurate dating, and comparative morphological analyses of hominid fossil remains. Increasing in importance, however, is the accumulating wealth of genetic data on human population relationships.

Human Evolution in the Context of Animal Evolution

Increasing attention is being given to the biological and behavioral changes that led to the emergence of *Homo sapiens sapiens*—the last major event in human evolution. Mounting evidence continues to push backward in time the point at which modern *Homo sapiens* made his appearance in the evolutionary scheme. The finds at Qafzeh, for example, indicated that modern man arose fifty thousand years earlier than had previously been thought. A clearer understanding of the evolutionary history of modern *Homo sapiens* has not only helped to define the place of the modern human species more accurately in relation to the rest of the animal kingdom but also helped to illuminate the pressures, adaptations, and changes that have made humans what they are.

The accumulating data on the evolutionary appearance of *Homo sapiens* have allowed biologists and anthropologists to see the rise of modern man as part of the evolutionary development of the animal kingdom in general and of primates in particular. The primates that exist today make up a remarkable gradational series that links *Homo* *sapiens sapiens* with small mammals of very primitive types.

Through the pressures and process of evolution (including adaptation and natural selection), *Homo sapiens* has become one of the most successful and adaptive animals that ever lived, because he came to possess an elaborate culture (culture is based on learned behavior). The key is *Homo sapiens*' superior mental capacity. Only human beings can assign arbitrary descriptions to objects, concepts, and feelings and can then communicate them unambiguously to others. In the late Middle Pleistocene, the hominid branch that gave rise to early *Homo sapiens* witnessed an increase in brain size, complex social organizations, continual use of fire, and perhaps even language. As to what initiated these changes, many have suggested tool use and, in turn, a hunting economy.

In a classic article published in 1960, entitled "Tools and Human Evolution," Sherwood Washburn argued that the anatomical structure of modern man is the result of the change, in terms of natural selection, that came with the tool-using way of life. He stated that tools, hunting, fire, and an increasing brain evolved together. Washburn also argued that effective tool use led to effective bipedalism—another significant characteristic of *Homo sapiens:* Man is different from all other animals because he became a user of increasingly complex tools.

The other behavioral pattern that is seen to have been of utmost importance to sapient evolution is big-game hunting. Early *Homo sapiens* was undoubtedly a big-game hunter, as were all of his successors until approximately 8,000 years ago. It has been argued that human intellect, interests, emotions, and basic social life are the evolutionary products of the success of hunting adaptations. Success in hunting adaptation dominated the course of human evolution for hundreds of thousands of years. The agricultural revolution and the industrial and scientific revolutions are only now releasing human beings from conditions characteristic of 99 percent of their evolutionary history.

Scholars have suggested that research into human origins and development is much more relevant than is often realized. It has been argued that, although man no longer lives as a hunter, he is still physically a hunter-gatherer. Some investigators in the field of stress biology, the study of how the human body reacts to stressful situations, feel that man is biologically equipped for one mode of life (hunting) but lives another. Thus, there would be some link between an emotional reaction, such as explosive aggression, and human evolutionary history. Tools and more efficient hunting helped produce great change in hominid evolution and made man what he is. Humans continue to be users of increasingly complex tools, such as computers, and perhaps this continued development of technology may determine the future evolutionary path of *Homo sapiens*.

—*Andrew C. Skinner*

See also: Apes to hominids; Convergent and divergent evolution; Evolution: Animal life; Evolution: Historical perspective; Extinction; Fossils; Gene flow; Genetics; Hominids; Neanderthals; Natural selection; Nonrandom mating, genetic drift, and mutation; Primates; Systematics.

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HORMONES AND BEHAVIOR

Type of animal science: Physiology
Fields of study: Ethology, neurobiology

Hormones exert a tremendous influence on behavior by heightening perceptions, altering motivational levels, and controlling drives, including hunger, sex, and the urge to migrate.

Principal Terms

ABLATION: the technique of removing a gland to determine its function and observe what effects its removal will precipitate

ANDROGENS: masculinizing hormones, such as testosterone, responsible for male secondary (anatomical) sex characteristics and masculine behavior

BEHAVIOR: an animal's movements, choices, and interactions with other animals and its environment

BIOLOGICAL CLOCK: a timekeeping mechanism that is "endogenous" (a part of the animal) and capable of running independently of "exogenous" timers such as day-night cycles or seasons, although the clock is normally set by them

ENDOCRINE SYSTEM: a collection of glands that secrete their products into the bloodstream

ESTROGEN: a feminizing hormone responsible for female secondary (anatomical) sex characteristics and sex-related behaviors

PROLACTIN: a hormone responsible for secretions of milk from the mammary glands of mammals and from the crops of birds

RECEPTOR MOLECULE: a molecule on the cell membranes of target tissues that binds to the hormone molecule and initiates the action of the hormone

Behavioral differences are usually attributed to two causes: differences in experience (learning) and differences in heredity (genes). Hormonal interaction involving an organism, its experience, and the highly specific behaviors that result are well illustrated by Daniel Lehrman's 1964 study of the ring dove, a small relative of the domestic pigeon.

A male ring dove begins courtship by bowing and cooing to the female when they are placed together in a cage. Toward the end of the first day of courtship, the birds choose a location and start building a nest. The doves court, nest-build, and mate, and the female lays an egg about five o'clock in the afternoon on the seventh to eleventh day. A second egg is laid about nine o'clock the next morning. The male sets for about six hours at midday, and the female occupies the nest the rest of the time. After fourteen days of incubation, the eggs hatch, and the parents feed the squabs crop milk, secreted from the lining of the adult dove's crop (enlarged gullet). At about two weeks of age the squabs (fledgling birds) begin pecking at grain, and the adults feed them less and less. With feeding chores diminished, the male begins bowing and courting, the pair start nest-building, and the cycle repeats itself.

The Hormonal Triggers of Behavior

The simplicity of this description belies the hormonal ferment going on beneath the placid exterior. The courtship ritual causes the production and release of estrogen and progesterone, hormones responsible for setting behavior and for the development of the oviduct. The oviduct develops from eight hundred milligrams, when the doves are placed together, to four thousand milligrams, when the first egg is laid. Birds presented with nests already containing eggs when they are first paired will build nests on top of the eggs. Even if the eggs are returned to the top of the nest by the investigator, the doves will not set until they have engaged in nest-building for five to seven days. On the other hand, if the doves are first injected with progesterone, 90 percent will set within three hours after pairing. Courtship and nest-building play a vital role in creating the hormonal conditions necessary for setting behavior. Development of the crop is, in turn, initiated when setting begins. Setting behavior causes the release of prolactin, which stimulates crop development and feeding behaviors. Unpaired doves injected with prolactin will develop crop milk and will feed squabs when exposed to them even if they have not mated. While they will feed squabs, however, they will not sit on eggs, because they have not courted, engaged in nest-building, or developed the hormonal balance necessary to support setting behaviors.

This ring dove study indicates that the behavior of one individual can alter the behavior and the hormonal balance of another individual; that an individual's behavior can alter its own hormonal balance and, hence, its own behavior; and that inanimate aspects of the environment (nest and eggs, for example) can alter an individual's hormonal balance and, hence, its behavior. The interactions among these three factors are complex. For example, the male's behavior (courting) changes the female's behavior (nest-building), which changes her hormonal balance (estrogen and progesterone), which causes her to alter the external environment (lay eggs in the nest), which affects the pair's behavior (setting), which changes their hormonal balance (prolactin), which stimulates them to feed the squabs.

Fetal Hormones Affecting Adult Behavior

Hormones produced by developing organisms have marked effects on adult behaviors. In mammals, the fetal testis becomes active and produces testosterone, then becomes inactive before birth and remains so until puberty. The changes resulting from this brief surge of testosterone are remarkable. They include the anatomical features that distinguish male and female genitalia, changes in neural anatomy, and the sensitivity of nervous (and other) tissues to adult hormones.

Rat and mouse fetuses have several littermates, which develop side by side in a common uterus, like peas in a pod. Male mice that develop between two male embryos are more aggressive as adults than males developing between females. Similarly, females that develop between two male embryos are more aggressive as adults than females that develop between other females. In another study, females from litters that were predominantly male showed more masculine behavior (such as the mounting of other females) than females from predominantly female litters. The explanation is that testosterone produced by the male embryos' testes is absorbed into the bloodstream of sibling embryos, altering their nervous systems and hence their behaviors. In cattle, testosterone produced by a bull calf twin affects the development of his heifer twin to the extent that she is usually sterile.

Scientists have shown that pregnant rhesus monkeys treated with testosterone produced offspring that showed rougher play and more threat behavior than usual. Male rhesus monkeys experience a decrease in blood testosterone levels within six hours after losing a fight to another male and are more submissive. These studies indicate that hormones play an important role in determining male-female behavioral differences.

Many biological phenomena are repeated or change intensity over and over again throughout the life of an individual. Examples include sleep-wake cycles, menstrual cycles, and the migration cycles of birds; these are repeated approximately once a day, once a month, and once a year, respectively. The regularity of these cycles led biologists to propose a "biological clock." The golden-mantled ground squirrel avoids freezing temperatures by going into hibernation once a year. Even if these squirrels are kept in constant conditions of light and temperature to deprive them of seasonal cues, they will enter hibernation once a year. These and other data lead researchers to believe that the clock resides within the animal. Although it can be reset by environmental cues, it can also run independently of them.

Hormones, Seasons, and Mating Behavior

A white-crowned sparrow, nesting in central Alaska, experiences dramatic seasonal changes and migrates to the southern United States or Mexico (more than three thousand kilometers) to avoid freezing. Central Alaska's short summer demands that the sparrow fly north as early in the spring as is safe and that it be prepared for mating and rearing chicks when it arrives. During the winter, the gonads atrophy to 1 percent or less of their breeding season weight. The bird's ability to sense the approach of spring depends on its sensing the increase in daylight. During the short winter days, the sparrow is content to stay in Arizona or Mexico, but as day length increases to fourteen or fifteen hours, the bird's hypothalamus releases hormones that stimulate the pituitary to release prolactin and gonadotropic hormones. The gonads respond by increasing in size and producing additional hormones, which stimulate the bird to begin its long migration.

When the male white-crown arrives at his breeding grounds in central Alaska, he chooses a nesting territory, attacks any male territorial intruders, and attempts to attract a mate with his constant singing. Each female chooses a mate and helps him defend the nesting site. In the next few days she feeds to gain nutrients for egg production, and her estrogen levels rise rapidly, stimulating her to solicit mating. Once the eggs are laid, the gonads of both birds begin to atrophy, estrogen and testosterone levels decline, and prolactin levels increase and stimulate feeding of the young. As the gonads atrophy, the birds become less aggressive and the male stops singing.

As the young become independent, both parents enter a "sexual refractory period," during which the gonads will not respond to artificially increased day length as they would in the spring. The birds feed voraciously, increasing body fat, which serves as fuel for the long trip south. In the next year, by early spring, the birds will have passed through the refractory period and be primed to respond to the increasing day length with a fresh hormonal flurry which will set them off on the long journey north.

Recognizing the existence of a refractory period is important. It underscores the ideas that while birds do respond to environmental conditions (day length), there is a given set of events through which the physiological machinery passes and that specific time parameters are dictated by the biological clock. White-crowned sparrows can be expected to show hormonal changes and migratory restlessness during springtime even if they had been caged and maintained in constant conditions. It is to the bird's advantage, however, to experience and recognize the seasonal changes in day length, because biological clocks tend to run a bit fast or slow. The actual measuring of day lengths allows the bird to reset that clock and arrive in Alaska at the most advantageous time for rearing a family of sparrows.

Studies of a closely related bird, the white-throated sparrow, indicate that the changes of behavior and physiology are primarily the result of two hormones: corticosterone from the adrenal cortex and prolactin from the anterior pituitary. Both hormones have daily peaks of secretion, but the timing of these daily peaks (relative to each other) changes with the seasons. If injections of these hormones are given with timing differences characteristic of specific seasons, the physiological and behavioral changes seen in the birds are characteristic of the seasons that the injections mimic.

Experimental Endocrinology

The earliest report of experimental endocrinology, in the mid-nineteenth century, demonstrated that replacements of testicular tissue would maintain comb growth and sexual behavior in castrated roosters. Techniques for determining endocrine function used today include ablation and replacement.

Hormones trigger many kinds of animal behavior, including bird migration. (Digital Stock)

Ablation (removal) of endocrine tissue results in deficiency symptoms. The effects of ablation are not always unambiguous. If the testes and accessory tissues are not completely removed when a horse is castrated, for example, tissue capable of producing testosterone remains, and the consequence is an infertile gelding that behaves like a stallion.

Hormones produced by different glands can have similar physiological effects. Both the adrenal glands and the testes produce androgens (masculinizing hormones). Sexually experienced male cats do not lose their sex drive if castrated, and researchers do not have a satisfactory answer as to why this occurs. Perhaps the adrenal hormones are sufficient to maintain established feline male sexual behavior but not sufficient to initiate it in inexperienced cats. The ablation of the adrenal glands, however, has severe consequences in terms of electrolyte and blood glucose imbalances that are life threatening. Replacement of ablated endocrine tissue can reinstate normal function. If a male cat is castrated as a kitten, it will not develop normal male sexual behaviors. If, however, a normal testis is later transplanted to the abdominal cavity (or elsewhere), normal behavior will develop.

In the early 1960's, Janet Harker became convinced that the "biological clock" controlling the daily activity cycle of the cockroach was contained in the subesophageal ganglion, a patch of nervous tissue the size of a pin head resting just below the esophagus. When she ablated this ganglion, the cockroach became arrhythmic. Harker removed the legs from a normal roach and glued the roach on top of the arrhythmic roach, surgically uniting their body cavities so that the same body fluids circulated through both roaches. The arrhythmic roach ran about the cage with an activity rhythm dictated by the rhythm of hormones released into the body fluids by the legless roach on its back.

Most hormone and behavior studies involve nonhuman species and most involve sexual behaviors. Most behaviors are oriented toward perpetuating one's species. Only those individuals with behaviors conducive to rearing offspring will provide the genetic basis for behaviors represented in the next generation. It may seem that wild, unrestrained mating would be selected for, but that makes no real sense. Mate selection, shelter-seeking, feeding, maintenance of social position, and a host of other behaviors are critical to the success of one's progeny. Individuals that produce more offspring than they can feed or protect usually rear fewer than those who produce fewer to begin with. Many predator species (owls and wolves, for example) tend not to mate in years when prey is scarce. This ultimately maximizes reproduction by reserving energies that can best be spent later. This restraint is mediated by adjusting hormonal levels. Hormones have been called the ultimate arbiters of sexual behavior.

The Endocine System, the Nervous System, and Behavior

The nervous system is usually thought of as the mediator of behavior, but the endocrine system is also a major player. Arguing that one system is more important would be like deciding whether height, width, or depth is more important in describing a box. It is useful, however, to discuss their differences. The nervous system has a shorter response time. Nerve impulses travel at speeds of up to 120 meters per second. Hormonal effects are much slower but are less transitory. If frightened by a false alarm, an animal may jump and run as a direct consequence of nervous system activity, but even after it recognizes that there is no real threat, it will be "keyed-up." This is a consequence of hormonal activity: Fright triggered the release of epinephrine (adrenaline) and norepinephrine from the adrenal glands. These hormones cause increased cardiac output; increased blood supply to the brain, heart, and muscles; decreased blood flow to the digestive tract; dilation of airways to breath more efficiently; and a significant increase in metabolic rate.

This is called the "fight or flight reaction," and it will affect behavior for several minutes and possibly for hours. These hormones enhance perceptions and elevate the responsiveness of the nervous system. In the final analysis, the understanding of hormones, what determines their ebb and flow, how they are affected by the environment, how hormones interact with one another, and how their levels are controlled by genetic programs of the individual and of the species is essential for the understanding of behavior.

—Dale L. Clayton

See also: Brain; Communication; Courtship; Endocrine systems in invertebrates; Endocrine systems in vertebrates; Hormones in mammals; Instincts; Mating; Nervous systems of vertebrates; Nesting; Pheromones; Reproduction; Reproductive systems of female mammals; Reproductive systems of male mammals; Rhythms and behavior; Sex differences: Evolutionary origins; Smell; Territoriality and aggression.

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HORMONES IN MAMMALS

Type of animal science: Physiology
Fields of study: Developmental biology, zoology

Mammals use chemical messengers called hormones for information transfer and control between different body regions. These molecules, produced and secreted from endocrine glands into the bloodstream for transport, play important roles in mammalian development from conception to death.

Principal Terms

ENDOCRINE SYSTEM: an array of ductless glands scattered throughout the mammalian body that produce and secrete hormones directly into the bloodstream

HOMEOBOX: a set of genes that encode proteins involved in development of a wide range of animal species, from nematodes to insects to mammals

HOMEOSTASIS: the maintenance of constant conditions within the internal environment of an organism, a process controlled by antagonistic hormone pairs

HYPOPHYSIS: the pituitary gland, or "master" gland, which produces and secretes at least eight protein hormones influencing growth, metabolism, and sexual development

HYPOTHALAMUS: a brain region just below the cerebrum that interconnects the nervous and endocrine systems of mammals, thereby controlling most hormone production and many body functions

NEUROTRANSMITTER: a signaling molecule that provides neuron-to-neuron communication in animal nervous systems; some double as hormones

PROTEIN HORMONE: a hormone type composed of protein, a long chain of amino acids encoded by a gene

STEROID HORMONE: a hormone type derived from cholesterol, a type of fat molecule

Mammals are vertebrate animals that have fur (hair) and that nourish their young with milk by means of mammary glands, which are modified sweat glands. Mammals include, among other animals, primates (such as humans and chimpanzees), cetaceans (such as whales and dolphins), and marsupials (such as kangaroos, koalas, and opossums). Mammals are sexually reproducing and diploid (having two copies of every chromosome). During fertilization, a sperm from the male parent unites with an egg from the female parent to produce a diploid single-celled zygote. The zygote contains all the genetic information for all the cells of the future individual. The zygote divides first into two cells, then four, eight, sixteen, thirty-two, and so on.

As the cells divide, they begin to specialize, so that different groups of cells assume unique functions. Some cells become nerve cells, others skin cells, and others blood cells. A number of factors, including hormones, contribute to differentiation.

Throughout the development of the organism, profound changes such as birth, puberty, menopause, aging, and death occur. Progressive changes in cell functions contribute to these sequential processes. Many of these developmental changes are controlled by hormones, chemical messengers that provide communication between cells located in different portions of the body via the bloodstream.

The Endocrine System

Hormones fall into the two principal categories of protein hormones and steroid hormones. Protein hormones are composed of protein—long chains of amino acids encoded by genes. Steroid hormones are derivatives of cholesterol. Both hormone types function in the same fashion: They control genes. Hormones are produced and secreted from a source endocrine gland and are then transported through the bloodstream to a target tissue, where they penetrate cells and concentrate on the control regions of genes located on chromosomes. Once at a control region, a given hormone either activates or inactivates the gene. If a gene is activated, messenger RNA will be produced, leading to protein production. If a hormone inactivates a gene, protein production will cease. A given hormone may activate certain genes and inactivate others.

Endocrine glands are ductless glands (glands that lack channels for secreting their products) that produce and secrete hormones into the bloodstream. Major mammalian endocrine glands include the hypothalamus, hypophysis, thyroid, parathyroids, thymus, pancreas, adrenals, and gonads. The hormones secreted from these glands influence many cells and each other during mammalian development.

Homeostasis, the maintenance of a constant internal environment, is a major objective of endocrine hormones. They work antagonistically (against each other) to maintain various body conditions (such as blood sugar and calcium levels) in equilibrium. Endocrine hormones work principally, but not exclusively, by negative feedback. For example, a region of the brain called the hypothalamus reacts to various body conditions by releasing hormones that stimulate the nearby hypophysis (the pituitary gland) to release certain of its hormones. The hypophyseal hormones direct other glands and tissues to respond in a particular fashion. Once bodily conditions are back to normal, the hypothalamus terminates its initial stimulatory hormones, thereby stopping the entire sequence of events.

The hypothalamus controls a number of critical body functions, including the activities of endocrine glands, body temperature, wake and sleep cycles, and appetite. Ultimately, all these functions involve some type of hormones. When various conditions occur in the body (for example, hyperthermia, which is increased body heat), genes in certain hypothalamic cells synthesize special proteins called releasing factors that are sent into the bloodstream to activate target cells in glands (in the example cited, sweat glands) located elsewhere in the body. Often, the target of hypothalamic releasing factors is a nearby endocrine gland called the hypophysis, also known as the pituitary, or "master gland."

Regulating the Reproductive Cycle

The eight hormones known to be released from the hypophysis gland are vasopressin (the "antidiuretic hormone"), oxytocin, prolactin, growth hormone, thyrotropin, adrenocorticotropic hormone (ACTH), follicle-stimulating hormone (FSH), and luteinizing hormone (LH). Vasopressin is released in response to low water levels in the blood; it stimulates the kidneys to retain water, reduce urine output, and increase blood pressure until blood water levels return to normal, upon which it will no longer be produced. Oxytocin causes muscular contractions in the uterus during childbirth and in the breast for the secretion of milk for an infant. Prolactin is present in males and females, but it is functional only in females. It stimulates milk production from fat deposits in the breast. Growth hormone causes growth in children; it is present in adults, but contributes only to the control of metabolic rate. Thyrotropin stimulates the thyroid gland to produce and secrete various hormones that control metabolism (examples: thyroxine and triiodothyronine). Adrenocorticotropic hormone stimulates the adrenal cortex, located above each kidney, to release its metabolism-controlling steroid hormones. At puberty, follicle-stimulating hormone stimulates the female ovarian follicle to mature and begin producing the steroid hormone estrogen; it directs the male testes to begin producing sperm. Also at puberty, luteinizing hormone stimulates the ovary to begin producing eggs and the steroid hormone progesterone; it directs the testes to begin producing the steroid hormone testosterone.

The hypophyseal hormones, all proteins encoded by genes, have a major impact upon metabolism and development in mammals. This is especially true for the sexual-cycle hypophyseal hormones FSH and LH. In females, puberty begins with the first menstrual cycle. Each menstrual cycle is the female body's way of preparing for a possible pregnancy. At the beginning of the cycle, the hypophysis produces high concentrations of FSH, which stimulates the ovarian follicle to develop and produce estrogen, a steroid hormone that increases body fat in regions such as the buttocks and breasts. Simultaneously, increased LH production matures the egg in the ovarian follicle and stimulates progesterone production. Progesterone causes the endometrium (the lining of the uterus) to increase its blood vessel content and thickness for receiving and maintaining a fertilized egg and for the subsequent long gestation period (nine months in humans). If the egg is fertilized by sperm, it will adhere to the endometrium, and progesterone will continue to be secreted to maintain the endometrium and the pregnancy. If the egg is not fertilized, progesterone levels will drop, estrogen levels will rise, the endometrium will be sloughed away (menstrual bleeding will occur), and the cycle will start all over again.

The primate female menstrual cycle is only one very complex example of how hormones are intricately involved in mammalian developmental processes. There are many subtler aspects of the menstrual cycle that still are not well understood, such as the identity of the hormonal signal from the fertilized egg that stimulates the female ovary to continue progesterone production for continuation of the pregnancy. All mammalian hormones are interconnected by cause-and-effect relationships. Tremendous research remains before a clear and complete picture of hormonally controlled mammalian development will emerge.

Regulating Other Functions

The thyroid gland, located in the throat region, produces several hormones (examples: thyroxine and triiodothyronine) that elevate the body's metabolic rate. The thyroid also secretes a hormone called calcitonin, which works antagonistically with the hormone parathormone produced by the adjacent parathyroid glands. When blood calcium is high (as in a condition called hypercalcemia), the calcitonin gene in thyroid cells begins producing the protein hormone calcitonin, which stimulates bone cells called osteoblasts to build more bone, thereby removing calcium from the bloodstream. Once blood calcium levels are back to normal, calcitonin production halts. In hypercalcemia, the parathormone gene in parathyroid cells begins producing parathormone (also a protein hormone) that stimulates bone cells called osteoclasts to break down bone, thereby restoring blood calcium levels but possibly contributing to osteoporosis (bones that are brittle because of calcium deficiency) and other bone-related disorders. Parathormone production is stopped once blood calcium levels are back to normal.

The islets of Langerhans in the pancreas secrete two antagonistic protein hormones, insulin and glucagon. In response to high glucose levels in the blood (as in hyperglycemia), genes in beta cells produce and secrete insulin, which directs body cells, especially liver cells, to absorb glucose and store it as a polysaccharide called glycogen. Insulin production will stop once blood glucose levels are reduced to normal. An insulin deficiency leads to prolonged hyperglycemia, a serious and often fatal disorder called diabetes mellitus. When blood glucose levels are too low (as in hypoglycemia), genes in the alpha cells of the islets of Langerhans produce and secrete glucagon, which directs body cells to break down their glycogen reserves and begin releasing glucose back into the bloodstream until normal blood glucose levels are reached, upon which glucagon production ceases.

Further endocrine glands include the adrenal cortex, located on top of each kidney, which secretes three major classes of steroid hormones: the glucocorticoids such as cortisol, which controls fat and protein metabolism; the mineralocorticoids such as aldosterone, which controls blood sodium levels; and the androgens (male sex steroids). The adrenal medulla, located internally to the adrenal cortex, is derived from nervous tissue and secretes two hormones, epinephrine and norepinephrine, that double as excitatory neurotransmitters at nerve axon endings; chemical energy transmission between nerve cells occurs at synapses, or gaps, between adjacent neurons. Neurotransmitters are protein hormones that relay electrical impulses from one neuron (nerve cell) to another throughout the trillion-cell nervous systems of mammals. Other neurotransmitters include the excitatory acetylcholine and inhibitors glycine, enkephalin, and gamma-aminobutyric acid.

The kidney secretes the protein hormone erythropoietin when the blood has a low red blood cell level; erythropoietin stimulates the undifferentiated stem cells called hemocytoblasts in the red bone marrow of flat bones (ribs, sternum) to differentiate and develop into mature red blood cells. Platelet-derived growth factor (PDGF) is released from damaged blood vessels to activate platelet cells to begin blood clotting. Macrophage colony stimulatory factor and eosinophil chemotactic factor are two hormones that both activate and attract certain respective immune system cells to the site of an infection or allergic reaction. Histamine is released from damaged tissue and causes blood vessel dilation, so that the vessels are more leaky, thus allowing hormones and other molecules to reach the injury site, eventually leading to the inflammation and itching associated with wound healing.

The hormone prostaglandin helps inflammation and contracts some smooth muscles located throughout the body; nerve growth factor stimulates the growth of sensory nerves throughout the body; and epidermal growth factor stimulates the growth of the epidermis, the outermost skin layer that is constantly being shed and replaced. Sunlight exposure to skin produces cholecalciferol, or vitamin D, which helps to stimulate bone growth and maintenance.

The hormone prolactin is responsible for stimulating milk production in mammals. (PhotoDisc)

Developing the Full Hormonal Picture

The tally of mammalian hormones extends well beyond the molecules just discussed. What is most puzzling is how the many hormones are interconnected during the control of development. Hormones control gene activities of target cells, and some simple hormone systems act antagonistically (calcitonin-parathormone, insulin-glucagon). Yet there has not emerged a clear and complete picture of the overall interactions. Hormones control an incredibly complex array of cellular activities from conception to death.

Mammalian developmental hormones have been studied using a variety of biochemical and physiological experiments: isolation and purification experiments, injection into experimental animals, studies of metabolic disorders in animals, and molecular genetics experiments. Protein structures based upon genetic and biochemical studies are well understood. Steroid hormone structures have been unraveled from studies of cholesterol biochemistry.

Dissections of experimental animals yield intact endocrine glands (such as the thyroid and pancreas) that can be used to show function. Chemical secretions from these glands can be extracted and separated into the various hormone components by several biochemical techniques such as electrophoresis, chromatography, and centrifugation. The isolated hormones can be further purified by rerunning them through these separatory techniques.

Electrophoresis involves the separation of molecules in an electric field based upon their sizes and charges. Large molecules move slowly, whereas small, compact molecules move more quickly. Protein hormones move from the negative pole to the positive pole in electrophoretic gels. Affinity chromatography involves placing membrane hormone receptor proteins on a vertical column containing a porous resin. The specific hormone type that binds to this particular target receptor protein will stick to the resin. Nonbinding hormones will wash through the column. Finally, ultracentrifugation separates molecules based upon size in incredibly high-spinning gravity fields measuring about 100,000 times the earth's gravity. These three techniques, plus a few others, are very effective in isolating and purifying hormones as well as other important molecules.

Isolated hormones have been injected into experimental organisms and organ extracts, followed by observation and recording of the animal's physiological responses. For example, injection of vasopressin reduces an animal's urine output while simultaneously producing a slight blood pressure rise. Injection of insulin lowers blood sugar levels, which is why diabetics are prescribed insulin. Such experiments require the use of experimental animals, and extracts from these animals, which has sparked considerable controversy and debate concerning animal rights. These studies are important in understanding the physiology of the human body.

Genetic studies such as cloning and DNA sequencing have identified genes that may encode other developmental hormones. Discovery of the homeobox within the genes of all mammals indicates that there are some proteins (hormones) that control basic pattern development in mammals during early embryonic development. Some researchers believe that there may be certain hormones that accelerate aging and cause death in later life.

Hormones as a Key to Understanding Genes

All mammals start as a single-celled zygote—an egg that has been fertilized by a sperm—that undergoes a rapid sequence of mitotic divisions until it reaches the stage of a hollow, microscopic ball of identical cells called the blastula. Signaling molecules called hormones stimulate the blastula to fold in upon itself and form layers of tissue that gradually become differentiated into organs because of the presence of other hormones, which affect the tissue in sequence. Still other hormones later influence the interactions of organ systems for the smooth function of the organism. Knowledge of the chemical mechanisms and sequences through which hormones exert their effects will provide the key to understanding the action of genes, which in a more fundamental way are responsible for the various stages of life. Hormones direct cellular differentiation and development in the organism for the rest of its life. Hormones will be crucially involved in fetal development, birth, early growth and development, puberty, reproductive cycles, aging, and eventually death. Hormones control virtually all aspects of an organism's life.

If certain relevant mammalian developmental hormones can be identified, then target cells—cells that respond to the hormones in discrete but interrelated ways—may also be determined. A "developmental profile" for any organism would then be a real possibility, and the control of any organism's development, even behavior, could result, although this may pose ethical problems.

Currently, there is some detailed knowledge of the functions of many developmental hormones. Many hormones remain to be identified, however, and the overall scheme of hormonal control of development is still sketchy. Extensive research will be needed in the future.

—*David Wason Hollar, Jr.*

See also: Aging; Communication; Development: Evolutionary perspective; Endocrine system of vertebrates; Estrus; Gametogenesis; Genetics; Growth; Hibernation; Lactation; Mammals; Mating; Morphogenesis; Regeneration; Reproductive system of female mammals; Reproductive system of male mammals; Rhythms and behavior.

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HORNS AND ANTLERS

Type of animal science: Anatomy
Fields of study: Anatomy, physiology, zoology

Horns are hard, pointed outgrowths from the frontal bones of the heads of male ruminant herbivores, used for protection and to attract mates. They are permanent (true horns) or temporary (antlers) appendages. Antlers are shed yearly. In a few cases, horns are made of fused hair.

Principal Terms

ANDROGEN: a male hormone (especially testosterone) made by the testes
FRONTAL BONE: the bone which, vertically, makes up the forehead and is important, horizontally, to formation of the top (roof) of the orbital and nasal cavities
KERATIN: a tough, fibrous protein which is a major component of hair, nails, hooves, and the outer covering of true horns
PEDICLE: a small bone spur from which an antler grows (for example, in deer)
RUMINANT: a hoofed animal, with a stomach divided into four parts, that chews a cud of regurgitated, partly digested food
TRUE HORN: the permanent horns found in animals such as cattle, sheep, and goats

Horns are found in many ruminant herbivores. They are hard, pointed outgrowths that arise at the front of the heads of many herbivores. Horned animals include cattle, deer, giraffes, antelope, and rhinoceroses. In some cases, horns are permanent appendages that enlarge the bony front of the skull, as in cattle. In others, they are temporary bones arising on—but separate from—the skull, falling off every year, as in deer. In yet other cases, such as rhinoceroses, they are permanent groups of fused hairs, which become very hard.

Regardless of species, horns serve very important protective functions, both for the individuals having them and for the family groups or herds to which the individuals belong. Often, males use their horns to fight other males in the group for ascendency. In many horned species, an ascendant male does not fight much but faces down rivals with gestures, including displaying and threatening to use his horns.

The protective function of horns may explain why, most often, it is the males within a species who have horns, while the females are hornless. The males protect the herds or other family groups from predators. Although horns are most often found in males, females may have horns as well, for example, giraffes and oxen. When females of a species have horns, they are almost always much smaller than those found in males of the same species.

The nature of horns also differs from species to species. For example, in deer, their temporary horns, or antlers, are made of naked bone. In contrast, the permanent horns of cattle are made of bone covered with hard tissue. In the giraffe, the bony horns are covered with hairy skin. Also, in some cases a horn is not made of bone—the rhinoceros horn is made of hair.

The True Horns

True horns are pointed, permanent, bony structures most often seen on the heads of male ruminant mammals. The horns of females, where present, are smaller. Most horned animals—cattle, sheep, goats, and antelope—have paired horns. True horns have cores of bone which are extensions of the skull's frontal bone. Atop the bone core is a layer of skin, rich in a very tough, fibrous protein, keratin. The high keratin content in this skin makes it an extraordinarily tough and durable covering for the underlying bone.

Males and females of many animal species grow horns. The horns range from straight spikes to elaborately curved varieties. However, except in pronghorn antelope, the horns do not form branches, as in deer and other animals which shed their antlers every year. Animals having horns keep them for life. In pronghorn antelope the horn coverings are shed and grow again every year. This allows horn enlargement that would otherwise not occur.

Antlers

Antlers are horns which are shed each year and then grow again. In most antlered species only males have antlers. Like true horns, antlers grow out of the bones of the skull. They arise from permanent frontal bone structures called pedicles. At first the antlers have soft, velvetlike coverings of skin over their bone. Instead of hardening, as in true horns, this covering dies off and is rubbed away by the animal. The rubbing is believed to be due to itching caused by the dead velvet. Many zoologists propose that an advantage associated with rubbing off dead velvet is the development of good spatial perception of a stag's antler size and shape that helps to keep him from entanglement in underbrush and forests. Antlers have the same functions as true horns: protection, and use or display to develop ascendancy in a herd.

Antlers begin their growth in early summer, on the skull's frontal bone. They begin as small nubs that increase in length over time. The growing antler, sensitive to the touch, is covered with velvet, soft, smooth, and full of blood vessels. This gives it an abundant blood supply, carrying to growing antlers all the nutrients required for the two to three months of the growing period. At first, antlers are made of connective tissue. As time goes on, this tissue calcifies and becomes solid bone.

Antler growth is greatest in the late summer. At that time, hard tissue grows around the base of each antler, cutting off its blood supply. This kills the velvet, which loosens and is rubbed off by the stag. Antlers reach their full glory in the mating season, when they can be used to impress potential mates and to vanquish other males. Zoologists observe that the blood running through antler velvet cools down and this cool blood makes stags and bulls more comfortable on hot days. Antlers are shed between January and February, just following the mating season, when they are no longer useful.

Bone

Horns and antlers are made mostly of bone. About 70 percent of the matter in bone is an inorganic mineral material, hydroxyapatite, composed of calcium phosphate and calcium carbonate. Much of the remainder is a fibrous protein, collagen. The mineral and the protein together are called bone matrix. Within bone matrix, three types of specialized cells ensure its formation, its remodeling as needed, and its continuity throughout the life of any organism having a bony skeleton.

The first cell type, the osteoblast, produces bone matrix and surrounds itself with matrix, making collagen and stimulating mineral deposition. The second type, the osteocyte, is branched and becomes embedded in bone matrix. Osteocytes are interconnected and act to control the mineral balance of the body. Finally, osteoclasts destroy bone matrix whenever it is remodeled (rebuilt) during skeleton growth or the repair of bone breaks and fractures.

The conversion of connective tissue to bone begins when connective tissue cells arrange themselves in rows, enlarge, and change. This is followed by the synthesis of collagen and by mineral deposition around them. Osteoblasts needed for bone formation develop below the inner surfaces of a membrane that surrounds bone-to-be. Simultaneously, osteoclasts set the stage for formation of additional bone.

Who Has Horns and Antlers?

Bighorn sheep have true horns in individuals of both genders. Rams' huge, back-curved horns show growth rings that tell their age. Ewes have smaller, lighter horns that they use to protect their offspring. Rams use their horns to attract females, assert ascendancy, and battle predators.

Caribou of both genders have antlers, though those of females are small. Males shed their antlers in the winter, while females do not do so until spring. Females may use this advantage to oust males from winter feeding areas, in order to assure the continuation of the species by their offspring.

Elk antlers occur only in males. Bull elk use them to battle any predators who seek to harm the herds they lead, display them to attract females, and use them to assert ascendancy.

Moose antlers occur only in males. The huge, scoop-shaped antlers are mostly for show and to attract mates. Moose do not travel in herds and have relatively weak familial instincts.

American pronghorns of both genders have permanent horns that share attributes of both true horns and antlers. Doe antlers are short spikes. In males, the pronghorns—true horns—can become quite large. The coverings, but not the horns, are shed yearly. This leaves bone cores attached to the head. Then the bare core enlarges and its covering grows again. The horns of males have the usual protective, display, and assertive functions.

The first growth of antlers occurs when a stag or bull elk is one to two years old. At first, the antlers are small, straight, and spikelike. At that time young males are often called spikehorns by hunters. As an antlered male grows older its yearly antler crop branches out, having more prongs (points). In old, antlered males these horns may spread to widths of six feet and be several feet tall.

Antler growth is regulated by hormone secretions from the pituitary gland and the testes. The growth begins outside of the breeding season, when the testes are inactive. When the testes begin to make androgens, in preparation for breeding, both antler calcification and velvet tissue death occur. Decreased androgen production in winter leads to shedding of antlers.

Antlers, Horns, and Species Life Cycles

In the fall (September to October), American elk—called wapiti by Native Americans—mate, after crashing battles between bull elk, who joust with many-pointed antlers. This identifies winners, who thoroughly impress cow elk. Then each bull mates with his harem of cows and they wander off to form part of a huge winter herd of elk of both genders and all ages.

By early winter, bull elk shed their heavy, four- to six-foot-wide antlers, unneeded burdens that would diminish their chances of surviving the cold winter. Winter passes and by the late spring (May and June) the cows give birth to young, usually one per mother. At this time, new antlers begin to sprout from the pedicles on foreheads of bulls over a year old.

The antlers of elk follow the same growth pattern as in deer, leaving the bull elk with a strong bony rack of antlers in the fall, just right for jousting at the mating season. With some variation, in other antlered species—pronghorns who never lose bone cores of horns, and horned sheep, goats and bovines—the overall story is about the same. Offspring are conceived in the fall after jousts using antlers, pronghorns or horns, and life goes on. In some species females have horns or antlers, and in others small family groups are formed. Sometimes males hardly interact with females after copulation. However, a common thread to all their lives is the possession of true horns, pronghorns, or antlers.

—Sanford S. Singer

See also: Anatomy; Beaks and bills; Bone and cartilage; Brain; Circulatory systems of invertebrates; Circulatory systems of vertebrates; Claws, nails,

Horns are used for display, defense, and to establish an individual's place in the social hierarchy. (Corbis)

and hooves; Digestive tract; Ears; Endoskeletons; Exoskeletons; Eyes; Fins and flippers; Immune system; Kidneys and other excretory structures; Lungs, gills, and tracheas; Muscles in invertebrates; Muscles in vertebrates; Nervous systems of vertebrates; Noses; Physiology; Reproductive system of female mammals; Reproductive system of male mammals; Respiratory system; Sense organs; Skin; Tails; Teeth, fangs, and tusks; Tentacles; Wings.

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HORSES AND ZEBRAS

Type of animal science: Classification
Fields of study: Anatomy, genetics, zoology

Horses and zebras are herbivorous, hoofed mammals that represent five species of the Equidae family.

Principal Terms

CECUM: pouch in intestinal tract
CROWN: external tooth surface above gums
GELDING: castrated male
HAND: ten-centimeter (four-inch) measuring unit
UNGULATE: hoofed animal

Horses and zebras, members of the Equidae family, share common anatomical traits such as hard hooves, strong spinal columns, muscular arching necks, sloping shoulders, wide hindquarters, high-crowned teeth, slender legs, and elongated heads. Size and coloration varies according to specific horse breeds developed through selective breeding. Similar differences in zebra species have evolved due to natural selection and environment. Horses and zebras are related to wild asses and donkeys and represent five species of the genus *Equus*.

Anatomy Development

Eohippus was the ancestor of both domestic and wild horse species. A leaf-eating mammal as small as a fox, *Eohippus* lived during the Eocene epoch and had several toes on its feet. Descendants gradually grew larger, lost toes, and became grass grazers. Przewalski's horse, indigenous to Mongolia but not seen in the wild since 1968, links ancient and modern horses. Because it has sixty-six chromosomes and domestic horses have sixty-four, Przewalski's horse is a separate wild horse species and not an ancestor of modern horses. A hybrid produced by a horse and a Przewalski has sixty-five chromosomes and is fertile.

Modern horses and zebras are distinguished by a single hoof on each foot. Vestigial remains of prehistoric toes are located above hooves. Horses and zebras have long skulls and jaws that hold approximately forty to forty-four permanent teeth, including incisors to bite grass and molars to chew roughage. The teeth have long crowns that slope with age and can be examined to determine how old an animal is. Horses use their teeth to eat, groom, and fight.

The horse's digestive system is bigger and more efficient than that of carnivores, and has approximately 40 meters (131 feet) of intestines with a meter-long cecum attached to the colon. Horses and zebras live on grasslands ranging between sea level and mountains and eat mostly fibrous food such as hay, grain, and oats. Food ferments in the cecum, which can hold as much as thirty-eight liters (ten gallons). Horses eat an average of sixteen hours per day to sustain their systems.

The average horse's heart weighs about 3 kilograms (6.6 pounds), and the surface area of a horse's lungs measures approximately 2,500 square meters (8,200 square feet). Horses' weight varies from minimums of nearly 500 kilograms (1,000 pounds) to maximums of more than 908 kilograms (1 ton). Fifty-one vertebrae are in horses' spines from the top of the skull to the base of the tail.

Horses' eyes are placed on the sides of their heads, enabling them to see the horizon without moving their head. Their eyesight is better than that of dogs. Horses depend on hearing more than sight, but rely most on the sense of smell. The flehmen response is when the horse raises its upper lip to indicate it has smelled something interesting.

Social Behavior

Depending on the age, female horses are called fillies and mares, and males are colts, stallions, and geldings. Horses attain sexual maturity at two to three years old and usually produce a single foal after eleven months of gestation. Multiple births are rare, with twins occurring on average once per 1,500 births. Foals are able to stand within an hour of birth. Stallions fight while competing for mares, and one stallion may mate with several mares during a season. Mares usually come into heat one week after giving birth. Foals are weaned before they are one year old.

Horses are herd animals and rely on this social relationship, as well as on speed and endurance, as protection from predators. Domesticated horses enjoy the companionship of horses and other animals. Wild horses form a family group of one stallion, several mares, and their offspring. Young stallions sometimes form a bachelor group led by an older stallion. These groups forage in an area where they can find food, water, and shelter, and a pecking order maintains a hierarchy of rank within the group. Several groups often share the same range. Horses communicate by whinnying and nickering.

Vulnerable to wild animals, horses can run an average speed of forty-five to sixty kilometers (twenty-eight to thirty-seven miles) per hour. Their legs are slender and angled forward so that their weight is carried forward to enhance quick motion. Horses' shoulders absorb shock, while their powerful hindquarters provide impulsion. Horses naturally move at the gaits of walk (four beat), trot and pace (two beat), canter (three beat), and gallop (an extended canter), with several other natural gaits including pacing and the running walk.

Horse and Zebra Facts

Classification:
Kingdom: Animalia
Subkingdom: Metazoa
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Subclass: Eutheria
Order: Perissodactyla
Suborder: Hippomorpha
Family: Equidae
Genus: Equus
Subgenera: Equus (horses), *Asinus* (asses), *Hippotigris* (zebras), *Dolichohippus* (zebras)
Species: Equus przewalskii (Przewalksi's horse), *Equus caballus* (domestic horse), *Equus africanus* (African ass), *Equus hemionus* (Asiatic ass), *Equus burchelli* (plains zebra), *Equus zebra* (mountain zebra), *Equus grevyi* (Grevy's zebra)
Geographical location: Horses can be found on all continents except Antarctica; zebras live in southeastern Africa
Habitat: Grasslands in tropical, temperate, and subarctic regions
Gestational period: Eleven months for horses; thirteen months for some zebras
Life span: Ten to twenty-five years, up to thirty-five in captivity
Special anatomy: One-toed feet, high-crowned teeth

Appearance

Domesticated horses are described by three types: heavy or draft, light, and pony. Humans genetically developed specific breeds for different tasks and degrees of hardiness, stamina, and versatility. Most horse breeds are derivatives of Arabians and thoroughbreds. Draft horses (often referred to as cold-blooded, which is not physiologically accurate), usually stand over sixteen hands high at the withers (the ridge between the shoulder blades) and have sturdy, thick dimensions, useful for pulling loads. Light horses, sometimes called hot bloods, are at least 14.2 hands high and tend to be streamlined. Ponies are shorter than 14.2 hands and vary in conformation according to breed. Welsh ponies tend to be more delicate, while

Each zebra has a distinctive pattern of stripes as individual as human fingerprints. (Corbis)

Shetland ponies are more rotund. Miniature horses are extremely small ponies that are often less than one meter tall.

Coat colors range from shades of brown and red to solid black and white, with some horses, such as Appaloosas and pintos, having spots and others being gray or roan. Spotted patterns are linked to genes that also often produce mottled noses, eyelids, and genitalia, blue eyes, and striped hooves. Lipizzans are born black and turn completely white by age two years. Some horses have dorsal stripes and zebra stripes on their legs. Various white facial and leg markings also distinguish horses.

African Cousins

Zebras belong to the horse family and are represented by three species, the plains, Grevy's, and mountain zebras. Several subspecies exist according to geographic range, herd behavioral differences, and physical variations such as dewlaps. Zebras are smaller than horses and have erect manes, longer ears, and thinner tails. The average zebra stands 140 centimeters (55 inches) high and weighs 300 kilograms (660 pounds). These striped animals exist in herds that graze in southeastern Africa's grasslands and also live in nearby deserts.

Each zebra species is determined by a specific stripe pattern of black, brown, and white markings. Individual zebras have unique striping somewhat like the uniqueness of human fingerprints. Scientists have determined that zebras, from the moment of birth, are drawn to striped objects, a type of imprinting which has led to speculation that stripes might be a factor in herd cohesiveness and sociability. Previous hypotheses that stripes are for camouflage and to confuse predators have been discredited. The exact purpose of stripes remains a scientific mystery. Researchers are aware that abnormally striped zebras are often shunned by herds, which threatens their survival.

Herds can include several zebras, often a male and females with their offspring or a group of

North American Wild Horses

Considered the symbol of the freedom of the American West, mustangs roam prairies, in addition to isolated areas along the East Coast and in the Midwest. In the early twentieth century, the federal government ordered the extermination of mustangs. Velma "Wild Horse Annie" Johnston lobbied Congress in the 1950's to stop wild horse slaughters. Congress passed the Wild Free-Roaming Horse and Burro Act in 1971 to protect wild horses under the jurisdiction of the Bureau of Land Management (BLM). The Wild Horse Act of 1999 assured federal protection for a feral horse herd in Missouri.

Although wild horses are romanticized in books and movies, realistically they pose problems such as uncontrolled population increase, encroachment on urban areas, and destruction of rural landscapes. They also are at risk from animal predators, microscopic diseases, and human poachers. Droughts and wildfires in the late twentieth century depleted food sources, resulting in many mustangs starving. Roundups by helicopters drive wild horses toward government corrals, where they are fed and offered for adoption to the public. Approximately forty-six thousand wild horses roamed the American West in 1999, and seven thousand were adopted.

Such dispersal, however, is controversial. Some of the mustangs are actually sold for slaughter because horse meat is a popular food in Asia and Europe, due to concerns about bovine spongiform encephalopathy (mad cow disease). Critics of the BLM suggest that agency will inadvertently cause the extinction of America's wild horses.

young males. Herds can expand to hundreds of zebras. Typically passive animals, male zebras occasionally fight for females during breeding season by kicking, biting, and shoving each other. Female zebras attain sexual maturity at age three and usually reproduce annually throughout their lives, while males reach breeding age at five years. Gestation lasts approximately eleven to thirteen months, and twins are rarely foaled. The life span of wild zebras can extend to twenty-two years, and zebras kept in captivity can live longer.

Zebra foals weigh approximately thirty-two to thirty-six kilograms (seventy to eighty pounds) at birth. Able to stand soon after being born, zebra foals eat grass which adds about 0.45 kilograms (1 pound) of body weight per day until they reach physical maturity. Zebra foals develop more quickly than horse foals and become independent sooner.

Defense Mechanisms

The herd protects zebras from predators, primarily large cats, such as lions and cheetahs, in addition to hyenas. Humans also hunt zebras for their hides. While other zebras sleep, a guard zebra watches for potential hazards and is aided by its keen night vision, comparable to an owl's, and tall ears which can rotate to pick up sounds. Zebras' primary defense mechanism is to run away from danger, and they can reach speeds as high as sixty-five kilometers (forty miles) per hour, which is much slower than most of their enemies.

Zebras also are at risk from reduced water resources and grasslands due to ranching and farming and compete with livestock for basic nutritional needs. While the common zebra remains abundant, the Grevy's zebra and the mountain zebra are considered endangered species and another type of zebra, the quagga, became extinct in 1883. A century later, the Quagga Breeding Project attempted to revive the quagga because genetic researchers determined that quagga and plains zebra deoxyribonucleic acid (DNA) was similar, and hypothesized that the quagga was not a separate species but rather a variation of the plains zebra. Zebroids are horse-zebra hybrids that are sterile.

—Elizabeth D. Schafer

See also: Camouflage; Claws, nails, and hooves; Domestication; Endangered species; Fauna: Africa; Fauna: Asia; Herds; Imprinting; Locomotion; Ungulates.

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HORSESHOE CRABS

Type of animal science: Classification
Fields of study: Anatomy, invertebrate biology, marine biology, systematics (taxonomy)

Horseshoe crabs are not crabs at all, being more closely related to spiders and scorpions. They have been around for at least 400 million years—before dinosaurs walked the earth—and have changed relatively little in that time.

Principal Terms

CEPHALOTHORAX: the forward segment of the horseshoe crab's body
CHELATE: pincerlike
CHELICERAE: appendages with pincers
DIOECIOUS: having separate sexes
EXOSKELETON: the external shell of horseshoe crabs and their relatives
GNATHOBASE: the part of the leg closest to the horseshoe crab's body

There are four species of horseshoe crabs, and all are members of the class Merostomata, aquatic animals with two body segments and a spikelike telson at the tail end. Perhaps the best-known representative is *Limulus polyphemus*, the common horseshoe crab native to the northwest Atlantic coast and the Gulf of Mexico. These animals live in shallow water to depths of one hundred feet and prefer soft sand or mud bottoms, through which they slowly plow as they scavenge for food.

Horseshoe crabs, unlike true crabs, do not have antennae. However, like crabs, they do have jointed appendages and a hard shell, or exoskeleton, made of chitin, which must be periodically shed to accommodate the growing body of the individual.

Horseshoe Crab Anatomy

The body of horseshoe crabs is divided into two segments: a large, helmet-shaped, forward section called the cephalothorax or prosoma, and a rear abdomen or opisthosoma, to which is attached the lancelike telson. Despite its threatening appearance, the telson is not used for defense, but rather for pushing and righting the body if the animal is overturned.

There are two lateral and two median eyes on the upper surface of the prosoma. Although horseshoe crabs may be able to detect movement, there is little evidence that they can form images. The unique and relatively simple anatomy of horseshoe crab eyes make them favorite subjects for nervous system research.

Under the cephalothorax there is a pair of small, pincerlike chelicerae, followed by five pairs of walking legs. The first four pairs are chelate and the fifth pair is for pushing away mud and silt during burrowing. The first four pairs also have spines along the joints closest to the body. These gnathobases are used to shred and macerate food and move it toward the mouth.

The abdomen has six pairs of appendages, five of which are modified as thin, flaplike gills. In addition to providing oxygen to the animals, the gills function as paddles during upside-down swimming in small individuals.

Reproduction in Horseshoe Crabs

Horseshoe crabs are dioecious, meaning there are separate sexes. During warm months, females migrate into the intertidal zone to rendezvous with the smaller males. The males crawl onto the shell of the females and cling to them while the females scoop out depressions in the sand and deposit two hundred to three hundred small green eggs, which the male then fertilizes. The location of this

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egg burying is of critical importance: too high up the beach and the eggs will dry out; too low and they will die in the oxygen-poor sand.

After a lunar month a small (about one centimeter), swimming larva hatches which little resembles the adult. After successive molts the adult body form is eventually achieved, with sexual maturity being reached after three years.

Economic and Scientific Importance of Horseshoe Crabs

The economic value of horseshoe crabs has been recognized since at least the nineteenth century, when millions were harvested annually from Delaware Bay to be ground up as fertilizer. By the 1950's, the population of horseshoe crabs had decreased to the tens of thousands. Since then, controls have been put in place to protect this animal. In Japan, it has been declared a national monument to shield it from extinction.

Today the horseshoe crab is used for bait in the fishing industry. It is also valuable in biomedical research because of its blue, copper-based blood. An extract of this blood, called limulus amebocyte lysate (LAL), is used in detecting bacterial contamination of drugs and medical devices. There are many other chemicals derived from horseshoe crabs that may prove useful against human diseases.

—Robert T. Klose

See also: Arthropods; Marine animals; Marine biology; Molting and shedding; Shells.

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Horseshoe Crab Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Arthropoda
Subphylum: Chelicerata
Class: Merostomata
Subclass: Xiphosura
Order: Xiphosurida
Suborder: Limulina
Family: Limulidae
Genus and species: Limulus polyphemus

Geographical location: *L. polyphemus*, the most common species, is distributed along the northwestern Atlantic coast and the Gulf of Mexico; other species are native to Asian coasts, from Japan and Korea south through the East Indies and the Philippines

Habitat: Shallow water with soft bottoms

Gestational period: One lunar month for the eggs to hatch

Life span: Approximately thirty-five years

Special anatomy: Two distinct body segments, a rigid telson at the tail end, four eyes, a median frontal organ

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HUMAN EVOLUTION ANALYSIS

Type of animal science: Evolution
Fields of study: Anthropology, evolutionary science, genetics, human origins, systematics (taxonomy)

The study of human evolution traces the descent of the hominids from their primate ancestors and focuses particularly on the most recent stages that led to modern Homo sapiens.

Principal Terms

DEOXYRIBONUCLEIC ACID (DNA): the large molecular chains of nucleic acid that make up genetic material

GRACILE: slender and light-framed, as opposed to robust

HOMINID: belonging to the taxonomic family Hominidae, which includes all humans and their evolutionary ancestors as far back as the split from the great apes

MITOCHONDRIA: self-replicating units in a cell that are responsible for the metabolic generation of energy for cell processes

About fifteen million years ago, there was a great flowering of diversity among the primates. One branch of this evolutionary spurt gave rise to the family Pongidae (gorillas, orangutans, and chimpanzees). A second branch led to the family Hominidae. Fossil evidence suggests that the hominids diverged from the common ancestral primate at about the same time as the pongids, but according to molecular analysis of the genes of modern humans and gorillas, the divergence may have been much later—perhaps as recently as two million or three million years ago. The earliest known examples of the hominid family have been named *Ramapithecus*. Fossils of this creature, more ape than human, have been found in India, Greece, Africa, Turkey, and Pakistan. It is likely that this genus evolved into another hominid group, *Australopithecus*. Many australopithicine fossils have been found, mostly in Africa, and the genus is divided into two types, the large, heavy-boned robust species and the smaller, gracile types exemplified by "Lucy," the nearly complete skeleton discovered by Donald Johanson in 1974. The current view is that the robust australopithicines became extinct but that the smaller forms gave rise to the genus *Homo*, leading to modern humans.

The earliest discovery of a fossil of the *Homo* genus was given the species name *erectus* by its discoverer, Eugène Dubois, in 1891. It was found not in Africa but in Java. Dubois believed that Java man, as he called his find, was the first hominid to walk erect. Later discoveries showed that the more primitive *Australopithecus* had already achieved the erect stance of modern humans, but the name *Homo erectus* persists for the link between *Australopithecus* and more modern hominids.

Tool Use and Culture

The genus *Homo* was the first to leave clear evidence of toolmaking. Pebble tools of *Homo erectus* were described by Louis Leakey, and he named the collection of artifacts "Oldowan" culture, from the Olduvai Gorge where some of his most famous excavations were done. On the basis of his collection of African fossils dated to between one million and two million years ago, Leakey proposed a new species, *Homo habilis*, which would be intermediate between *Homo erectus* and *Homo sapiens*, but there were too few fossils from this critical period to make the sequence clear. In any case, the simple pebble tools of the earliest members of the human genus were gradually supplanted by somewhat more sophisticated implements made by chipping both sides, along with a growing preference for flint over softer stones. There are many more examples of flint tools than there are of actual bones of human ancestors from this period. The techniques used for making these tools were evidently handed down from generation to generation, and the patterns were quite conservative, so tools from a given culture can be identified wherever they are found. The tools and artifacts of the later members of *Homo erectus* are known as the Acheulian culture. The most characteristic tool of this culture is the hand axe, used for chopping, cutting, scraping, and possibly even as a weapon.

The species to which modern humans belong first appeared between 200,000 and 300,000 years ago. In 1856, when the first example of *Homo sapiens* was discovered, it was named Neanderthal man because the skeleton was found in a cave by the Neander Valley near Düsseldorf, Germany. Neanderthals were a robust species with a somewhat larger brain than modern humans. They wandered widely, leaving their remains over much of Europe, Asia, and Africa. The name Mousterian culture was coined to describe their artifacts, which were much more sophisticated than Acheulian tools.

Finally, perhaps as recently as fifty thousand years ago, Neanderthals were replaced by fully modern humans. The two groups can be separated into the subspecies *Homo sapiens neanderthalensis* and *Homo sapiens sapiens*. At about the same time the Neanderthals disappeared, the Mousterian artifacts were replaced by much more complex and widely varied implements of the Aurignacian culture. The explosion of cultural innovation—including cave paintings, carvings, and other artistic and technological inventions—had a remarkable effect on life.

The first fossils of the *sapiens* subspecies were found in a limestone cliff at Cro-Magnon in southern France in 1868. They and numerous later finds from the same period were given the name Cro-Magnon man, and from the very beginning, they were recognized as being fully modern in form.

Evolutionary Controversies

Controversy over the relationship between the modern human subspecies and the Neanderthals centers around the fact that the two groups overlapped in time. Evidently some subpopulation of Neanderthal evolved into Cro-Magnon while the more primitive type was still flourishing. For some unknown period, both types existed, but eventually—quite abruptly on a geological time scale—Neanderthals vanished from the face of the earth, and *Homo sapiens sapiens* reigned alone. Some anthropologists put the divergence between Neanderthals and the *sapiens* subspecies quite early and suggest that most of the known fossils of Neanderthals represent a dead end of evolution and not human ancestors. A few fossils that appear to be of the modern human type are tentatively dated much earlier than fifty thousand years ago, which is the time most of the fossil evidence would indicate that modern humans first appeared. Whether humans evolved from early or late Neanderthals, there is certainly no other candidate for an immediate ancestor nor any evidence of an alternative link between *Homo erectus* and modern humans.

The Neanderthal question is one of three major controversies about the details of human evolution. Another is over the site of major stages in human evolution. The "out-of-Africa" view is that Africa, with its rich store of fossil evidence, had to be the place where, successively, *Australopithecus*, *Homo erectus*, and modern humans emerged. Countering this is the fact that fossils and artifacts of each stage of human evolution are found in many regions of the globe. Some authorities feel that it is more probable that this mobile, adaptive, wide-ranging species was already dispersed during the final million years or so of human evolution rather than exclusively in Africa.

The third major disagreement among anthropologists is about how to interpret evidence from molecular biology. The random mutation of deoxyribonucleic acid (DNA) chains provides a molecular clock because the mutations cause a genetic drift. In an interbreeding population, the genetic changes are shared by all members, but if a population divides, the genetic changes vary between the two groups, resulting in more and more differences as the time since the separation increases. Studies of DNA differences among humans and between humans and the great apes suggest that the genetic divergence between humans and the gorillas has taken only about three million years. This is a much shorter period than fossil evidence would indicate. However, the time scale for DNA changes is not well enough established to persuade many of the geologists and fossil hunters to give up their chronology. In 1987, the even more disturbing claim was made that all living humans had descended from one woman and that this "Eve" had lived in Africa as recently as 200,000 years ago. The work that led to this announcement was based on the study of mitochondrial DNA, which is much less variable than the DNA in the nucleus of the cell.

Each tiny mitochondrion has its own set of genes, and they divide independently of the cell nucleus. Because the sperm does not contribute any mitochondria to the fertilized egg, mitochondrial DNA is inherited only through the female line of descent. In one study, mitochondrial DNA from 147 individuals, representing populations in Africa, Europe, Asia, Australia, and New Guinea, was compared. The samples seemed to fall into two major groups when analyzed by a computer program: a group containing the African samples and one holding all the rest. The group containing the African individuals appeared to be the more primitive. From the rate of mutations in mitochondrial DNA, it was calculated that the observed variations in the samples would have occurred over a time span of about 200,000 years.

The convergence of molecular evidence and fossil interpretation has given a boost to the out-of-Africa hypothesis for human origins. Africa is certainly a rich source of fossils of the earliest progenitors of the human species. It is also the home of most of the great apes. The controversy is mainly about when the migration of humans or proto-humans into the rest of the world occurred. Fossils of every stage of human evolution have been found in many parts of Europe and Asia and even Australia. It is possible, of course, that sample populations of each stage of human evolution emigrated from Africa, leaving their bones and their tools scattered all over Eurasia, only to be replaced by successive waves of emigrants from later stages. There is no hypothesis to suggest why the further evolution of these intermediate species should not have taken place outside Africa.

Fossils and Paleoanthropology

The major technique for the study of human evolution is the analysis of fossils and the artifacts associated with human activities. Fossil hunting is more an art than a science, and many of the major finds have been accidental. However, knowing where to look and the use of systematic excavation have been very fruitful. Dating the fossils and artifacts is the most critical part. When fossils are excavated from undisturbed layers of sediment, the dating can be determined by knowledge of the geological strata. Layers of lava from volcanic eruptions, sediment from floods, the presence of other fossils of plants or animals of known periods all contribute to the determination of the age of the deposit. Radioactive decay provides another method. Radioactive carbon-14 is continuously produced in the upper atmosphere and is absorbed by plants. The carbonate in fresh bone contains about one atom of radioactive carbon for every one hundred forty atoms of the inactive isotope. The radioactive isotope decays at a constant rate and is reduced to half of its original concentration in about five thousand years. The radioactivity of bones (or charcoal or other organic debris) can be measured, and the older the sample, the smaller the proportion of radioactive to nonradioactive carbon atoms will be. Unfortunately, the sensitivity of the method limits its usefulness to materials less than about thirty thousand years old. Also, it is often hard to rule out the possibility of contamination by groundwater or organic sources of "fresh" carbon. Older materials can sometimes be dated by other radioactive isotopes such as argon. Another dating method is to use the accumulation of atomic dislocations caused by cosmic ray bombardment in hard materials, especially stone and pottery. Such dislocations "heal" when the material is heated, so measuring the amount of cosmic ray damage in a material can reveal its age since the last heating. This method is good for much longer time periods than radiocarbon dating.

Molecular biology is relatively new, and its use as a method for studying human evolution is still experimental. The basic premise on which it operates is that mutations of DNA molecules are random events, relatively independent of environmental factors, and therefore relatively constant in time. Although exposure to natural or artificial radiation or certain chemical mutagens can increase the rate of DNA change, it is assumed that such factors would not be likely to affect a whole population; therefore, the assumption of a uniform slow rate of genetic drift is probably justified statistically.

DNA molecules are very large, and with modern techniques, it is possible to detect small changes in the molecule that may not produce any observable mutation in the organism. This means that chemical comparison of DNA samples from two individuals is a much more sensitive measure of their degree of relatedness than simple comparison of visible features. Analysis of DNA differences (and similarities) correlates well with older techniques of classification. Human DNA, for example, is much more similar to sheep DNA than to earthworm DNA. Monkey DNA is much closer to human DNA than is sheep DNA. By assuming that DNA changes at a uniform rate, these differences can be interpreted in terms of evolutionary time since humans and monkeys or humans and sheep shared a common ancestor.

The Implications of Human Origins

The study of human origins has social, intellectual, religious, and philosophical implications. The fact that humans are all one subspecies, with a remarkably homogeneous genetic makeup, should minimize the importance of race, culture, or language differences. Anthropology is the discipline that studies the origins of humans. Anthropologists also study living human cultures, and there is a two-way transfer of information between cultural anthropologists and physical anthropologists. Knowledge of human descent deepens understanding of the diversity of cultures and capabilities among living humans. Studies of contemporary and recent cultures give great insight into how Stone Age ancestors might have lived and worked. Even the study of developmental psychology provides insights into the ways the modern mind might have evolved.

Naturalist Charles Darwin's theory of human evolution met with powerful resistance not only

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because it was contrary to a literal interpretation of the Christian scriptural story of human creation but also because it seemed to make humans helpless products of random processes. Humans may be powerless to control their biological evolution, but they are fully in control of the spectacular cultural evolution that provided people with language, knowledge, and civilization.

Although many people still see a conflict between religious beliefs about human origins and the scientific view, others have been able to reconcile the two doctrines and are comfortable with both their religious faith and their scientific knowledge.

Philosophers have always discussed what it means to be human and the origins of humankind. Scientific knowledge of human origins has had immeasurable impact on philosophy. Modern philosophy emphasizes the importance of language to humans, and anthropological studies of human evolution also point to the critical importance of language development in the final stages of human evolution. There is a growing conviction that the acquisition of language was the single most important step in the final evolutionary jump from Neanderthal to modern human. Language made it possible for humans to communicate with others and to pass along the accumulated wisdom and experience of one generation to the next. Language helped the pace of cultural development accelerate to a point where further biological evolution became irrelevant. Clothing and fire substituted for fur in a cold climate. Weapons were better than sharp claws and long teeth. Human evolution thus became cultural evolution.

—Curtis G. Smith

See also: Adaptations and their mechanisms; Apes to hominids; Convergent and divergent evolution; Development: Evolutionary perspective; Evolution: Historical perspective; Gene flow; Hominids; *Homo sapiens* and human diversification; Language; Neanderthals; Nonrandom mating, genetic drift, and mutation; Population genetics; Primates.

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HUMMINGBIRDS

Types of animal science: Anatomy, behavior, classification, physiology, reproduction
Fields of study: Ornithology, physiology, population biology, wildlife ecology

Hummingbirds are found only in North and South America. Classified in the general order Apodiformes, they have unique coloration and many of their feathers are iridescent. The rapid beating of their wings, which enables them to hover, produces a distinctive, recognizable hum.

Principal Terms

BANDING: technique for studying the movement, survival, and behavior of birds
COVERTS: small feathers at the base of the wings and tail
GORGET: patch of feathers between the bird's throat and breast
PRIMARY FEATHERS: flight feathers on the outer joint of the wing
RECTRICES: tail feathers
SECONDARY FEATHERS: flight feathers on the inner wing

Over four hundred species of hummingbirds have been identified in North and South America, forming the Western Hemisphere's second largest family of birds. These exceptionally small birds have the greatest comparative energy output of any warm-blooded animal. In one day, they often consume more than half their total weight in food and twice their weight in water. The smaller species have the fastest wing beat of all birds. Unlike other birds, their wing upstroke is as powerful as their downstroke. They can fly forward, backward, and briefly, upside down.

The range of the hummingbird stretches from Alaska to Tierra del Fuego, Chile. Because of a constant supply of nectar and insects, tropical hummingbirds rarely migrate. Those hummingbirds that do migrate sometimes travel enormous distances. The rufous hummingbird flies over two thousand miles from its winter home in Mexico to the Pacific Northwest and Alaska.

Physical Characteristics of Hummingbirds

Hummingbirds are extremely small, weighing from two to twenty grams. The bee hummingbird is the world's smallest bird. Their long, slender bills, which are often slightly decurved, and their long bitubular tongues give them easy access to flower nectar, their main source of food.

Although their feather structure is among the most specialized of birds, hummingbirds have the fewest feathers. The primary flight feathers de-

The hummingbird's long, pointed beak and bitubular tongue allow it to suck nectar from deep within trumpet-shaped flowers. (Corbis)

Hummingbird Facts

Classification:
Kingdom: Animalia
Phylum: Chordata
Class: Aves
Order: Trochiliformes
Family: Trochilidae (hummingbirds, sixty-two genera, eighty-eight species)
Geographical location: North and South America, with most living near the equator
Habitat: Wooded areas, mountain slopes, plateaus, canyons, often near water
Gestational period: Usually one breeding cycle in a year
Life span: Average is five years, though observations of banded and captive birds show they can live ten or more years
Special anatomy: Ten primary flight feathers; six to ten secondary wing feathers; ten rectrices; extremely large sternums; long bills, often decurved

crease in size from the outer feathers inward toward the secondary feathers. Hummingbirds are able to rotate each of their wings in a circle. To hover, they move forward and backward in a repeated figure eight. They can move in any direction instantaneously. Their feet, which are more suited for perching than walking, have three toes directed forward and one pointed back.

Hummingbird feathers are iridescent. Depending on the viewing angle, the colors will change from red to gold or from green to turquoise. Adult males have the most intensely colored feathers and in full sunlight seem to glow. Some feathers are also modified to produce sound, so that as the birds fly, a soft humming sound is heard.

Reproductive Biology and Behavior

Hormonal changes prompt the female hummingbirds to begin nest building as ova ripen in their ovaries. In the male, hormonal changes enlarge their testes to many times their normal weight. Following mating, the female takes from one day to two weeks to complete building her nest, and soon after, she lays her eggs. Most hummingbirds lay two eggs, two days apart. The tiny, elliptical white eggs weigh less than 0.02 ounce. Depending on the species, incubation lasts fifteen to twenty days. Newly hatched hummers are featherless and do not open their eyes for two weeks. By two and a half weeks they are covered with feathers and can groom themselves. After testing their wings, at three weeks they are able to leave the nest, although the mother continues feeding them for two to four more weeks.

Hummingbirds are highly territorial. Particularly when they are migrating, they aggressively protect their sources of nectar. A nesting female will attack any interloper approaching her nest.

Hummingbirds have adapted to living in diverse areas. Like most birds, hummingbirds eat vast quantities of food. They have taste receptors on their tongues and salivary glands, and prefer flower nectars with a high sugar content. Throughout the day, hummingbirds eat frequently. At night, in order to conserve energy, they enter a state of torpor, which is a short-term form of hibernation. In this state they are unable to flee from predators. To resume a normal state requires enough energy to warm their organs and tissues. The birds need to monitor their energy reserves so they can recover from their torpid state.

—*Susan E. Hamilton*

See also: Beaks and bills; Birds; Domestication; Feathers; Flight; Molting and shedding; Nesting; Respiration in birds; Wildlife management; Wings.

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HYDROSTATIC SKELETONS

Types of animal science: Anatomy, evolution, physiology
Fields of study: Anatomy, invertebrate biology, physiology, zoology

Hydrostatic skeletons use the incompressibility of water to create a transient skeleton. This is accomplished in animals by contracting muscles around a fluid-filled space.

Principal Terms

CIRCULAR MUSCLE: muscle fibers that run in a circular pattern around the body perpendicular to the long axis of the body

COELENTERON: the fluid-filled gastrovascular cavity of Cnidarians

COELOM: the body cavity of higher invertebrate and vertebrates, where mesodermal tissues enclose a fluid-filled space

LONGITUDINAL MUSCLE: muscle fibers that run along the longitudinal or anterior-posterior axis of the body

PSEUDOCOEL: a fluid-filled body cavity that is bounded by mesodermal muscle on the outside and endodermal epithelium on the internal boundary

The most primitive form of skeletal support evolved is mostly hydrostatic skeletons because no mineralization process is necessary for their formation. Hydrostatic skeletons have been evolved in a wide range of organisms including plants, protists, and animals. The basis of all hydrostatic skeletons has to do with the material properties of water. Water cannot be compressed under biological conditions and thus can act as a support and locomotory transient skeleton. Essentially, all hydrostatic skeletons act in a similar fashion, that is, water is contained in a compartment and is subjected to pressure. In this way, the compartment can become stiff and act as a skeleton. The method used to create the pressure differs among groups.

Among the Protozoa, hydrostatic skeletons are found in the members of the phylum Sarcomastigophora. Within this group are the amoeboid types that form pseudopodia, false feet that are transient structures formed by hydrostatic pressure within the cell. It is hypothesized that contractile proteins within the cell direct fluid toward the cell periphery in channels, and in so doing cause the cell membrane to bulge outward as a pseudopod. Thick pseudopodia, termed lobopodia, are found in the shell-less amoebas. In this case, there appears to be a chemical difference in the fluid used in pseudopodia formation. Plasmasol has less viscosity and is pushed into the pseudopodia; when it is distributed laterally it turns to plasmagel. In thin pseudopodia termed actinopodia, cytoplasm is forced along microtubules termed axonemes. These types of pseudopodia are normally found among foraminiferan and radiolarian amoebas.

Worm Hydrostatic Skeletons

In the animal phyla, hydrostatic skeletons are developed in the Cnidaria and function in relationship to the gastrovascular cavity. In the polyp forms of colonial forms and especially within the Anthozoa, such as sea anemones, the myoepithelial cells surrounding the coelenteron make up a circular muscle band and thus are able to put pressure on the water in the coelenteron to extend the body or maintain the form of the polyp. This coelenteron extends into the tentacles of these forms and thus, via contraction of the myoepithelium, can elongate the tentacles to capture food.

Various types of flatworms comprise the phylum Platyhelminthes. Despite the lack of a coelom, these worms are still considered to have a hydrostatic skeleton. Since the longitudinal and circular muscles lie external to fluid-filled parenchyma tissue, the pressure exerted by this muscle extends the body by elongating this tissue. In this way, the worms can undulate in swimming or have peristaltic motion while moving along a substrate.

The nematode worms as well as other members of the Pseudocoelomate group have developed a fluid-filled body cavity. This cavity in most members of this group has a space with an outer boundary of mesodermal muscle and an inner boundary composed of endodermal cells. In nematodes, the muscle layer is arranged in a longitudinal pattern beneath a cuticle that is composed of layers, including fibrous collagen to maintain the shape of the worm under muscular pressure. Although less flexible than in true worms, contraction of the muscle layer can act against the pseudocoel fluid, thereby causing the body to undulate. Most nematodes need to act against a surface to have effective locomotion.

A more effective method of locomotion using a hydrostatic skeleton has been developed by annelid worms. These worms are segmented and have developed a true coelom. This means that the body cavity or coelom is bounded on all sides by mesodermally derived tissue: circular and longitudinally arranged muscles on the external boundary and membranes wrapping the gut tube. In addition, the coelom is divided in each segment into right and left halves and each segment has a membrane that separates the coelom in one segment from that of another segment. Thus, the circular musculature can constrict one side of the body while the other side is relaxed and stretched. As a result, undulation is more effective in this group than in the pseudocoelomates. When such bending is coupled with setae or segmentally arranged parapodial extensions on the body, the undulations could be used for crawling and swimming, although the latter locomotory ability is poor in some groups.

Using the hydrostatic skeleton in burrowing necessitates another evolutionary strategy involving the coelom. Here the intersegmental partitions or septa are lost or are perforated. This accomplishes the movement of coelomic fluid between segments during muscle contraction. Thus, circular muscles in posterior segments can drive fluid anteriorly, swelling and elongating the anterior portion of the animal. The posterior segments left behind can catch up with the anterior segments when the longitudinally arranged fibers contract. In this way burrowing is effected. Similar contractile wave patterns are used by terrestrial oligochaetes such as earthworms to create peristaltic-type contractions that drive the animal forward. The contraction of circular and longitudinal muscles alternate to create thick and thin areas of the body. This corresponds with elongation and subsequent contraction of the body segments. In earthworms, the segments retain their intersegmental septa. The Hirudinida or leeches have done away with their intersegmental septa and thus the coelomic space is continuous. Constriction of the circular muscles extends the body forward and the subsequent contraction of the longitudinal muscles will bring the rest of the body to meet it. The movement is accomplished by first attaching the posterior sucker, then elongating, attaching the anterior sucker and then pulling the rest of the body forward in the direction of the anterior sucker.

The Hydrostatic Skeletons of Arthropods, Bivalves, and Echinoderms

The development of an exoskeleton requires a change from a coelom-driven locomotion to one that uses muscles. The reduction of the coelom is a characteristic of the diverse arthropod taxon, but hydrostatic skeletons are still used in certain body areas. Flying insects, when attaining their adult state, emerge from their cocoons with folded wings. The insect must pump hemolymph into veins within the wing in order to expand them before they harden. These veins remain in the wings, and their walls and hydrostatic pressure may act to maintain the shape of the wing during flight. The ability of spiders to run fast even though they do have eight legs may lie in the hydraulic systems in their legs. Spiders have replaced extensor muscles with hydraulic spaces that, under pressure, automatically extend the legs. Thus, muscles are normally only used for flexion of the leg segments, and the legs can be moved faster than if muscles were used in both extension and flexion of the leg segments.

Although mollusks have a reduced coelom, hydrostatic skeletons are developed in certain members of this phylum. Bivalves normally burrow into the substrate and send up siphons through which water is brought in and out of the clam. In some species, water pressure is used to open and extend these siphons. In addition, the foot of the clam contains a blood sinus that, under pressure, fills with blood and expands in two ways. The foot can be extended into the substrate with subsequent swelling of the distal end. This action anchors the foot so that the clam can pull itself into the substrate. Among other mollusks, it is thought that the extension of tentacles to capture prey by squid and cuttlefishes is based upon hydraulic action of muscles on these structures.

Most echinoderms have a well-developed water vascular system derived from the coelom. This system is composed of sieve plate opening to the water. This plate is then connected via a stony tube to a ring canal. In asteroids or sea stars, this ring canal extends into the arms via radial canals. From the radial canal located in each, there extend bilaterally arranged lateral canals that enter a tube foot structure. The tube foot has two functional parts, an upper, bulblike ampulla and a lower tube foot. Contraction of the ampulla drives water into the podium, extending it and causing its tip to form a suctionlike disc that attaches to the substrate or prey. Relaxation of the ampulla withdraws water back into the ampulla, retracting the podial portion of the tube foot. In this way many echinoderms move along the ocean bottom and manipulate prey.

Vertebrate Hydrostatic Skeletons

Like mollusks and arthropods, vertebrates have largely abandoned the coelom. Their endoskeletons have taken the place of hydrostatic skeletons. However, hydrostatic skeletons still occur, particularly in the reproductive system. The penis or hemipenes of mammals and reptiles contain spongy tissue that can engorge with blood. Venous return of the blood is largely prevented, extending the length and stiffness of the intromittent organ so that it may be inserted into the female's reproductive tract.

—Samuel F. Tarsitano

See also: Endoskeletons; Exoskeletons; Locomotion.

How Hydrostatic Skeletons Work

Although hydrostatic skeletons operate on the basis of fluid pressure, there are certain constraints as to how this pressure can be generated and on the makeup of the body wall resisting the pressure.

First, sets of muscles that will exert the pressure on the body must be located external to the fluid compartment or tissue that will function as the hydrostatic skeleton. Second, there have to be reinforcement fibers arranged in a helical pattern around the hydrostatic tissue or space. If fibers are just arranged in a circular or longitudinal pattern, bending of the structure may cause the creation of kinks or possibly bulges in the wall, due to pressure exerted on the body wall. In both cases, deleterious effects can occur on body organs or an aneurysm may form in the wall that may lead to compromising the structure through its rupture. To prevent such adverse conditions, fibers are arranged in a helix around the body wall. This same type of reinforcement is seen in the construction of the walls of high-pressure hoses. Since the fibers are wound at an angle around the structure, bending does not cause an aneurysm to form and there is no chinking of the wall. This type of fiber arrangement is found in the walls of annelids, nemertines, and flatworms, among others. The fibers are often composed of collagen, a helical protein.

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HYENAS

Types of animal science: Classification, ecology, reproduction
Fields of study: Anatomy, ecology, zoology

Hyenas are wolflike carnivore-scavengers whose useful ecological functions derive from their diet of carrion and live animals from termites to antelope.

Principal Terms

CARRION: dead animals
GESTATION: time in which mammalian offspring develop in the uterus
MUSK: bad-smelling liquids made to mark territory or for self-defense
PERINEAL: located between scrotum and anus in males or equivalent region in females

Hyenas comprise four carnivore species of the family Hyaenidae, with body shapes similar to wolves; awkward-looking hind legs shorter than the front legs; good hearing; good vision; and a good sense of smell. Sizes range from small aardwolves to large spotted hyenas. All inhabit grasslands and shrubby areas in Africa, the Middle East, and Arabia.

Some species form packs; others live alone. Most scavenge anything they find, including carrion. Aardwolves eat carrion but prefer termites. Hyenas mate year round and have two- to four-month gestation periods, depending on species.

Physical Characteristics of Hyenas

The physical characteristics of three of the four hyena species are exemplified by the spotted hyena, the largest, strongest species. Their maximum length is six feet, height three feet, and weight 175 pounds. Spotted hyena hind legs are shorter than their front legs, making them look awkward. They also have four-toed paws and manes of coarse hair on the neck, shoulders, and back. The adults are a brown-gray with brown spots, and have large heads, bone-crushing jaws, and an eerie, "laughing" cry, like hysterical human laughter.

Laughing (spotted) hyenas were long thought to be carrion-eaters only. It is now clear that they are major predators of live herbivores such as zebras. They attack in packs at night, bite their victims, and hold on until the prey stumbles. They

Hyena Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Carnivora
Family: Hyaenidae (hyenas and aardwolf)
Genus and species: Crocuta crocuta (spotted hyena); *Hyaena brunnea* (brown hyena), *H. hyaena* (striped hyena); *Proteles cristatus* (aardwolf)
Geographical location: Asia, Africa, and parts of the former Soviet Union
Habitat: Deserts, grasslands, shrubby areas, forests, and mountains
Gestational period: Depending on species, two to four months
Life span: Fourteen to twenty-five years in the wild, twenty-five to forty-five years in captivity
Special anatomy: Manes; four- or five-toed paws; hind legs shorter than forelegs; most have teeth able to crush bones, but the aardwolf eats only insects

kill by tearing open the belly of the prey. Spotted hyenas kill other carnivores as well, such as striped and brown hyenas.

Striped and brown hyenas have manes, short hind legs, and bone-crushing teeth. They are smaller and less aggressive than laughing hyenas, inhabiting grassy and shrubby areas of Africa, India, and the former U.S.S.R. Their gray-brown, black-striped fur is fine camouflage. Like other hyaenids, striped hyenas eat carrion. They also eat fruit, small mammals, birds, and sometimes large herbivores, such as antelope. They grow to maximum lengths of 5.5 feet, heights of 2.5 feet, and weights of 125 pounds. Spotted hyenas hunt at night in small packs.

Brown hyenas are dark brown with gray heads and striped legs. Their maximum length is 4.5 feet, and they reach 120 pounds. They inhabit the dry, rocky Southern African deserts, usually traveling alone. As scavengers they eat anything available, including carrion and bones picked clean by vultures, using strong teeth to crack bones for marrow.

Aardwolves, honorary hyenas, inhabit much of Africa. They are hyaenid by appearance, as their backs slope down from shoulder to tail due to short hind legs. They have reddish, black-striped fur and manes on their necks and shoulders. When attacked, aardwolves erect the mane to look fiercer and spray evil-smelling musk from perineal glands.

Aardwolves differ from hyenas in having five-toed front feet. Aardwolf teeth are small and suitable only for eating their main food, termites and other insects. Their maximum length is 2.5 feet, their height is 1.5 feet, and their weight is twenty-five pounds. The termites that aardwolves eat are active at night, so aardwolves are nocturnal and eat termites with their long, sticky tongues. Aardwolves live alone and mark territories with musk, denning in empty burrows of other animals.

The spotted hyena's maniacal, eerie cry has led to it being called the "laughing" hyena. (Digital Stock)

The Life Cycle of Hyenas

There are similarities and differences in hyena species lives. Spotted hyenas form groups of up to one hundred: a few males, many females, and numerous young. Females conceive year round, birthing two or three pups that can see and run immediately, after a four-month gestation. Females, larger than males, select short-term mates. Striped hyenas fight within groups, sometimes killing group members. Maximum life spans are twenty-five years in the wild and forty years in captivity.

Like spotted hyenas, striped hyenas mate year round. They live in small groups or alone. A three-month gestation yields two to five young born with the eyes not yet open. Mothers nurse offspring until they can feed themselves. Life spans are up to twenty-five years in captivity. Brown hyena life cycles and reproductive habits are nearly the same as in striped hyenas. However, they live alone except when mating or nursing young.

Aardwolves live in groups. They have a mating season when males fight for females and winners mate. Gestation is two months and yields two to five young, nursed for two months. Aardwolves live for fifteen years in captivity.

Spotted, striped, and brown hyenas eat carrion, preventing its decay and its endangerment of humans and other animals. Aardwolves eat termites, preventing damage to the wilderness and human habitations. These activities are their main ecological function. As spotted and striped hyenas eat live food, they also kill injured or weak members of other species, helping the species eaten to enhance their long-term survival.

—Sanford S. Singer

See also: Carnivores; Dogs, wolves, and coyotes; Fauna: Africa; Packs; Predation; Scavengers.

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HYRAXES

Types of animal science: Anatomy, classification, reproduction
Fields of study: Anatomy, zoology

Hyraxes, rabbit-sized, furry mammals, look like rodents but are more closely related to elephants. Their foot pads optimize traction on rocks and in trees.

Principal Terms

DIURNAL: active during the day
GESTATION: duration of pregnancy
NOCTURNAL: active at night
PELAGE: animal fur
SOLITARY: lives alone

Hyraxes are rabbit-sized mammals that look like rodents. Strangely, they are closely related to elephants. There are three kinds of hyraxes, all found in Africa: rock hyraxes, bush hyraxes, and tree hyraxes. These vegetarians eat different kinds of food and differ in social interactions. Some live in groups and others are often solitary.

Image Not Available

Physical Characteristics of Hyraxes

Hyraxes are one to two feet long and weigh three to fourteen pounds. They have stumpy tails, brown to gray fur on their backs, and lighter pelage on their sides. Hyrax fur is short on individuals living in warm, dry regions, and thick and soft on those living in colder areas.

The three types of hyraxes walk on all fours and are excellent climbers, because their feet end in rubbery pads having sweat glands. When hyraxes run, their feet sweat, and the resultant lubrication improves traction on rocks or trees. However, hyraxes also have small hooves on the first and third toes of their hind feet. All hyraxes have a gland in the middle of the back, surrounded by a ring of erectile, dark brown to yellow fur. When a hyrax becomes excited, this hair stands on end.

Life Cycles of Hyraxes

Bush and rock hyraxes are social animals which live in family groups of up to three dozen members. Each group is led by a dominant male. Its other members are adult females and young of various ages. Group members care for each other. The dominant male marks off their territory and defends it, using scent markers to warn off other hyraxes.

Single groups of bush and rock hyraxes may share a territory peacefully, even using the same burrows. They cluster together for warmth. The young of both species play together. Part of the basis for this coexistence is that they do not compete for food. Although hyraxes can eat grasses or other soft plants, bush hyraxes eat soft plants but not grasses, and rock hyraxes eat grasses. However, while the two species live together, they do not interbreed, since both their mating behaviors and the anatomy of their sex organs differ.

Tree hyraxes differ from the other types in being usually solitary. However, they may live with one or two others. They never live in large groups or with other kinds of hyraxes. This is partly due to their habitats in trees. Rock and bush hyraxes are diurnal, while the tree hyraxes are nocturnal.

In all types of hyrax, mating season depends on species and habitat. Gestation is seven to eight months. All females in a family group of rock or bush hyraxes give birth within a few weeks of each other, each having one to four young which are nursed for five months. Tree hyraxes litter one or two young. The offspring of all species can mate at approximately sixteen months old. Females join rock or bush hyrax groups, and males leave by age 2.5 years. Tree hyrax offspring are solitary after weaning. Hyraxes can live for nine to twelve years.

The Three Types of Hyrax

Rock hyraxes (dassies) live in diurnal family groups among rocks and boulders, from dry lowlands to mountains 14,000 feet high. They inhabit and hide in rocks or their crevices. Dassies are one to two feet long and weigh four to fourteen pounds. Their back fur is light to dark brown and the erectile fur around their midback glands is dark brown or yellow-orange. Rock hyraxes eat grasses. Their eyes can look right into the sun, enabling them to escape avian predators. They can live for nine to twelve years.

Bush hyraxes are diurnal and live amid rocks and boulders or in hollow trees from south to northeast Africa. Up to two feet long, they weigh three to twelve pounds, have light gray back fur, and yellow fur around the midback glands. These hyraxes eat soft plants and live in groups of up to thirty-four. Often they share territory with rock hyraxes. They can live for ten to twelve years.

Tree hyraxes (dendrohyraxes) live in Africa. Eastern tree hyraxes inhabit Kenya's coast and Zanzibar. Southern tree hyraxes inhabit southeastern and East Africa. Western tree hyraxes live in West and Central Africa. All make tree nests in savannas, rain forests, and evergreen forests at altitudes up to 12,000 feet. They are up to two feet long, and weigh three to nine pounds, less than rock or bush hyraxes. Their long, dark brown back fur and dark yellow erectile fur around midback glands blend with shadows in trees. They eat soft plants, are nocturnal and hide during daylight, are most often solitary, but may live with one or two others.

Hyrax Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Hyracoidea (hyraxes)
Family: Procaviidae
Genera: Procavia (rock hyrax, five species); *Heterohyrax* (bush hyrax, three species); *Dendrohyrax* (tree hyrax, three species)

Geographical location: Africa and the Middle East up to Syria

Habitat: Among rocks and boulders, from dry lowlands to mountains fourteen thousand feet high, in trees near coasts, in rain forests, and evergreen forests twelve thousand feet high

Gestational period: Seven to eight months

Life span: Nine to twelve years

Special anatomy: Feet with rubbery pads containing sweat glands; rudimentary hooves on the first and third toes of the rear feet; a midback gland, surrounded by erectile fur

Hyraxes and Their Predators

Hyraxes are of relatively little interest to humans, though some Africans eat them. All hyraxes are preyed on by eagles, lions, leopards, jackals, hyenas, and snakes. Other predators are more selective in hyrax predation, due to their different habitats. For example, special predators of tree hyraxes include civet cats, servals, and caracals.

—Sanford S. Singer

See also: Elephants; Fauna: Africa; Groups; Nocturnal animals; Rodents.

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ICHTHYOSAURS

Types of animal science: Anatomy, classification, evolution
Fields of study: Anatomy, paleontology

Ichthyosaurs are extinct marine reptiles of the Mesozoic era. They were highly adapted to the marine habitat, having evolved a dorsal fin, flippers, and a tail fin. These fleshy features are often preserved in spectacular fossils from the Holzmaden and Solnhofen deposits in Germany.

Principal Terms

CARANGIFORM SWIMMING: a method of swimming where the tail is moved while the body is held rigid

DIAPSID: having two bone openings in the temporal region used for jaw adductor attachment; a supratemporal opening and an infratemporal opening

EURYAPSID: having only a single temporal bone opening above the squamosal and postorbital bone; the supratemporal opening of a diapsid condition

HYPERDACTYLY: a condition whereby the number of digits is increased above the normal five to create a wing

HYPERPHALANGY: a condition whereby the number of phalanges is increased in each digit

INIA TYPE: ichthyosaurs with a tunalike tail fin and possible carangiform swimming or forelimb flyer

NEOCERATODUS TYPE: ichthyosaurs with undulating tails and forelimb wings

Ichthyosaurs were the most marine-adapted type of all the reptiles. When they first make their appearance in the fossil record in the Triassic, they are already recognizable as ichthyosaurs adapted to an aquatic existence. For this reason, their ancestry has remained a mystery since their discovery in the eighteenth century. Ichthyosaurs ranged in size from less than a meter to over ten meters in length. Early ichthyosaurs had already modified their forelimbs and hindlimbs into winglike structures. The limbs in ichthyosaurs had hyperphalangeal conditions, whereby there was an increase in the usual number of phalanges in each finger. Some ichthyosaurs expanded the width of the wing by adding extra rows of fingers, a condition known as hyperdactyly. The tails had reevolved a fin that either extended from the middorsal surface to the midventral surface or formed a semilunate tail. In these ichthyosaurs, the body plan already was porpoiselike, with a barrel-shaped thorax and tapering tail. Along these lines, icthyosaurs reevolved a dorsal fin. The skull, with its beaklike rostrum, had a narrow snout with large orbits, with sclerotic plates for maintaining the shape of the eyes. The nostrils had migrated backward to lie in front of the orbits and the temporal region was reduced. The skull behind the large eyes was much reduced. The ichthyosaurs retained one large temporal fenestra (bone opening) that housed the pseudotemporalis muscle. The other main jaw adductor, the pterygoideus, originated on the palate. Based upon the temporal fenestral pattern, these forms were classified as either their own class of reptiles or were considered to be a member of the Euryapsida. Evidence from the skull and reproductive strategy point to another ancestry. The ichthyosaur skull shows the loss of the lower temporal opening of the diapsid skull condition. In addition, ichthyosaurs were live bearers of their young, with a placenta-like structure. The only reptilian group with the loss of the lower temporal fenestra and loss of the eggshell is the diapsid Lepidosauria. All other reptilian groups use the eggshell for the main source of cal-

Ichthyosaur Facts

Classification:
Kingdom: Animalia
Phylum: Chordata
Subphylum: Craniata
Class: Reptilia
Subclass: Lepidosauria
Order: Ichthyopterygia
Family: Ophthalmosauria
Genus and species: Ophthalmosaurus icenicus
Geographical location: Oceans of the Mesozoic Era
Habitat: Marine
Gestational period: Unknown
Life span: Unknown
Special anatomy: Limbs transformed to flippers (wings) that employ hyperphalangy to elongate flipper; reevolve dorsal fin and tail fluke in some; smooth skin without scales; rostrum elongate with conical labyrinthodont teeth; live-bearing

cium for the skeletal development of the embryo, and thus the eggshell cannot be eliminated in their reproductive cycle.

Types of Ichthyosaurs
Ichthyosaurs are typed according to their mode of locomotion or by the morphology and shape of the pectoral flippers. The *Neoceratodus* type, or lungfish type, is so called because their straight tails resembled the tails of lungfish. These types had equally sized pectoral and pelvic flippers. It is considered that these forms had a flexible body with some degree of tail undulation possible for locomotion. The winglike forelimbs, with their hyperphalangy condition, gave them a hydrodynamic shape, and may have been their main propulsion system, acting as wings. Jurassic ichthyosaurs saw the development of a tunalike semilunate tail fin. These types, known as *Inia* type, named after the Amazon dolphin, were considered to be faster and more maneuverable swimmers than the *Neoceratodus* type. The hind limbs are reduced in these forms, and it is considered by some that the forelimbs were used as wings and the tail was used as a steering device. Others consider that the semilunate tail was used in a form of swimming used by tunas, known as carangiform swimming, using rapid movements of the tail. The vertebral column here extended into the lower lobe of the tail. A cartilage ray extended into the leading edge of the upper lobe of the tail, as seen in beautifully preserved tail found in the upper Jurassic deposits around Solnhofen, Germany. These forms also had a well-developed dorsal fin to aid in the prevention of rolling during swimming. It is thought that these ichthyosaurs had a more rigid body and thus had less drag on the body during swimming. Another ichthyosaur form, the *Leptopterygius* type, had well-developed hind limb flippers and pelvic girdle, and slightly reduced pectoral flippers. Undulation of the tail was con-

Image Not Available

sidered the main propulsion system of these ichthyosaurs. Finally, in the *Mixosaurus* type, undulation of the body seems to have been the mode of locomotion. In this body form, a series of elongated neural spines supported the tail fin. There seem to be two opposing views of ichthyosaur swimming speed and prey capture. Some authors believe that ichthyosaurs were high-speed swimmers, while others feel that ichthyosaurs were slower moving but highly maneuverable, and perhaps capable of short, high-speed swimming bursts.

Much is known about the diet of ichthyosaurs through the preservation of stomach contents. Many ichthyosaur species relied heavily on squid and, to a lesser degree, fish. There are reports of pterosaur remains preserved in the guts of ichthyosaurs as well.

Surprisingly, much is also known concerning the reproductive habits of ichthyosaurs. Because of their wing limbs and their round-girthed bodies, it is unlikely that ichthyosaurs came out of the water. How then did they give birth? The answer to this question lay in some of the most spectacular fossils of ichthyosaurs housed in the Stuttgart Museum in Germany. Female ichthyosaurs were preserved in the act of giving birth, whether from problems arising in the birthing process or possibly from poisonous dinoflagellate blooms that killed the ichthyosaurs during the birthing process. In some of these fossils the preserved offspring can be seen lying in a placenta-like structure expelled from the female's body. Other baby ichthyosaurs are often seen in the abdominal area of the ichthyosaur, and were previously thought to be the result of cannibalism. However, it is more likely that these were developing fetuses.

—Samuel F. Tarsitano

See also: *Allosaurus*; *Apatosaurus*; *Archaeopteryx*; Dinosaurs; Evolution: Animal life; Extinction; Fossils; Hadrosaurs; Paleoecology; Paleontology; Prehistoric animals; Pterosaurs; Sauropods; Stegosaurs; *Triceratops*; *Tyrannosaurus*; Velociraptors.

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IMMUNE SYSTEM

Type of animal science: Physiology
Fields of study: Cell biology, immunology, pathology

The immune system distinguishes "self" from "nonself" in the body, fighting off foreign invaders such as bacteria, viruses, and parasites. It works through the production of proteins called antibodies, and of cells that recognize and kill foreign pathogens.

Principal Terms

ANTIBODY: protein produced by lymphocytes, with specificity for a particular antigen

ANTIGEN: chemical that stimulates the immune system to respond in a very specific manner

CELL-MEDIATED IMMUNITY: production of lymphocytes that specifically kill cells with foreign antigens on their surfaces

HUMORAL IMMUNITY: production of antibodies specifically reactive against foreign antigens carried in body fluids (humors)

LYMPHOCYTE: white blood cell that produces either cell-mediated or humoral immunity in response to foreign antigens

MACROPHAGE: mature phagocytic cell that works with lymphocytes in destroying foreign antigens

An animal must keep itself distinct from its environment, recognizing its own tissues and keeping them from being invaded or mixed with tissues of other organisms. There are two types of protection used by animals in keeping out invaders and resisting foreign substances, nonspecific and specific defenses. In both types, the body distinguishes between cells that belong to the animal, which are "self," and anything that does not belong, or "nonself."

Nonspecific Defenses

Even animals as primitive as sponges have the ability to recognize and maintain self-integrity. Scientists have broken apart two different sponges of the same species in a blender, intermixing the separated cells in a dish. Cells crawled away from nonself cells and toward self cells, reaggregating into clusters of organized tissues containing cells of only one particular individual. Phagocytic cells that engulf and destroy foreign invaders were first identified by a scientist who had impaled a starfish larva on a thorn. He observed that, over time, large cells moved to surround the thorn, apparently trying to engulf and destroy it, recognizing it as nonself. Even earthworms have the ability to recognize and reject skin grafts from other individuals. If the graft comes from another worm of the same population, the skin is rejected in about eight months, but rejection of skin from a worm of a different population occurs in two weeks. Phagocytic cells in earthworms have immunological memory, enabling a worm to reject a second transplant from the same foreign source in only a few days.

Barriers, chemicals, and phagocytic cells are nonspecific protective mechanisms, which do not distinguish among different kinds of invaders. Tough outer coverings such as skin, hide, scales, feathers, or fur provide surface barriers. Nonspecific defenses also include secretions of mucus, sweat, tears, saliva, stomach acid, and urine, as well as body-fluid molecules, such as complement and interferon. Damaged tissues or bacterial invaders signal other cells to produce inflammation, a nonspecific response characterized by heat, redness, swelling, and pain. Cellular defenses associated with inflammation include phagocytes such as neutrophils and macrophages, which engulf and digest bacteria and debris, and natural killer cells, which destroy cancer cells or virally infected cells by poking holes in them.

Immunity

The only specific defense in vertebrates is provided by the immune system, in which the component parts react against particular antigens on invaders, such as individual strains of bacteria or types of viruses. This more sophisticated protection is produced by lymphocytes that provide either cell-mediated or humoral immunity against particular antigens. Cell-mediated immunity depends on T lymphocytes (T cells) that become mature as they pass through the thymus, from which they get the "T" of their name. Humoral immunity is the function of antibodies, proteins released by B lymphocytes (B cells) that have matured and developed into plasma cells. The B lymphocytes reach maturity in the bursa of Fabricius in birds, where they were first recognized and from which they were named. Other vertebrates lack the bursa of Fabricius, and B cells mature in the bone marrow instead, so the name "B lymphocyte" still applies.

Antigen molecules are usually proteins or glycoproteins (proteins with sugars attached) that generate either an antibody response or a cellular immune response when they are foreign to the responding animal. So-called self antigens are molecules on cell membranes that identify the cells as belonging to the animal itself. An animal would not normally produce an immune response against its own antigens, but the same antigens would generate an immune response if placed in another animal to whom they were foreign. These antigens are the means by which self and nonself distinctions are made by the immune system, so the system can determine whether to ignore cells or attack them. Occasionally, self antigens, for some reason, are no longer recognized by the animal's immune system, and are attacked as if they were foreign. This causes an autoimmune disease, where the immune system destroys the body's own tissues.

Scientific understanding of how the immune system functions is largely dependent on work done using laboratory animals, including rabbits,

Five Classes of Antibodies

IgM is produced first in a response to foreign antigen, but its concentration declines rapidly. With five Y-shaped monomer subunits forming a pentamer structure, IgM is very effective in binding many copies of the same antigen and agglutinating them, but is too big to cross the placenta.

IgG is the most abundant class of antibodies in circulating blood, a monomer capable of passing through vessel walls to protect cells and tissues. In some species, including humans, it crosses the placenta to pass on the mother's immune protection to the fetus. Produced after IgM in an immune response, it is much more effective against bacteria, viruses, and toxins.

IgA is secreted as a dimer (two subunits) into milk, sweat, saliva, and tears. It is especially important in colostrum, the secretion before milk production begins that is the only way some newborn animals receive their mother's antibodies. IgA prevents bacteria and viruses from binding to epithelial cell surfaces, especially in the digestive tract.

IgE antibodies bind to the surfaces of mast cells and basophils with the arms of the Y-shaped monomer extended. Foreign antigens bind to the ends of the Y arms and trigger these cells to release histamine and other chemicals that cause the inflammation of allergy. IgE is also the antibody that attacks parasites inside the body, such as worms.

IgD molecules are monomers located mainly on the surfaces of B cells, apparently acting as receptors for the antigen that is recognized by each B cell and triggers its activation.

mice, and hamsters. Laboratory mice have been highly inbred into strains where all the animals are genetically identical and their genes and antigens are well known. Studies on these mice have been essential in determining how the immune system normally works, and how it fails to work in autoimmune diseases and the inability to prevent cancer cells from proliferating.

Antigen Presentation and Receptors

Central to the functioning of the immune system in mammals is a system of genes called the major histocompatibility complex (MHC). These genes encode a collection of cell-surface glycoproteins that are the self antigens by which the immune system recognizes its own body cells. Class I MHC molecules are expressed on the surfaces of all nucleated cells, while Class II MHC markers are produced only by specialized cells, including cells of the thymus, B lymphocytes, macrophages, and activated T lymphocytes. Both Class I and Class II MHC molecules identify the cells bearing them as self, and these also serve as the context in which the immune system recognizes foreign antigens that are presented on the cell surface. Cells with self antigens are tolerated by the immune response of that individual animal, while cells that show foreign antigens are attacked and destroyed. Rejection of a graft or transplanted organ is reduced with more closely matched tissues, which are better tolerated by the immune system.

When bacteria evade protective barriers and chemicals to enter an animal's body, the animal's macrophages attack, engulfing and digesting the invaders. One bacterium may have thousands of different antigenic segments that can be recognized on its surface or inside the cell. Small parts of these digested cells, the individual antigens, are joined to the macrophage's newly formed MHC Class I and Class II before they are exposed on the cell surface. The foreign antigens fit into a space or pocket within the MHC molecule and are recognized by T cells that have the same MHC molecules and can respond specifically to the foreign antigen. Cytotoxic T cells (T) react to antigens held in the pocket of a Class I molecule, while helper T cells (T) respond to those presented by Class II molecules. T cells are the agents of cellular immunity, producing perforin molecules that puncture and kill cells bearing the foreign antigen against which the T cells are specific. T cells, when activated by encountering their specific antigens presented with Class II molecules, release cytokines that help to activate both T cells and B lymphocytes. Activated B cells divide to produce memory B cells and lymphocytes that mature into plasma cells, which secrete about two thousand antibody molecules per second over their active lifespan of four or five days.

Both T and B lymphocytes can react with their specific foreign antigens because the antigen-MHC complex binds to receptor molecules on the lymphocyte surfaces. Each clone of lymphocytes has the genetic ability to respond to a particular shape that fits its receptors. There may be millions of different receptors among the lymphocytes of a single animal, capable of binding millions of different antigens, even artificial chemicals not existing in nature. This enormous variability in response capability makes the immune system of each animal protective against many kinds of foreign invaders. Since each individual has its own set of immune responses, a population is less likely to have all its members die in an epidemic. Certain animals will be more resistant to the pathogens, so some will survive to reproduce and keep the population from extinction.

Primary and Secondary Immune Responses

When a foreign antigen is encountered by an animal for the first time, both T and B cells that can bind the antigen are activated, but not immediately. In a series of reactions, macrophages first break down the antigen-bearing cell, processing and presenting the antigen on its surface with MHC. The T cell specific to that antigen then encounters the antigen-MHC complex on the macrophage and divides to produce a clone of memory T cells and a clone of effector (activated) T cells. Activated T cells release cytokines that activate T and B cells so that they can attack the same foreign antigen. The first encounter with antigen produces a slow primary response, taking more than a week to reach peak effectiveness. During the time needed to generate this response, pathogenic bacteria or viruses can produce disease in the animal under attack. The memory T and memory B cells remain alive but inactive until the same foreign antigen is encountered again, even years later. The secondary response that results immediately when these memory cells are activated occurs so quickly that the disease process does not recur.

The importance of the immune system is seen in humans who lack its function, those with acquired immunodeficiency syndrome (AIDS). Human immunodeficiency virus (HIV) is the causative agent of AIDS, and is similar to viruses that attack other species in the same way. Most who die with AIDS really succumb to one of many opportunistic infections that cause diseases in HIV-positive individuals, but which are eradicated by the immune system in normal individuals.

—*Jean S. Helgeson*

See also: Anatomy; Beaks and bills; Bone and cartilage; Brain; Circulatory systems of invertebrates; Circulatory systems of vertebrates; Claws, nails, and hooves; Digestive tract; Diseases; Ears; Endoskeletons; Exoskeletons; Eyes; Fins and flippers; Kidneys and other excretory structures; Lungs, gills, and tracheas; Muscles in invertebrates; Muscles in vertebrates; Nervous systems of vertebrates; Noses; Physiology; Reproductive system of female mammals; Reproductive system of male mammals; Respiratory system; Sense organs; Skin; Tails; Teeth, fangs, and tusks; Tentacles; Wings.

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IMPRINTING

Type of animal science: Behavior
Fields of study: Ethology, neurobiology, zoology

Imprinting is the process of very rapid attachment between parents and offspring during a brief period that alters the offspring's behavior permanently. Imprinting involves behavior that is necessary to the survival of the animal under natural conditions.

Principal Terms

CONSPECIFICS: animals of the same species

CRITICAL PERIOD: a very brief period of time in the development of an animal during which certain experiences must be undergone; the effects of such experiences are permanent

INNATE: inborn, unchangeable

NIDIFUGOUS BIRDS: ground-nesting birds

PRECOCIAL: possessing, as infants, well-developed sense organs, the capability of locomotion, and the ability to contribute substantially to the establishment of bonds between them and their parents

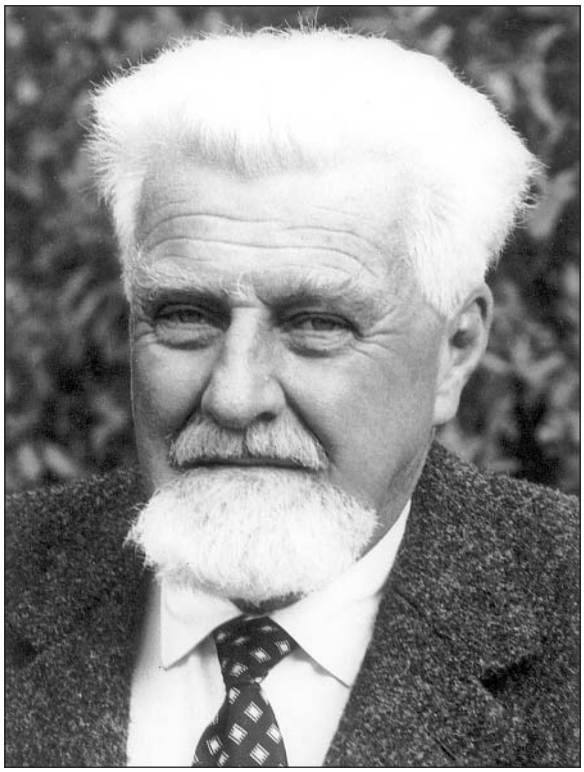
RELEASER: a stimulus that releases a sequence of reflexes that always occur in the same order and manner

SCHEMA (pl. SCHEMATA): an innate releasing mechanism; a neural process that programs an animal for receiving a particular sign stimulus and causes a specific behavioral response

SENSITIVE PERIOD: a period during which a given event produces a stronger effect on development or in which a given effect can be produced more rapidly than it can earlier or later

Imprinting is the process of very rapid attachment between parents and offspring, during a brief sensitive period, that alters the offspring's behavior permanently. This period is found only in precocial birds and a very few mammals. The significance of imprinting is the development of behavioral patterns that will enable the animal, as it matures, to recognize its own species (for future mating), to socialize and cooperate with other conspecifics, and to locate food and territory.

Konrad Lorenz, the first scientist to investigate the phenomenon of imprinting thoroughly, drew attention to the process by which young duck-



Konrad Lorenz's studies of imprinting in young animals contributed to his sharing the Nobel Prize in Physiology or Medicine in 1973. (Nobel Foundation)

Konrad Lorenz

Born: November 7, 1903; Vienna, Austria
Died: February 27, 1989; Altenburg, Austria
Fields of study: Ethology, physiology, zoology
Contribution: Lorenz, the founder of ethology, developed a deep understanding of the behavior patterns in animals, notably imprinting in young birds.

Konrad Lorenz, the son of an orthopedic surgeon, received a medical degree in 1928 and a Ph.D. in zoology in 1933. Both were earned at the University of Vienna. Lorenz studied animal behavior by means of comparative zoological methods, a field now known as ethology. Many of his observations came from establishing and watching colonies of birds, particularly the jackdaw and greylag goose. He published numerous papers based on his observations of these birds.

In the mid 1930's, Lorenz reported his findings about learning behavior in young ducklings and goslings. The survival of a young bird requires an extremely rapid establishment of the behavioral bond between it and a parent. Lorenz discovered that a newly hatched bird learns within a few hours to follow real or foster parents. This process, known as imprinting, may occur with a human, or even an inanimate object, if the bird's parent is not present. Although the behavior itself is genetically determined, the bird learns the object. Through imprinting, many young animals follow the first moving object they encounter.

To demonstrate the process of imprinting, Lorenz imitated a mother duck's quacking sounds in the presence of newly hatched mallard ducklings. The ducklings responded to Lorenz as their mother and followed him accordingly. After numerous studies, Lorenz concluded that when a young bird is imprinted to a member of another species, the imprinted bird will adjust its own functional cycles to that of its adopted parent. Once accomplished, the behavior pattern is very stable and may be irreversible in some cases.

In 1937, Lorenz taught comparative anatomy and animal psychology at the University of Vienna and became the coeditor of the leading journal for ethology. After World War II, Lorenz headed the Institute of Comparative Ethology at Altenberg, Austria. From 1961 to 1973, he served as the director of the Max Planck Institute for Behavior Physiology in Seewiesen, Austria. Lorenz developed the concepts of animal behavior that led to the modern scientific understanding of how behavioral patterns evolve in a species. He advanced the concepts of how these patterns develop and mature during the lifetime of an individual organism.

In 1963, Lorenz published his book *Das sogenannte Böse* (1963; *On Aggression*, 1966), in which he argued that the aggressive behavior in humans may be modified or channeled, but in other animals, it is primarily survival motivated. Based on his insights and discoveries associated with animal behavioral patterns, Lorenz shared the 1973 Nobel Prize in Physiology or Medicine with Karl von Frisch and Nikolaas Tinbergen.

In 1973, Lorenz was appointed as the director of the department of animal sociology at the Institute for Comparative Ethology of the Austrian Academy of Sciences in Altenberg, where he continued to apply his ideas about the behavior of humans as members of a social species. In 1978, he published *Vergliechende Verhaltensforschung: Grundlagen der Ethologie* (*The Foundations of Ethology*, 1981), a comprehensive review and assessment of his major contributions to science.

—Alvin K. Benson

lings and goslings follow the parent soon after hatching. By doing this, the young become sensitive to the visual and auditory stimulus pattern presented by the parent. This process is remarkably confirmed when a young bird fostered to a parent of another species establishes a permanent bond with the foster species and excludes members of the bird's own kind. The bond is so lasting that Lorenz called the process which gives rise to it *Prägung*, or imprinting. This single experience imprints the pertinent object of the infantile instinctive behavior patterns in a young bird that does not recognize the object instinctively. The object can be imprinted only during a quite definite period in the bird's life. From this observation, Lorenz set forth two principles of imprinting: First, that there is a critical time period in which the young offspring must form the attachment and after which no imprinting stimulus is effective, and second, that once formed, the attachment to a specific object, whether it be to its parent, a person, or an inanimate object, is permanent and irreversible. Several ethologists who have since studied imprinting do not totally accept Lorenz's conclusions that imprinting is irreversible and unchangeable, believing instead that the "critical period" is more flexible and is not necessarily dictated by inheritance. Thus, the term, "sensitive period" has gained popularity and become more widely accepted.

The Imprinting Process

Imprinting processes occurring during this sensitive period are basically different from the processes that occur after the sensitive period is over. The differences can be observed both in the immediate behavior and in the long-range effects of these experiences. The order in which these imprinting events occur has little relevance to the sequence in which they are later manifested. In jackdaws, the sensitive period for sexual imprinting comes well before the sensitive period for imprinting of the approach and follow responses. In this bird, sexual imprinting occurs while the nestling sits in the nest still half-naked, showing no responses to conspecifics other than that of gaping at its parents when they arrive to feed it. The sensitive period for imprinting of following behavior occurs immediately before fledgling. The effect of sexual imprinting, however, does not become obvious until two years later, whereas the following response is observable only a few days after imprinting.

A variety of stimuli may elicit the imprinting responses; most responses are to either auditory or visual stimuli. Some authors have suggested that auditory imprinting is especially important in the song-learning of birds. In many species, the song is completely innate, while in others it is learned; in still others, a combination of learned and innate factors is necessary. In some species where there are learned components, there seems to be a sensitive or receptive period during which songs are normally learned permanently and irreversibly. Lorenz found that ducklings respond to both visual and auditory stimuli but that the strongest responses are to their mother's call. More often, however, when both auditory and visual cues are provided, the extent of successful imprinting exceeds that attained with either stimulus provided singly. Not to be ignored are those cases in which the olfactory sense plays a role in imprinting, particularly in those animals with high olfactory acuity. In these animals, the olfactory sense may regulate relationships between members of the same species (as in sexual behavior), promote predator or prey recognition, and help identify food or territory when conspicuous visual aspects are absent.

Experimenting with Imprinting

The law of effort says that the more energy a bird expends during the primary attachment formation, the stronger the imprinting will be. To observe this effect, researchers may manipulate the energy expenditure in at least three ways: by using a moving object rather than a nonmoving one, by providing continuous rather than spaced training sessions with the object being imprinted, and by having longer training sessions using a stimulus that moves around the arena more quickly. Ducklings placed in a runway with ten-centimeter hurdles were forced to exert more effort than animals that followed an object in an ordinary runway; it was found that birds compelled to go over the hurdles in order to keep up with the moving model later achieved higher imprinting scores than did control birds.

Other experiments seem to indicate that movement by the subject is not always necessary for imprinting to take place. In one such study, ducklings were exposed to a moving object but were not allowed to follow it, while control subjects were permitted to follow the object. Both experimental and control animals exhibited poor responses to the new object. The role of movement in imprinting was also tested by placing ducklings in wooden stocks that restricted movement, then exposing them individually either to a moving object or to a stationary one. Despite the restriction of their movement, the animals became imprinted. The way the object was moved made no difference to the extent of approach and follow-on testing, but ducklings that had been exposed to a stationary object did not follow as well. This experiment showed that, while movement of the subject was immaterial, movement of the object was important for imprinting. In most cases, birds that expend more energy are more successfully imprinted.

Recognition and discrimination are the primary means to determine whether imprinting has occurred: If a bird is given a choice between known and unknown figures, it will choose the known. This is considered the standard test for imprinting; birds will usually run to their mother. Observations other than recognition and discrimination may also be worthwhile in assessing the amount of imprinting. One of these is distress at separation. Young chicks and ducklings, when separated from the mother or companions, make specific distinctive calls. Another evaluation can be made upon recognition at reunion: Approach and follow responses are clearly shown by birds that, upon hatching, are visually exposed to that figure. When a chick or duckling is placed in a runway with a moving object and is left there for a number of hours or even days, it will eventually stop following the object and otherwise occupy itself, maybe eating or drinking or wandering about. Disruption of the familiar, however—by a noise, by placing a piece of paper on one of the runway walls, or by the appearance of a strange object—will cause the bird to run to the familiar object, where it will remain for a time.

Theories to explain the ending of the ability to imprint can be divided into four categories. The first category is end of sensitivity because of maturation; that is, the tendency to approach and follow naturally decreases as the animal ages, and this lessened tendency is internally determined, rather than being caused by any impact of experiences. The second category is inhibition through socialization. Evidence so far presented indicates that the sensitive period for imprinting is likely to continue until a firm imprinting experience has occurred. Once imprinting of the approach and follow responses to a particular stimulus has occurred, it tends to inhibit approach and imprinting to new figures. Third, growth of timidity or fear responses eventually represses approach and follow responses. This is perhaps the most popular theory. Last, the ending of imprinting may be shown by an end to varied, restless activity that is not performed to achieve a goal.

Innate Versus Learned Behavior

That imprinting behavior occurs is not debatable, but controversy has arisen pitting Lorenz and his followers, who believe that the process is wholly innate, against a host of later investigators who conclude that imprinting is actually a form of learning. Those who say that imprinting is innate base their opinion on observations that the drive to imprint is strikingly different from other instinctive behavior patterns, whose releasing schemata are not innately determined but are acquired like conditioned reflexes. Lorenz states that imprinting is different from learning in that imprinting can occur only during a very definite, and perhaps short, period in the animal's life and, therefore, is dependent on a specific physiological developmental condition in the young bird. He further asserts that imprinted recognition, even after the critical period, is the same as innate behavior because the recognition response cannot be forgotten (as opposed to learned processes, which can be forgotten). Others, however, believe that imprinting involves a behavior that is absolutely necessary for the survival of the animal under normal conditions. In the case of both social and food imprinting, this is clear. The desire to follow the parent or to want to eat a particular food (as well as to learn what objects are the targets) motivates these behaviors. The urge to learn these objects is so strong that the associated processes which fulfill this learning are contradictory to those associations usually involved in this rote-type learning.

If imprinting is a learned behavior, then can it be considered conditioning? Conditioning involves the building of associations between stimuli and responses. A wide variety of stimuli may initiate the imprinting process by innate unconditioned approach responses. The particular stimulus continues to elicit filial responses, but eventually any new stimuli begin to be ignored and later even feared. There is no selective pairing of stimuli and responses, as in conditioning. In imprinting, the primary bond between stimuli and responses continues to be strengthened and becomes exclusive.

The Study of Imprinting

The earliest documentation of the imprinting process was by the seventh century English monk Saint Cuthbert, who spoke of it as "object fixation." Sigmund Freud later discovered the process independently of ethologists, but several ethologists take credit for its discovery and subsequent investigations. Most means of study practiced by ethologists investigating this phenomenon have been patterned after techniques employed by Eckhard Hess. Experiments have usually been conducted using models that do not closely resemble any real animals, let alone the parent model. Each subject is individually "trained" with a particular figure. Then, all the subjects are individually presented with a situation in which they can choose between two figures. Imprinting has occurred when an animal is drawn to the figure that is familiar. (If only one figure were used to train all the animals, a later choice test would be invalid because, if the figure was favored on the test, the investigator would not know whether the attraction was caused by imprinting or by some other impression of the figure.) Earliest observations showed that moving animals, persons, or even inanimate objects could evoke approach and follow responses in newly hatched nidifugous birds. Goslings, for example, have been found to follow people if the mother goose is absent. Incubator-hatched ducklings will follow anybody who encourages them to do so by tapping the ground and/or calling while moving away from them.

Another much-copied method that Hess used employs ducklings hatched in the dark and kept isolated until trained to the test stimulus. They then are placed on a circular track and allowed to follow a moving, sound-producing object around the runway for a determined time or distance. Later, the ducklings are tested for adequacy of the imprinting by allowing them to choose between two models to see which is approached. It is important to know what external stimuli arouse the strongest following response. The stimulus may be size of the object: If the object is too large, the duckling will flee. The duckling will simply peck at an object that is too small. Another factor is color; blue objects are the first choice for chicks, followed by red, then yellow. A third aspect is shape; strangely, adding immovable wings, tail, and head to a sphere actually reduces its effectiveness in generating a response.

Early investigators attempted to model releasers after parent birds. They discovered that a noisy moving object tended to elicit stronger responses than a silent one. Approach and follow responses in ducklings succeed intermittent noises, but to be most effective the noises should be simple, rhythmical, and monosyllabic, and given in rapid succession. Such stimuli are, overall, quicker than visual stimuli in eliciting approach from ducklings. In fact, ducklings that fail to imprint to moving models occasionally do imprint to noise-making ones—enough so that they will continue to follow its movement even when the noise ceases. Generally speaking, it is necessary for sound to accompany visual stimuli, though ducklings and goslings do not appear to imprint on sound alone.

Some scientists wonder whether all this laboratory study has really been relevant to the study of natural imprinting. Laboratory procedures are undoubtedly useful in helping to determine the behaviors of young animals; however, because the animals are given such an overwhelming number of inappropriate stimuli, it may be difficult to assess how the animal would react under normal conditions. Observations of animals in their natural settings are difficult to make and analyze, but the known data reveal several differences from laboratory tests. For example, hatched ducklings normally stay in the nest with the female mallard long past the earlier laboratory-assigned critical period, and, as a result, they are both visually and auditorially attached to the parent by the time they leave the nest. This enhances their ability to survive on their own. Continued investigation into imprinting must occur, but it should take place in an animal's natural setting.

The Complexity of Imprinted Behaviors

The imprinting process has a much broader significance for the animal than merely giving it the tendency to follow moving objects. Behaviors usually associated with imprinting are following and approach responses, sexual identification, species recognition, and socialization among conspecifics. Following behavior is far from a simple behavior; there are many degrees, from close, nonfearful following, through hesitant following mixed with fear responses, to strong escape behavior in which only a minimum of following can be observed. Following can also be balanced by aggressive behavior, and the actual behavior of the young bird is largely determined by the interplay between these competing tendencies. Following behavior is important to those duck species that build their nests at a distance from the water, the eventual home of the birds; mother and young may move to the water within several weeks of hatching. The use of species-specific visual or auditory signals in imprinting may enable young birds to follow the mother successfully through dense vegetation from the nest to the water. When the young are ready to leave the nest, generally located several feet above the ground in a tree hole or other suitable site in a pond or swamp, the mother goes down to the water and calls her ducklings. In response to the call, the ducklings jump to the nest opening and then down to the water to follow the mother. The same imprinting patterns may also aid the ducklings in avoiding predators. Quickly following the mother to safety in a few seconds between the time the predator is sighted and an attack may mean the difference between life and death.

Imprinting may serve as a species-identifying mechanism and, even more narrowly, as a species-isolating mechanism. The sexual preferences of birds have been shown, by appropriate exposure to an imprinting stimulus and later testing, to be imprinted to stimuli to which they were exposed. For virtually all species in nature, encounters with birds of other species during the first few days or even weeks after hatching are limited; this alone ensures that young birds will imprint on members of their own species and that when, as mature adults, they begin to engage in reproductive activities they will court only conspecifics. Therefore, imprinting helps guarantee that reproductive energy investments and gametes are not wasted on nonproductive mating endeavors. The overall recognition of conspecifics that can occur as a result of imprinting may also be important for the socialization of young birds and for general cooperation of conspecifics in a social organization. Associating with conspecifics, in turn, may be a significant means of increasing survival, by aiding in processes such as locating food, finding shelter, and migrating.

—Iona C. Baldridge

See also: Communication; Ethology; Instincts; Learning; Mating; Rhythms and behavior.

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INFANTICIDE

Types of animal science: Behavior, evolution
Fields of study: Ecology, ethology, wildlife ecology, zoology

Infanticide, the killing of immature members of the same species, is one of the more disturbing phenomena seen in animals, including humans. However, it follows from the evolutionary logic of individuals striving to maximize reproductive success.

Principal Terms

CONSPECIFIC: a member of the same species
GENERA: plural of genus, a grouping of animals above the species level
GESTATION: the period when the young are nourished within the mother's body; pregnancy
LACTATION: the period when mammal mothers produce milk to nourish their infants
OVICIDE: killing of fertilized eggs
RAPTORS: predatory birds such as hawks and eagles
SIBLICIDE: infanticide committed by the siblings of the individual killed

Infanticide is the intentional killing of dependent immatures by a member of the same species, or a conspecific. Victims may be as young as fertilized eggs or nearing independence from their parents. The infanticidal attackers may be strangers or relatives. The motive is always selfish competition, but sometimes the young are direct competitors and sometimes indirect competitors with the killers. Infanticide occurs in every class of animal, but mammals and birds seem to have evolved the most pervasive and pernicious form, sexually selected infanticide. Wherever it is seen, infanticide reveals the darker side of evolutionary adaptation. There are three scientific explanations for infanticide, each of which applies to particular circumstances.

Infanticide by Genetic Relatives

The first circumstance occurs when related individuals kill dependent young. For example, extreme sibling rivalry occurs in spotted hyenas (*Crocuta crocuta*) and many raptors. The unpredictability of resources or extreme competition for parental care may lead siblings to fight to the death in the den or nest. Even parents may act infanticidally. When parents have larger numbers of offspring than they can feed, the parents themselves may neglect or inflict damage on the smallest or least vigorous young, so as to reduce the number of offspring and increase each survivor's chances of success. Sibling rivalry and parental neglect or abuse of young can lead to infanticide in extreme cases when resources, such as food or parental time and energy, are in short supply. The brutal logic of natural selection shows that selfishness and lethal competition can divide even close kin. However, in most animal species, unrelated individuals are more dangerous to the young.

Infanticide by Direct Competitors

The second circumstance in which infanticide arises is referred to as local resource competition. When immatures use resources that unrelated animals need, aggression may be severe and directed to killing the infants. All ages of infants are vulnerable, even independent juveniles. In the burying beetle (*Nicrophorus orbicollis*), male and female pairs compete for access to rotting meat in which to lay eggs. If defenders of such a resource are displaced by an intruding pair, the intruders proceed to kill and eat the eggs (ovicide) or larvae of the previous pair. Similarly, many birds, such as black-and-white casqued hornbills (*Bycanistes subcylindricus*), compete for rare tree hole nesting sites. If adults encounter another nest with eggs in such a tree hole, they will roll these eggs out or crush them and lay their own eggs. Finally, cannibalism of unrelated young has been seen in many amphibians, fish, reptiles and even in chimpanzees. Stepchildren suffer much higher rates of severe neglect and homicide than a parent's biological children. All of these cases represent extreme competition where resources are scarce and vulnerable young are eliminated or eaten by unrelated killers. The behavior patterns seen in this type of infanticide often resemble predation, are directed at young of any age, and can be performed by adults of either sex.

Sexually Selected Infanticide

The third circumstance in which infanticide occurs is motivated by sexual competition among adults. In a wide range of mammals, including over twenty genera of primates, adult males will kill unrelated infants if they can then mate with the mother. The mother of that infant does not usually reject the infanticidal male even though he has inflicted a tremendous cost on her. Typically, it takes female mammals many months—even years—to nurse young to independence. During this period of infant dependency, the mother is generally physiologically incapable of reproducing. An infanticidal male benefits if he can cut short this period so that he can fertilize the female's next egg. Therefore, a successful infanticidal male eliminates another male's offspring and advances his own reproductive career. Sexually selected infanticide is not restricted to mammals, although the best-documented cases come from lions (*Panthera leo*), langur monkeys (*Semnopithecus entellus*), and rodents (order Sciurognathi). Some birds may also behave infanticidally. For example, the wattled jacana (*Jacana jacana*) shows a fascinating reversal. In this species, the adult females may commit ovicide and infanticide against unrelated young. Adult male jacanas incubate eggs on the nest and protect the young from predators, so females strive to monopolize the parental care donated by males. To do this, a female must eliminate the young of another female and lay her own eggs in the care of the male. Typically, the behavioral patterns seen in sexually selected infanticide differ from those in local resource competition. The young are virtually never eaten and permanent separation of mother and young is the primary goal—whereupon attacks usually cease.

Evolutionary Consequences of Infanticide

Infanticide is widespread and may reach high frequencies in certain species, but it is not universal. Siblicide and parental neglect are found in a very restricted subset of birds and very few mammals. Local resource competition is more common, found in most classes of animals. Finally, sexually selected infanticide is most common in mammals, but even here there are many orders of mammals that never display infanticide. Species that have a very long period of lactation relative to their gestation period are most vulnerable to sexually selected infanticide. The reason for this is that infanticidal attacks are risky because of maternal defense and counterattacks by allies. Therefore, infanticidal behavior will only evolve when the males gain substantially by shortening lactational infertility of the mother.

Clearly, infants and their parents have a very strong motivation to avoid infanticide. Evolution has favored various mechanisms to reduce the risk. In general, infants avoid strangers, even in humans. In some primates, it seems that infants are born with unusual coat colorations that may impede males' efforts to determine which infants are theirs and which were fathered by other males. Parents are normally very protective of their young, both because of predators and because of the risk of attack by conspecifics. This parental protection is expressed through frequent proximity, carrying, and physical defense. One of the most fascinating consequences of a high risk of infanticide is the tendency for the father and mother to establish a long-lasting relationship whose primary benefit is protection of the young from conspecifics. This is seen in burying beetles and many primates. Alternatively, groups of mothers may cooperate in protection against infanticidal males, as in lions and langurs. Therefore, infanticide is one of the few evolutionary pressures that favors complex social relationships.

—Adrian Treves

See also: Altruism; Competition; Copulation; Courtship; Estrus; Fertilization; Lactation; Mating; Offspring care; Predation; Reproduction; Reproductive strategies; Sexual development.

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INGESTION

Type of animal science: Physiology
Fields of study: Biochemistry, ecology, neurobiology

Ingestion is the process of taking food into the body. The animal kingdom possesses myriad strategies for this process, reflecting the diversity of available food sources and how they are utilized.

Principal Terms

CARNIVORE: any organism that eats animals or animal tissues

DETRITUS: small bits of dead matter derived from decay of plants and animals

HERBIVORE: any animal that eats plants or plant material

INVERTEBRATE: any animal that lacks a backbone

OMNIVORE: any animal that eats both plants and animals or their tissues

PARASITE: any organism that lives on or in other living organisms and obtains its food from them

PLANKTON: microscopic plants and animals that float in water

PREDATOR: any organism that kills another living organism to eat it

PROTOZOAN: a single-celled animal-like organism

SAPROVORE: any organism that consumes dead or decaying plant or animal matter

TAXONOMY: a classification scheme for organisms based primarily on structural similarities; taxonomic groups consist of genetically related animals

Ingestion is the process of taking food into the body to satisfy nutritional and energy needs. Although basic nutritional requirements are remarkably similar for all animals, mechanisms of ingestion are exceedingly diverse. This diversity stems from the varied nature of available food sources and the resulting behavioral adaptations and specific body forms required to procure adequate nutrition. Because it is convenient to classify feeding strategies by the type of food consumed, organisms are often described as herbivores, carnivores, omnivores, and saprovores. Although very descriptive, these terms alone are not sufficient to describe fully the feeding adaptations used by animals, especially when considering invertebrates, which make up more than 97 percent of all animal species. Accordingly, this section will expand on these ideas by further categorizing ingestion by the type, size, and consistency of food, while also describing behavioral adaptations that lead to ingestion.

Small Particle Ingestion

Numerous animals live exclusively on a diet of very small particles that include bacteria, algae, plankton, and detritus. Although most small-particle consumers are relatively small animals, they range from the tiniest animal-like organisms (protozoans) to the largest (whales). Many mechanisms have evolved to permit ingestion of small food particles. One common method is by endocytosis. During this process, the outer membrane of a cell surrounds a food particle and engulfs it within the cytoplasm, forming a food vacuole (a cellular organelle used for digestion). This mode of ingestion is best illustrated by protozoans. The amoeba, for example, uses pseudopodia (extensions of its cell membrane) to surround and then ingest prey. Paramecia use cilia (tiny hairlike processes on cell membranes that beat in a coordinated manner) to guide food particles into an oral region prior to ingestion by endocytosis.

Multicellular animals may also ingest small food particles by endocytosis. Sponges use flagella (motile, whiplike structures resembling long cilia) to aid in the gathering of small particles of food. The body cavity of sponges is lined with flagellated cells called choanocytes, or collar cells. The beating action of their flagella creates currents that move water through the body cavity, where food particles are removed and incorporated by the choanocytes.

Filter feeding is another strategy that is commonly used to obtain small bits of food. Most often cilia, mucus sheets, flagella, tentacles, and nets are used as filtering devices. Rotifers (small aquatic invertebrates), for example, use a special double-banded ciliary system to transport water and filter out suspended food particles, which are conducted to the mouth by a third set of cilia. In general, sessile (immobile) organisms (such as sponges, rotifers, and some oysters) are called filter feeders, because they must wait for food to come to them, then extract it from the surrounding medium.

Numerous free-moving animals also use filtering devices to obtain food. Sea cucumbers (animals related to starfish) live on the bottom of the seabed. By extending and periodically retracting sticky tentacles, they capture and ingest small food items. Clams, mussels, and some snails produce a sticky mucus that covers ciliated cells. The mucus traps fine suspended food particles, which are transported to the mouth by ciliary action. Mussels, for example, continuously pass water between their mucus-covered gill filaments for respiration, simultaneously trapping food particles. Similarly, herring and mackerel (fast-swimming fish) possess special structures called gill rakers, which act as sieves to catch plankton from water that continually passes over their gills for the process of respiration. Basking sharks and whale sharks also feed on plankton that is strained from water that enters their mouth and flows over their gills. Baleen whales use a filter consisting of a curtain of parallel filaments (called baleen) attached to the upper jaw to feed. These whales en-

Elephants use their trunks to bring food and water to their mouths. (Corbis) gulf a mouthful of water containing krill (small, shrimplike plankton) and use their tongue to force the water out, trapping krill in the hairlike edges of the baleen. The mouthful of krill is then swallowed. Flamingos feed in a similar manner. They use specially adapted beaks lined with filaments to strain plankton from the muddy bottoms of their aquatic habitat. Some fast-water caddis fly larvae spin tiny silk nets that are used to filter small food items. The nets are then periodically gleaned. Finally, spiders may be considered filter feeders because they use their webs to "filter" flying insects from their environment.

Large Item Ingestion

In contrast with small-particle consumers, numerous animals ingest large food items. Some of these organisms are saprovores, such as earthworms. These worms consume large masses of soil and dead leaves, from which they obtain usable organic matter. Some planarians (flatworms) extend a long extensible tube (called a pharynx) from their mouth to ingest decaying material. Other examples of saprovores include millipedes, wood-eating beetles, some sea cucumbers, many roundworms, and a few snails.

An extraordinary number of animals have adapted to eat plants. Eating plants requires special structures to free plant material for ingestion. Although invertebrates lack true teeth, they have other structures to obtain plants or plant parts. Snails have a unique structure in their mouth called a radula, which acts as a miniature rasping file that scrapes plant material from surfaces and rasps through vegetation. The freed plant material is then ingested. Sea urchins scrape algae by using a highly developed oral apparatus composed of five large pointed plates. Termites use strong jaws made of chitin, the hard structural component of their external skeleton, to cut tiny chunks of wood for ingestion.

Birds use horny beaks to obtain and ingest plant material. Cardinals and grosbeaks, for example, are well adapted to hull and then consume the nutritional portion of large seeds. Herbivorous mammals use specialized teeth to obtain and chew plant material. Rodents (such as beavers, porcupines, and mice), rabbits, and hares have chisel-like front teeth (called incisors) that are used to gnaw, slice, or pull off plant material. Other herbivorous mammals (including cows, sheep, deer, moose, elk, and giraffes) lack upper incisors and therefore use their lower incisors pressed against the roof of their mouth to pull off leaves. The ingested food is then chewed by grinding with premolars and molars.

In contrast to herbivores, many animals capture other animals and eat them. To be effective, these carnivorous predators must have appropriate behavioral adaptations to find and capture prey as well as specialized structures to seize and hold their victims. Jellyfish use tentacles that are equipped with stinging cells to grasp and subdue animals, whereas the tentacles of squid and octopuses have suction-cup-like structures to grasp and manipulate prey. The giant water bug is a carnivorous insect that hunts and captures small fish, relatively large prey for an insect. To do this, water bugs use their legs to seize and hold fish, and their piercing mouthparts to suck juices from their victims. Fish, amphibians, and reptiles have pointed teeth to seize and hold prey. It also is common for many of them to swallow their food whole. Snakes, for example, swallow whole items such as birds' eggs and small mammals. In addition, a snake's jaws are held together by elastic ligaments, permitting it to spread apart and ingest victims larger than its own head. Some large tropical snakes actually consume small pigs and deer. Chameleons and frogs swallow their prey whole, but in contrast to snakes, they use a long and sticky tongue that rapidly shoots out to capture insects. Some predatory carnivores (such as lions, tigers, bears, and dogs) have long, pointed, daggerlike teeth called canines to pierce and kill their prey. Carnivores also may have knifelike molars (called carnassials) that are used to slice flesh from bones. Carnivorous birds (such as hawks, eagles, and owls) use long, sharp talons to seize and kill small animals. Their beaks can be used to tear small pieces of food for ingestion. Further, many carnivorous animals possess specialized mechanisms for paralyzing victims. Jellyfishes, centipedes, spiders, scorpions, and some snakes possess structures that inject toxins that inhibit the nervous system of their prey. Finally, some electric eels may locate and stun their prey with electrical discharges.

Liquid Ingestion

Surprisingly, many animals live exclusively on a liquid diet. Herbivores such as bees, butterflies, moths, hummingbirds, and some bats derive nutrition by consuming plant nectar. As a consequence of their feeding, these animals help plants reproduce by dispersing pollen. Hummingbirds have specially adapted long, narrow beaks and long tongues to suck nectar from flowers. Nectar-consuming bats also have long narrow faces and tongues. Aphids, and many other insects that consume plant sap, have highly specialized mouthparts that pierce plants and act as miniature straws to suck sap.

A number of carnivores also are adapted to consume a liquid diet. As ghoulish as it might sound, ingesting blood is the most common mechanism of feeding for these animals. Mosquitoes, for example, are equipped with a syringelike mouthpart called a proboscis. Although the male sips nectar, the female mosquito uses her proboscis to pierce skin and suck blood. As with most bloodsucking animals, mosquitoes secrete an anticoagulant that prevents blood from clotting (and also makes people itch). Some flies use a similar mode of feeding, but the common housefly generally laps up food and sugary solutions. Leeches are also well adapted for bloodsucking: They have a suction-cup-like mouth that clings tenaciously to a host while their jaws make a Y-shaped cut in the skin. Further, leeches have a muscular pharynx (throat) that literally pumps blood from their host. Ticks, which are related to spiders and scorpions, have tiny heads that are designed to burrow into the skin of their host and suck blood. Unfortunately, they also are vectors for potentially serious diseases such as Lyme disease and Rocky Mountain spotted fever. Although vampire bats consume blood, they do not suck it. Instead, they lap blood with their tongue as it oozes from a shallow scrape in the skin made by their teeth.

Spiders also are adapted to live on a liquid diet; however, they prey on insects that have a tough external skeleton that is not easily ingested. To feed, they first pierce the insect's exoskeleton with hollow jaws and pump in strong digestive juices that liquefy the internal contents of their prey. Later, the spider sucks the insect empty. Some young birds, such as pigeons and emperor penguins, feed on a regurgitated milklike secretion (called crop milk) that is produced by their parents' crop. In addition, all mammals begin their life as fluid feeders, ingesting milk produced by their mother.

Finally, endoparasites comprise a group of animals that consume a liquid diet by living inside other organisms. Some eat host tissues, while others rely on their host to digest food for them and, as a result, lack a digestive system. Tapeworms, for example, have a specially adapted anterior end with hooks and suckers to maintain a fixed position in their hosts' gut while they consume predigested food. In contrast, hookworms (a type of roundworm) do have a digestive system, and they use their mouth opening and toothlike structures to draw and ingest blood from the inside of their host.

Studying Ingestion

Much of what has been learned about ingestion has come from simple observation of feeding behavior combined with careful note-taking. In fact, observation and data collection, along with analysis and interpretation, are the most fundamental of all scientific activities. Most people have seen a robin use its beak to pull an earthworm from the ground or a cat capture a mouse. By closely watching the lifestyle and daily activities of animals, biologists have discovered what food items are eaten and how they are ingested.

The naked eye is insufficient for observing very small animals, and for this activity microscopes aid biologists. These tools have permitted observation of endocytosis of paramecia and bacteria by the amoeba as well as other feeding mechanisms of protozoans. Microscopic, inert latex beads are used to study the direction and power of feeding currents generated by cilia and flagella and the formation of food vacuoles. For example, paramecia will direct beads into their oral region by ciliary action and then engulf them by endocytosis. Dyes are also commonly used to study the direction and action of feeding currents. This method has revealed that flagellated choanocytes of sponges move water in through small pores in the sides of the sponge and out a single larger opening at the top.

Videotape and photographic film are routinely used to supplement simple observation. These procedures not only provide a permanent record of the event but also permit additional analysis to be conducted at some future time. Further, feeding mechanisms that occur very quickly are difficult to analyze with the naked eye. These events can be recorded by high-speed cinematography and later played back at a slower speed for analysis. This method of study has been used to observe the lightning-fast movement of a chameleon's tongue and the way bats catch insects with their wing membranes while in flight. Alternatively, very slow feeding events, such as endocytosis or a snake swallowing a rat, can be recorded by time-lapse photography and later viewed at a faster speed for analysis.

Mechanisms of ingestion may also be inferred by carefully analyzing the body design of an animal. For example, birds possessing beaks that have an arrangement of tightly packed vertical filaments, as found in flamingos, feed by filtering. In contrast, birds with long, pointed beaks, such as woodpeckers, probe for food in narrow places. Finally, the contents of the stomach and fecal samples from animals may be analyzed to determine the type and size of the food items that were eaten.

The Necessity of Food

Animals have an absolute requirement for food. Animals must ingest food items because, unlike photosynthetic organisms, they cannot manufacture all the necessary nutrients they require from raw materials. Animals require food both as a fuel source to provide energy for locomotion and metabolism and as building blocks for growth, maintenance, and repair. Obtaining sufficient food is of paramount importance for survival. Therefore, the limited availability of food is selected by animals that have the most-successful feeding strategies and body designs for procurement and ingestion of nutrients. Because different sources of nutrition are utilized, the selection pressures for obtaining food may result in vastly different feeding mechanisms among closely related animals. For example, giant water bugs, termites, and aphids are all classified as insects. Yet, they rely on different diets and therefore possess divergent methods of feeding and structures for ingestion. In addition, and conversely, selection pressures for obtaining food may result in the development of similar body structures in distantly related species (convergent evolution). Baleen whales and flamingos, for example, are classified in different taxonomic groups (mammals and birds) but have similar feeding methods and therefore similar structures for ingestion. Thus, specific feeding behaviors and structures for ingestion are primarily shaped by the nature of the food items being utilized, and the vast diversity of feeding mechanisms reflects a similar diversity in food sources.

Ultimately, the source of energy to create food comes from the Sun. Photosynthetic organisms use light to synthesize energy-rich organic compounds, such as glucose, from energy-poor inorganic compounds, such as carbon dioxide and water. One exception to this scheme occurs in certain regions of the ocean floor, near the thermal vents. Far removed from sunlight and organic material derived by photosynthesis, the food chain of oceanic thermal vents is based upon certain bacteria that synthesize organic compounds from inorganic substances emitted by these undersea geysers.

Unfortunately, there is an unavoidable loss in usable material and energy between links in a food chain. This loss occurs because much of the energy stored in food is irreversibly lost when it is used by organisms for growth, repair, and maintenance. Therefore, it is more efficient to have a lower number of links in a food chain between its base (usually plants or plankton) and its end (typically large carnivores). With that in mind, it is interesting to note that some of the largest fish (whale sharks) and mammals (whales) in the world are filter feeders of tiny organisms. These huge animals, which require a large amount of energy, avoid extra links in their food chain by feeding on plankton instead of other large animals.

—Douglas B. Light

See also: Carnivores; Digestion; Digestive tract; Food chains and food webs; Lactation; Nutrient requirements; Omnivores; Predation.

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INSECT SOCIETIES

Type of animal science: Behavior
Fields of study: Ethology, invertebrate biology

Ants, termites, and many kinds of bees and wasps live in complex groups known as insect societies. Studies of such societies have enriched scientific knowledge about some of the most successful species on earth and have provided insights into the biological basis of social behavior in other animals.

Principal Terms

BROOD: all the immature insects within a colony; these include eggs, larvae, and, in the Hymenoptera, the pupal stage

CASTE: one of the recognizable types of individuals within a colony, usually physically and behaviorally adapted to perform specific tasks

EUSOCIAL: referring to any of the truly social species characterized by division of labor, with a sterile caste, overlapping generations, and cooperative brood care

HAPLODIPLOIDY: sex determination found in the Hymenoptera, where males arise from unfertilized eggs and females from fertilized eggs

METAMORPHOSIS (COMPLETE): a transformation that occurs during the development of higher insects, in which a grublike immature form enters a resting (pupal) stage for major tissue reorganization; after pupation, the adult, which bears no resemblance to the larval form, emerges

PHEROMONE: a chemical produced by one member of a species that influences the behavior or physiology of another member of the same species

TROPHALLAXIS: the exchange of bodily fluids between nestmates, either by regurgitation or by feeding on secreted or excreted material

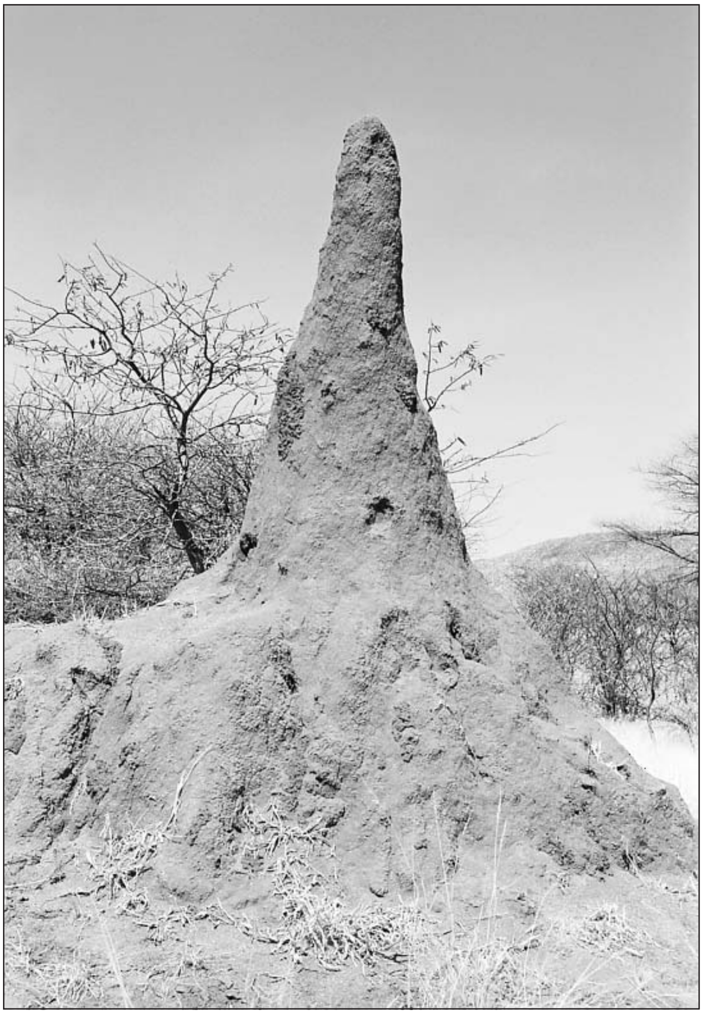
Many of the most robust, thriving species today owe their success in great part to benefits that they reap from living in organized groups or societies. Nowhere are the benefits of group living more clearly illustrated than among the social insects. Edward O. Wilson, one of the foremost authorities on insect societies, estimates that more than twelve thousand species of social insects exist in the world today. This number is equivalent to all the species of known birds and mammals combined. Although insect societies have reached their pinnacle in the bees, wasps, ants, and termites, many insects show intermediate degrees of social organization—providing insights regarding the probable paths of the evolution of sociality.

Ant, Wasp, and Bee Societies

Scientists estimate that eusociality has evolved at least twelve times: once in the Isoptera, or termites, and eleven separate times in the Hymenoptera, comprising ants, wasps, and bees. In addition, one group of aphids has been found which has a sterile soldier caste. Although the eusocial species represent diverse groups, they all show a high degree of social organization and possess numerous similarities, particularly with regard to division of labor, cooperative brood care, and communication among individuals. The organization of a typical ant colony is representative, with minor modifications, of all insect societies.

A newly mated queen, or reproductive female, will start a new ant colony. Alone, she digs the first nest chambers and lays the first batch of eggs. These give rise to grublike larvae, which are unable to care for themselves and must be nourished from the queen's own body reserves. When the larvae have reached full size, they undergo metamorphosis and emerge as the first generation of worker ants. These workers—all sterile females—take over all the colony maintenance duties, including foraging outside the nest for food, defending the nest, and cleaning and feeding both the new brood and the queen, which subsequently becomes essentially an egg-laying machine. For a number of generations, all eggs develop into workers and the colony grows. Often, several types of workers can be recognized. Besides the initial small workers, or minor workers, many ant species produce larger forms known as major workers, or soldiers. These are often highly modified, with large heads and jaws, well suited for defending the nest and foraging for large prey. Food may include small insects, sugary secretions of plants or sap-feeding insects, or other scavenged foods. After several years, when the colony is large enough, some of the eggs develop into larger larvae that will mature into new reproductive forms: queens and males. Males arise from unfertilized eggs, while new queens are produced in response to changes in larval nutrition and environmental factors. These sexual forms swarm out of the nest in a synchronized fashion to mate and found new colonies of their own.

With minor modifications, the same pattern occurs in bees and wasps. Workers of both bees and wasps are also always sterile females, but they differ from ants in that they normally possess functional wings and lack a fully differentiated soldier caste. Wasps, like ants, are primarily predators and scavengers; bees, however, have specialized on pollen and plant nectar as foods, transforming the latter into honey that is fed to both nestmates and brood. The bias toward females reflects a feature of the biology of the Hymenoptera that is believed to underlie their tendency to form complex societies. All ants, wasps, and bees have an unusual form of sex determination in which fertilized eggs give rise to females and unfertilized eggs develop into males. This type of sex determination, known as haplodiploidy, generates an asymmetry in the degree of relatedness among nestmates. As a consequence, sisters are more closely related to their sisters than they are to their own offspring or their brothers. Scientists believe that this provided an evolutionary predisposition for workers to give up their own personal reproduction in order to



Ant colonies can build huge mounds through their united efforts. (Corbis) raise sisters—a form of natural selection known as kin selection.

Termite Society

The termites, or Isoptera, differ from the social Hymenoptera in a number of ways. They derive from a much more primitive group of insects and have been described as little more than "social cockroaches." Instead of the strong female bias characteristic of the ants, bees, and wasps, termites have regular sex determination; thus, workers have a fifty-fifty sex ratio. Additionally, termite development lacks complete metamorphosis. Rather, the young termites resemble adults in form from their earliest stages. As a consequence of these differences, immature forms can function as workers from an early age, and—at least among the lower termites—they regularly do so.

Termites also differ from Hymenoptera in their major mode of feeding. Instead of feeding on insects or flowers, all termites feed on plant material rich in cellulose. Cellulose is a structural carbohydrate held together by chemical bonds that most animals lack enzymes to digest. Termites have formed intimate evolutionary relationships with specialized microorganisms—predominantly flagellate protozoans and some spirochete bacteria—that have the enzymes necessary to degrade cellulose and release its food energy. The microorganisms live in the gut of the termite. Because these symbionts are lost with each molt, immature termites are dependent upon gaining new ones from their nestmates. They do this by feeding on fluids excreted or regurgitated by other individuals, a process known as trophallaxis. This essential exchange of materials also includes, along with food, certain nonfood substances known as pheromones.

Insect Communication

Pheromones, by definition, are chemicals produced by one individual of a species that affect the behavior or development of other individuals of the same species that come in contact with them. Pheromones are well documented throughout the insect world, and they play a key role in communication between members of nonsocial or subsocial species. Moth mating attractants provide a well-studied example. Pheromones are nowhere better developed than among the social insects. They not only appear to influence caste development in the Hymenoptera and termites but also permit immediate communication among individuals. Among workers of the fire ant (*Solenopsis saevissima*), chemical signals have been implicated in controlling recognition of nestmates, grooming, clustering, digging, feeding, attraction or formation of aggregations, trail following, and alarm behavior. Nearly a dozen different glands have been identified which produce some chemical in the Hymenoptera, although the exact function of many of these chemicals remains unknown.

In addition to chemical communication, social insects may share information in at least three other ways: by tactile contact, such as stroking or grasping; by producing sounds, including buzzing of wings; and by employing visual cues. Through combinations of these senses, individuals can communicate complex information to nestmates. Indeed, social insects epitomize the development of nonhuman language. One such language, the "dance" language of bees, which was unraveled by Karl von Frisch and his students, provides one of the best-studied examples of animal behavior. In the waggle dance, a returning forager communicates the location of a food resource by dancing on the comb in the midst of its nestmates. It can accurately indicate the direction of the flower patch by incorporating the relative angles between the sun, the hive, and the food. Information about distance, or more precisely the energy expended to reach the food source, is communicated in the length of the run. Workers following the dance are able to leave the nest and fly directly to the food source, for distances in excess of one thousand meters.

Benefits of Cooperation

Living in cooperative groups has provided social insects with opportunities not available to their solitary counterparts. Not only can more individuals cooperate in performing a given task, but also several quite different tasks may be carried out simultaneously. The benefits from such cooperation are considerable. For example, group foraging allows social insects to increase the range of foods they can exploit. By acting as a unit, species such as army ants can capture large insects and even fledgling birds.

A second benefit of group living is in nest building. Shelter is a primary need for all animals. Most solitary species use naturally occurring shelters or, at best, build simple nests. By cooperating and sharing the effort, social insects are able to build nests that are quite elaborate, containing several kinds of chambers. Wasps and bees build combs, or rows of special cells, for rearing brood and storing food. Subterranean termites can construct mounds more than six meters high, while others build intricate covered nests in trees. Mound-building ants may cover their nests with a thatch that resembles, in both form and function, the thatched roofs of old European dwellings. Colonial nesting provides two additional benefits. First, it enhances defense. By literally putting all of their eggs in one basket, social insects can centralize and share the guard duties. The effectiveness of this approach is attested by one's hesitation to stir up a hornet's nest. Nest construction also provides the potential to maintain homeostasis, the ability to regulate the environment within a desirable range. Virtually all living creatures maintain homeostasis within their bodies, but very few animals have evolved the ability to maintain a constant external living environment. In this respect, insect societies are similar to human societies. Workers adjust their activities to maintain the living environment within optimal limits. Bees, for example, can closely regulate the internal temperature of a hive. When temperatures fall below 18 degrees Celsius, they begin to cluster together, forming a warm cover of living bees to protect the vulnerable brood stages. To cool the hive in hot weather, workers initially circulate air by beating their wings. If further cooling is needed, they resort to evaporative cooling by regurgitating water throughout the nest. This water evaporates with wing fanning and serves to cool the entire hive. Other social insects rely on different but equally effective methods. Some ants, and especially termites, build their nests as mounds in the ground, with different temperatures existing at different depths. The mound nests of the African termite, *Macrotermes natalensis*, are an impressive engineering feat. They are designed to regulate both temperature and air flow through complex passages and chambers, with the mound itself serving as a sophisticated cooling tower.

Finally, group living allows the coordination of the efforts of individuals to accomplish complex tasks normally restricted to the higher vertebrates. The similarities between insect societies and human society are striking. An insect society is often referred to as a superorganism, reflecting the remarkable degree of coordination between individual insects. Individual workers have been likened to cells in a body, and castes to tissues or organs that perform specialized functions. Insect societies are not immortal; however, they often persist in a single location for periods similar to the life spans of much larger animals. The social insects have one of the most highly developed symbolic languages outside human cultures. Further, social insects have evolved complex and often mutually beneficial interactions with other species to a degree unknown except among human beings. Bees are inseparably linked with the flowers they feed upon and pollinate. Ants have actually developed agriculture of a sort with their fungus gardens and herds of tended aphids. On a more sobering note, ants are the only nonhuman animals that are known to wage war. These striking similarities with human societies have led researchers to study social insects to learn about the biological basis of social behavior and have led to the development of a new branch of science known as sociobiology.

Studying Insect Society

Because of the diversity of questions that investigators have addressed regarding insect societies, many methods of scientific inquiry have been employed. In Karl von Frisch's experiments, for example, basic behavioral observations were cou-

Edward O. Wilson

Born: June 10, 1929; Birmingham, Alabama
Fields of study: Ecology, entomology, ethology, evolutionary science, genetics, zoology
Contribution: Wilson is recognized as the world's chief authority on social insects, particularly ants. He is also an expert on the genetic basis of the social behavior of all animals, including humans.

After his graduation from high school in Decatur, Alabama, Edward O. Wilson earned his bachelor's and master's degrees in biology at the University of Alabama at Tuscaloosa, concentrating his efforts on the study of ants. Continuing his educational pursuits at Harvard University, he earned his doctor's degree in zoology and received an appointment as a professor of zoology and curator of entomology at the Museum of Comparative Zoology at Harvard. Based on their study of insect societies, Wilson and W. L. Brown proposed the idea of character displacement: that after the populations of two closely related species come into contact, they undergo rapid evolutionary differentiation so as to minimize the chances of competition and hybridization between the two species.

Wilson's definitive work on ants and other social insects, *The Insect Societies* (1971), treats the societal behavior patterns of many species. It covers numerous aspects of insect societies, ranging from paleontology to formal genetics and from ethology to biochemistry. Providing an account of the natural history of social insects, with their great proliferation of genera, species, and behavioral types, Wilson incorporated concepts from the fields of modern genetics, selection theory, and biomathematics to explain the evolution of insect societies and their diversity in size and longevity. In *The Ants* (1990), Wilson and Bert Hölldobler published a comprehensive summary of current knowledge on ants.

Wilson's thorough study of insect societies led to his proposal that the biological principles governing animal societies extend to humans, which he explored in *Sociobiology: The New Synthesis* (1975). Wilson theorized that the preservation of the gene, versus the preservation of the individual, is the fundamental concept in evolutionary development. His argument was that social animals, including humans, behave according to rules written in their genes. Since this theory contradicts the belief in free will and suggests that some human groups may be biologically superior to others, it sparked much controversy among scientists and nonscientists alike. In *The Diversity of Life* (1992), Wilson further investigated how the world's living species became diverse, as well as the massive species extinctions produced by human activities in the twentieth century.

Wilson became the first and only person to receive both the highest award for science in the United States, the National Medal of Science, and the premier literary award, the Pulitzer Prize in literature. He received the latter award for his book *On Human Nature* (1978) in 1979. In 1990, he was awarded the prestigious Crafoord Prize by the Swedish Academy of Science for his work in ecology. In 1995, *Time* recognized Wilson as one of the twenty-five most influential people in America. An international poll in 1996 ranked him as one of the hundred most influential scientists of all time. His present research is focused on the concept of consilience, a controversial attempt to unify all knowledge by means of science so that explanations of differing kinds of phenomena are connected and consistent with each other.

—Alvin K. Benson

pled with simple but elegant experimental design to unravel the dance language of bees. The bees were raised in an observation colony. This was essentially a large hive housed between plates of glass so that an observer could watch the behavior of individual bees. Researchers followed specific workers by marking them with small numbers placed on the abdomen or thorax. Sometimes the entire observation hive was placed within a small, darkened shed to simulate more closely the conditions within a natural hive.

Bees learned to find an artificial "flower"—a glass dish filled with a sugar solution. Brightly colored backgrounds and odors such as peppermint oil were added to the sugars to provide specific cues for the bees to associate with the reward. Feeding stations were set up at fixed distances; observers could follow the exact movements of known individuals both at the feeder and at the hive. In this way, von Frisch was able to describe several types of dances (the round dance for near food sources, the waggle dance for feeding stations that were farther from the hive) and show that a returning bee could share information regarding the location and quality of a source with her nestmates. Scientists subsequently have developed robot bees that can be operated by remote control to perform different combinations of dance behaviors. This allows them to determine which parts of the dance actually convey the coded information.

The investigation of forms of chemical communication requires application of a variety of techniques. Chromatography is useful for identifying the minute amounts of chemical pheromones with which insects communicate. Chromatography (which literally means "writing with color") is particularly suitable for separating mixtures of similar materials. A solution of the mixture is allowed to flow over the surface of a porous solid material. Since each component of the mixture will flow at a slightly different rate, eventually they will become separated or spaced out on the solid material. Once the components of the pheromone have been separated and identified, their activity is assessed separately and in combination using living insects. Such bioassays allow researchers to determine exactly which fractions of the chemical generate the highest response.

Other biochemical techniques, such as electrophoresis, have been used to determine subtle behavioral differences, such as kin discrimination among hive mates. Each individual carries a complement of enzymes or proteins that catalyze biological reactions in the body. The structure of such enzymes is determined by the genetic makeup of the individual, and it varies among individuals. Because enzyme structure is inheritable, however, much as eye color is, the degree of similarities between the enzymes can be used as a measure of how closely related two individuals are. The amino acids composing the enzyme differ in their electrical charges, so different forms can be separated using the technique of electrophoresis. When a liquid containing their enzymes is subjected to an electrical field, the proteins with the highest negative charge will move farthest toward the positive pole. This provides a tool to distinguish close genetic relatives for use in conjunction with behavioral observations to test, for example, whether workers can discriminate full sisters from half-sisters, or relatives from nonrelatives, as kin selection theory would predict.

The Success of Social Insects

Social insects are among the most successful groups of animals throughout the world, especially in the tropics. Although the number of species is low when compared to all insects (twelve thousand out of more than a million species), their relative contribution to the community may be unduly large. In Peru, for example, ants may make up more than 50 percent of the individual insects collected at any site.

The study of social insects has provided scientists with new ways of looking at social behavior in all animals. Charles Darwin described the evolution of sterile workers in the social insects as the greatest obstacle to his theory of evolution by natural selection. In attempts to explain this seeming paradox, William D. Hamilton closely examined the social Hymenoptera, where sociality had evolved eleven separate times. Realizing that the haplodiploid form of sex determination led to sisters being more closely related to one another than they would be to their own young, Hamilton developed a far-reaching new theory of social evolution: kin selection, or selection acting on groups of closely related individuals. This theory, which provides insights into the evolution of many kinds of seemingly altruistic behaviors, arose primarily from his perceptions regarding the asymmetrical relatedness of nestmates in the social Hymenoptera. These insects, then, should be credited with providing the model system that has led to a subdiscipline of behavioral ecology known as sociobiology, the study of the biological basis of social behavior. Moreover, given their central roles in critical ecological processes such as nutrient cycling and pollination, it would be hard to imagine life without them.

—*Catherine M. Bristow*

See also: Altruism; Ants; Arthropods; Bees; Communication; Communities; Endocrine systems in invertebrates; Ethology; Groups; Herds; Hierarchies; Home building; Insects; Instincts; Invertebrates; Mammalian social systems; Packs; Pheromones; Symbiosis; Wasps and hornets.

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_______. *Sociobiology: The New Synthesis*. Cambridge, Mass.: The Belknap Press of Harvard University Press, 1975. A discussion of the evolution and structure of societies—both those of insects and those of higher animals. The format is very similar to that of Wilson's *The Insect Societies*, and the drawings and illustrations are of equal quality. The book is almost seven hundred pages long but is well indexed and suitable for browsing. An excellent source for anyone interested in comparing different social animals or in tracing ideas on the evolution of sociality.

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INSECTS

Type of animal science: Classification
Fields of study: Anatomy, ecology, entomology, invertebrate biology

More than one million species of insects have been identified, and countless others await discovery. Insects provide many valuable products and services within ecosystems, but some cause damage by eating crops or spreading disease to plants, animals, and humans.

Principal Terms

APTEROUS: insects without wings, such as fleas

ECDYSIS: molting; the shedding of the exoskeleton that allows for insect growth

HEXAPOD: six-footed, a general term for an insect

OVIPOSITOR: egg-laying apparatus on the female abdomen, modified into a stinger in bees

PUPA: intermediate stage between the larval and adult stages of the life cycle

SPIRACLES: openings on the outside of the insect abdomen that lead to breathing tubes

VECTOR: transmits pathogens from one host to another

The history of insects dates back to the Devonian period, about 400 million years ago. Today numbering more than one million different species, insects are the most diverse class of animals on earth. Insects populate almost every habitat except the deep oceans and permanently frozen land masses. Insects are specialized to live underground, in live or rotting trees, in fast-flowing rivers, or stagnant puddles. Parasitic insects live attached to the outside (hair, skin) or inside (stomach lining, respiratory tract) of other animals. Crafty insects modify their habitat by building their own houses. Spittlebugs mix air into slimy anal secretions to form shelters. Bagworms spin silk to hold leaves together around them. Some African termites glue soil particles together with saliva into colossal nests measuring six meters high and nearly four meters across.

Insect Anatomy

Along the relatively straight digestive tract of an insect there are regions specialized for food storage, grinding, chemical breakdown, and nutrient absorption. Before undigested remains leave the insect, water and salts are reclaimed. Insect waste, termed frass, is thus very dry. This last step of water conservation is very important to insects because they lose water rapidly due to their small size.

The insect respiratory system is also adapted to save water. The tracheal system is a collection of tubes that allows for gas exchange from the outside environment directly with individual tissues. The openings in the body wall, spiracles, can be closed to conserve water between breathing cycles.

The circulatory fluid of insects, hemolymph, functions in keeping tissues moist and transporting nutrients and hormones. There are no red blood cells or other oxygen-carrying molecules because the insect respiratory system is totally separate from the circulatory system. The circulatory system is open. Hemolymph enters a series of chambers, collectively termed the heart, through holes called ostia. Muscular pumping of the heart propels the fluid through the aorta, toward the insect's brain. In the vicinity of the brain, the hemolymph flows out into the general body cavity, or hemocoel. Hemolymph directly bathes internal organs on its way to and from the legs and wings, starting the cycle again by entering the heart ostia. There are distinct veins in the wings. Insects take advantage of fluid circulation in the wings to transfer heat, warming themselves or cooling off when needed.

Insects are noted for their jointed exoskeletons. Chitin makes this armor especially strong. The exoskeleton functions much like the internal bones of vertebrates, serving to protect internal organs and as sites of muscle attachment. The exoskeleton puts limits on the overall size that insects can attain and makes growth energetically costly. The insect must shed its old exoskeleton and form a new one in order to increase in size. The old exoskeleton may be eaten to reclaim some of the nutrients within it. While a freshly molted insect is waiting for its new outer covering to harden, it is particularly vulnerable to attack from predators. Molting insects tend to be white; the exoskeleton will also develop color as it hardens.

The Insect Diet

Phytophagous insects feed on living plants. Caterpillars are famous leaf eaters. Other insects feed on plant roots, shoots, flowers, stems, or fruits. When a large group of phytophagous insects occurs in the same area, the crop or forest damage that they cause can be extensive. Yet there is quite another side to the relationship between insects and plants. Insect-pollinated plants have evolved odors, shapes, and ultraviolet color patterns to attract these important visitors. When the butterfly, bee, or other pollinator stops to drink the plant's rich nectar, pollen from the male part of the flower sticks to the insect's body. When it visits another flower of the same species, it deposits the pollen on the female floral organ. Without this interaction, beans, tomatoes, tea, cocoa, and many other plants could not reproduce.

Scavengers also serve an important purpose by recycling nutrients found in dead plant and animal matter. Termites are a nuisance when they infest a house but are invaluable at breaking down dead wood in nature. Dung beetles have the curious habit of forming animal feces into balls and rolling them away to feed their young. Carrion feeders assist in the decomposition of animal corpses. A succession of flies and beetles reduce a corpse to bones.

Predators hunt and kill to eat. Some predators use powerful mouthparts to tear apart their prey. Other predators inject digestive enzymes into their prey, digest them externally and suck out the liquefied tissues through a specialized beak. The first pair of legs of the praying mantis are striking

Insect Facts

Classification:
Kingdom: Anamalia
Subkingdom: Bilateria
Phylum: Arthropoda
Subphylum: Uniramia
Class: Insecta
Orders: Common orders include Coleoptera (beetles); Diptera (flies, mosquitoes); Hemiptera (true bugs); Homoptera (cicadas), Hymenoptera (ants, bees, wasps); Isoptera (termites); Lepidoptera (butterflies, moths); Odonata (dragonflies, damselflies); Orthoptera (crickets, grasshoppers)
Geographical location: Every continent except Antarctica
Habitat: Mainly terrestrial, some aquatic, primarily freshwater
Gestational period: Highly variable; some insects produce one, two, or several generations per year; conversely, relatively large insects may take more than one year for larval development
Life span: Highly variable; adult mayflies live less than one week, while queen termites have been known to live for more than twenty years
Special anatomy: Major regions include the head, featuring one pair of antennae, the thorax, with three pairs of legs and up to two pairs of wings, and the abdomen, housing spiracles and genitalia; in some insects, one or both pairs of wings are modified for functions other than flight, such as protection or balance

Image Not Available

examples of raptorial modifications for grasping and holding struggling prey.

Dragonfly nymphs, the young aquatic stage, have a diet of insects, crustaceans, tadpoles, and even small fish. Adult dragonflies eat bees, butterflies, and mosquitoes. Harmless insects such as dragonflies, which consume pest insects such as mosquitoes, are good candidates for biological control programs. Biological control is a method of pest control that takes advantage of natural predators of the pest. Ladybugs are commonly used by gardeners to control plant-damaging aphid populations.

On the other hand, a good parasite does not kill its food source, the host. Parasitic insects typically ingest host blood, mucus, or tissues, with minimal irritation or harm to the host. Trouble begins if there is a heavy parasitic burden (a large number of parasites per host), or if the parasitic insect transmits disease-causing organisms to the host. Ectoparasites live on the outside of their hosts. In this category, fleas and lice are adapted to avoid detection by the host and deter removal during normal grooming processes. Endoparasitic fly larvae live in the digestive or respiratory tract, mainly of livestock. Endoparasites of invertebrates do not follow the rules. Because there is little difference in size between this parasite and host pair, the host routinely perishes in this relationship. Species of endoparasitic wasps inject their eggs into caterpillars. When the larvae hatch, they tunnel farther into the host and feed off of its tissues. Upon completion of larval development, the wasps emerge from the caterpillar, killing it in the process.

Some parasites spend their lifetimes closely associated with the host, but others only briefly visit the host. On the time continuum, lice not only form a constant, more-or-less permanent association with a single host, but many generations of lice may inhabit the same host. However, these parasites are transferred from host to host during mating, nesting, or other close contact between individuals. Unlike lice, fleas leave the host frequently between bloodmeals. On the other end of the spectrum, mosquitoes normally require multiple hosts to complete a single bloodmeal; they are here and gone before they can be slapped by hand or tail.

Insect Behavior

Much of what insects do, they do by instinct, a genetically preprogrammed response to environmental stimuli, none the less amazing in its elegance and effectiveness. Antennae and setae, hairlike projections through the exoskeleton, serve as two of the many receptors of external stimuli. The necessity of keeping these sensory organs clean is evidenced by preening, commonly using mouthparts and legs. Major categories of environmental stimuli signal friend or foe.

Many insects locate opposite sex conspecifics, individuals of the same species, by sight. Color patterns, especially in the ultraviolet (UV) spectrum attract potential mates. Fireflies (Coleoptera) use visual recognition of patterns of light flashes. In some species, females use signaling to attract males. In other species the male and female signal to each other with the proper code and response. Females of the genus *Photuris* mimic the flashing patterns of other firefly species. When the male approaches, she makes a meal of him.

Sound production and reception are also used for mate location. The sound generated by a female mosquito's beating wings in flight is picked up by the male mosquito's antennae. Male homopterans and orthopterans produce songs of courtship. Cicadas use abdominal muscles and a resonating chamber for sound production. Grasshoppers and crickets rub their wings and or legs together. Sound receptors, "eardrums" of females in these orders, are found on their forelegs or first abdominal segments. Sound production and reception vary with temperature.

Pheromones, externally broadcast chemical signals, are another means of attracting mates. In moths, glands near the tip of the female's abdo-

Vector-Borne Disease

Insects are carriers of major human diseases. Interaction between disease-causing microorganisms and the insect vector is an interesting and vital component of the transmission cycle. The bubonic plague, for example, is endemic (naturally occurring) in populations of rodents. The plague bacteria, *Yersinia pestis*, is transmitted to humans primarily by *Xenopsylla cheopis*, the Oriental rat flea. When a flea ingests infected blood, the bacteria multiply in its gut and stick together, rapidly forming a plug. When a blocked flea attempts to feed, it regurgitates infected blood into its host. Still hungry, a blocked flea will repeatedly attempt to feed, increasing the chances of it infecting many hosts.

While there are still small geographic pockets where plague is present today, malaria rages as a widespread, tropical epidemic. Malaria is caused by species of protozoa in the genus *Plasmodium*, and carried by mosquitoes in the genus *Anopheles*. These mosquitoes not only transport the disease from host to host, they provide the only environment in which the protozoa can complete its life cycle. *Plasmodium* exhibits both asexual and sexual reproduction, but it reproduces sexually within the mosquito gut and nowhere else. After development in the gut, the protozoa migrate, through the mosquito, to the salivary glands. While feeding, the mosquito then spits *Plasmodium* into a new host.

Chagas' disease is also caused by a protozoan, *Trypanosoma cruzi*, but the vector and mode of transmission are radically different from that of malaria. Like *Plasmodium*, *T. cruzi* requires residence in the insect gut in order to develop into an infective stage. However, the insects that *T. cruzi* are associated with are true bugs (Hemiptera, Reduviidae). The protozoan remains in the bug's digestive tract until excretion within fecal material. Transmission of Chagas' disease relies on the host scratching infected feces into the itchy bite wound.

Forensic Entomology

Scientists and law enforcement agents capitalize upon the predictable sequence of insect development on human corpses to provide clues in homicide cases. Species of *Calliphora* (blowflies) lay eggs on the body almost immediately postmortem. The eggs hatch in a given amount of time, then the larvae go through distinct growth stages and pupate. During these first weeks, other species of flies also colonize and develop in this specialized microenvironment. After the flies have done their work, beetles arrive. Forensic entomologist M. Lee Goff has done many experiments with the decomposition of pig carcasses. Using his work, data tables have been established to aid scientists in interpreting the story of the insects present, and in turn provide clues regarding the fate of the deceased victim. The size of the larvae of each species is adjusted for temperature and this data is used to estimate the length of time that the person has been dead. Larval development is calculated at 72 degrees Fahrenheit. Time is subtracted for exposure to warmer environments since insect development speeds up at higher temperatures. At 80 degrees Fahrenheit, a larval fly would appear to be older than it really is. Insect evidence can assist investigators in determining whether the body has been moved and yield clues about poisons or drugs present in the body at the time of death.

men release pheromones that are received by the antennae of the male moths. Certain male butterflies and moths have specialized scent-producing glands on their wings. The notable pair of black patches, or androconia, on the hindwings of the male monarch secrete aphrodisiac pheromones that increase the female's receptivity to mating. Pheromones can also make already-mated females unattractive to subsequent suitors.

Members of the class Insecta display numerous protective behaviors and defense mechanisms when threatened. Walkingsticks are capable of losing part of a leg in the grasp of a predator. The amputated appendage continues to wiggle when severed, thus distracting the predator, while the walkingstick gets away. Some beetles play dead until the predator loses interest. Blister beetles are capable of reflex bleeding. They squeeze drops of hemolymph through joints in their exoskeleton. Their hemolymph contains cantharadine, which irritates and repels the predator. Bombardier beetles spray a noxious repellant from their anal glands for distances up to one meter.

Another means of defense is coloration. Insects blend into the surroundings by resembling a leaf, twig, pebble, or flower. Some insects use bright colors to hide in plain sight. Large eyespots on wings can startle would-be predators, or at least trick them into taking a bite out of the wing rather than from the head or body. Color patterns of orange and black seem to warn vertebrate predators that the insects would not make a good meal. Some of these insects derive chemicals from their diet that make them distasteful, even harmful, to predators. Without possessing such chemicals, mimics derive protection from their resemblance to the group that does.

Social insects exhibit the most complex behavior, approaching learning. Honeybees can communicate direction of a food source, and distance from the hive, to other bees through a multipart waggle dance. Some ants are farmers, planting and nurturing fungus gardens. Mound-building harvester ants ensure that the colony's young are kept at the optimal temperature through vertical migrations. The young are transported to top levels within the mound to warm up in the morning and evening. During the heat of the day, the young are carried to lower levels to cool off. Kidnapping of ants from other colonies to serve as workers in the home colony may not be considered a socially advanced behavior, but it is a complex one. The other major group of social insects, the termites, work together to build huge mounds, called termitaria, some reaching heights of 6 meters and diameters of over 3.5 meters. They engineer series of chimneys into the structure that can be opened and closed to regulate airflow and maintain constant temperature.

—*Sarah Vordtriede*

Maria Sibylla Merian

Born: April 2, 1647; Frankfurt am Main, Germany
Died: January 13, 1717; Amsterdam, Netherlands
Fields of study: Developmental biology, ecology, entomology
Contribution: Merian's paintings are significant as natural history illustrations in seventeenth century Western art. Her detailed observations, particularly of insect metamorphosis, also contributed to the development of entomology as a science.

Maria Sibylla Merian, the German-born Dutch naturalist, was the youngest of three children born into a family of artists. Her father, Matthaus Merian the Elder, a publisher, engraver, and botanical artist, died when Maria was just three years old. Her older brother, Matthaus Merian the Younger, became a famous portrait painter. Maria's own artistic talent was noticed early on by her stepfather, Jacob Marrell, himself a trained painter. Her curiosity and observation of the natural world was also established early in life. She kept a detailed journal of her observations from her teenage years until just before her death at the age of sixty-nine.

Deviating from other seventeenth century artists, Maria Sibylla Merian sketched, painted, and engraved insects from real-life observations rather than as still-life symbols. In this way, she was able to put their behavior and development into ecological context. She bred and raised silkworms and, at age thirteen, illustrated the egg, larva, pupa, and adult stages of these creatures, as well as many other butterflies. Merian is credited with being the first person to record such detailed observations on insect metamorphosis. Although she did not realize it at the time, she also documented parasitoid infection of some of the caterpillars. The organisms that she described as small black flies emerging from butterfly pupa were likely small wasps that complete their larval development within the pupal case of the butterfly host.

In 1699, funded by the city of Amsterdam, Merian and her youngest, teenaged daughter traveled to South America to study and paint insects, birds, and plants. They spent two years exploring the natural wonders of the cities, plantations and rainforests of the country of Suriname (formerly Dutch Guiana). Observational records from this excursion were published in 1705 under the title "De generatione et metamorphosibus insectorum surinamensium" ("of the reproduction and the transformation of insects in Suriname"). Both before and after her trip, she published several books of illustrations and observations of plants and the insects associated with them. Two of her paintings are featured on thirty-two cent U.S. postage stamps. In addition to her artwork, she traded in preserved insects, and instructed others according to the proper preservation of specimens.

Maria Sibylla Merian left quite a legacy. Her daughters continued research on insects after their mother's death, and Merian's artwork and keen scientific observations, meticulously recorded, are preserved for all to learn from and enjoy. Six plants, nine butterflies, and two beetles bear her name, which is ultimately fitting, since Carolus Linnaeus is said to have consulted her work while establishing his binomial nomenclature system for naming the living organisms of the earth.

—Sarah Vordtriede

See also: Antennae; Ants; Bees; Beetles; Butterflies and moths; Cockroaches; Cold-blooded animals; Communication; Communities; Exoskeletons; Flies; Flight; Grasshoppers; Insect societies; Invertebrates; Metamorphosis; Mimicry; Molting and shedding; Mosquitoes; Praying mantis; Symbiosis; Termites; Wasps and hornets; Wings.

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INSTINCTS

Type of animal science: Behavior
Fields of study: Biochemistry, ethology, neurobiology

Instincts cover a range of inherited behaviors that are unlearned and are predictable for a species. Scientists are interested in locating the biochemical sources of instincts and analyzing the relationship between instincts and a species' biological success.

Principal Terms

ALTRUISM: a high degree of devotion to the interest of others that often includes self-sacrifice

ETHOLOGY: a branch of biology that studies behavior

FIXED ACTION PATTERN (FAP): a behavior whose timing and duration are invariable for all members of a species

INNATE: denotes an inherited and unalterable condition or ability in an organism

NEUROBIOLOGY: the study of the biology of the brain

NEUROETHOLOGY: the study of behavior as it relates to brain functions

PEPTIDE: a chemical combination of certain amino acids

SIGNAL: information transmitted through sound, such as bird calls, or through sight, such as body posture

STEREOTYPED BEHAVIOR: an unlearned and unchanging behavior pattern that is unique to a species

Instincts are patterns of behavior found in animals that are unlearned and that are inherited by successive generations of the species. Ethologists call these stereotyped behaviors fixed action patterns (FAPs). Over time, such patterns are shaped by evolution, but at any given moment, a species maintains a range of instincts that are unique to its members. A number of categories of stereotyped behavioral responses exist that apply to all organic forms. These include the basic drives such as reproduction, feeding, and protection from predators. The term "instinctive behavior," however, is generally reserved for animals and insects, while excluding plants, bacteria, and viruses. Simple forms of stereotyped responses include a variety of reflex actions in which sensory nerve cells are affected by conditions such as heat and light. The more complex forms of responses are studied in order to understand the sequence of responses and the process of evolution that selected these patterns.

The Study of Instincts

The study of instinctive behavior began in the nineteenth century with the development of clinical psychology. Scientists noticed a direct link between animal and human behavior, and since clinical experimentation of human subjects was not always possible or desirable, experiments were carried out on monkeys, mice, and guinea pigs. Experiments focused on the responses of test subjects to specific environmental conditions. An example of this type of experiment would be investigating the puzzle-solving ability of rats in a maze. The flexibility and nature of these responses were seen as part of a study of learning processes.

Meanwhile, the field of ethology began to formulate a different view of animal behavior. A European group including Konrad Lorenz, Nikolaas Tinbergen, and Karl von Frisch noticed that animals possess a specific innate capacity to perform complex activities in response to the environment. As a result, modern ethology shifted the study of animal behavior from learned responses to inherited patterns of behavior. From their beginning as "bird watchers," observing birds' courtship behavior, nest building, rearing of young, and territorial ownership, ethologists collected a body of scholarship that came to represent a respected field of study. A number of subfields have been created, ranging from neurology and genetics of behavior to ecology of species behavior. One element that links these diverse and distinctive fields of study is that of signals, language, and communications.

Charles Darwin gave the scientific world a theory of evolution, but he was also an avid observer of instinctive behavior. He observed domesticated pigeons and described how emotions are expressed by humans and animals. Other early pioneers in this field included Charles Whitman, who studied the family tree of a group of pigeons in Massachusetts, and Oskar Heinroth, who observed several species of waterfowls in Germany. Their observations led to the conclusion that members of a species not only share the same body functions and bone structures but also share behavior patterns.

The next step was to compare instinctive behavior across several closely related species. This work was accomplished between 1940 and 1960 by Lorenz and Tinbergen. Lorenz chose as his subject the courtship sequences of mallards, teals, and gadwalls. Recognition signals among ducks are a specific sequence of behaviors that include tail shaking, head flicking, and whistling. The exact sequence for different species is different, yet the components are the same. Through these studies, it is possible to conclude that courtship sequences originated in a single ancestral form, and crossbreeding between duck species produced variations in the pattern. Tinbergen arrived at a similar conclusion with his work on the calls, body postures, and movements of gulls. His study of the signaling behavior of more than fifteen species of gulls showed that their system of signals is similar. As a result of their work, Lorenz and Tinbergen provided a scientific basis both for the biological source of behavior and for an evolutionary source of instinctive reaction.

The Nature Versus Nurture Debate

Although few scientists of the time had objected to the notion that genetics contributed to instinctive behavior, there was an ongoing debate as to the extent of the genetic contribution. The scientific bias was on the side of learned behavior patterns in such areas as language, signals, and body postures. It seemed clear that higher animals learn how to transfer information among themselves. One example was that an isolated songbird, denied access to parental teaching, does not instinctively know the songs of its species. Consequently, the genetic component may play only a small part in the overall development of behavior. In this debate, the contribution of Karl von Frisch shifted the balance to the side of inheritance. Von Frisch showed that honeybees communicate both the direction and the

Nikolaas Tinbergen, one of the founders of the science of ethology and a Nobel laureate in 1973, conducted many experiments on the subject of instincts and behavior, especially in gulls. (Nobel Foundation) distance of a source of nectar through a sequence of dance patterns. A scouting bee returning to the hive can provide exact information to other bees. While it was argued that the larger brain sizes of higher animals contributed substantially to learning a system of communication, it was difficult to make the same argument for insects.

The debate on nature versus nurture produced extensive efforts to determine the extent to which instinctive behavior is shaped by inheritance or by learning. In the study of sea gull chicks, Jack Hailman created a series of experiments that added evidence to the side of learned behavior. The parent of a sea gull chick can elicit pecking from the chick either by pointing its bill downward or by swinging its bill from side to side. The chick will respond not only to a parent's action, however, but also to a model that has the shape of the parent. The initial feeding behavior of a newly hatched chick is a "hit and miss" affair. With growth, the chick responds more precisely to the figure of the parent and acquires greater coordination. Thus, the initial instinct is for the chick to peck at a variety of motions, but with maturity a learning component takes place to create greater discrimination.

Sequences of Behavior

During the 1950's and 1960's, researchers in instinctive behavior studied a number of animals and insects. Scientists began to understand that instincts are not a simple response to the environment but are a complex sequence of behavior. Scientists also began to find evidence suggesting that natural selection acts on behavior patterns as well as on an organism's biological makeup. The result of this research came to be categorized into three broad groups of instinctive behavior. One was the response of a simple instinct on the part of a single organ to some stimulus. An example is a nerve cell responding to light that triggers a reflex response. Other reflex reactions include locomotion and movement. Another type of stereotyped behavior was called fixed action patterns (FAPs). For example, the courting behavior of ducks can be classified as FAPs, wherein the pattern and timing of the responses are invariable for all members of the species. Similar FAPs are found in spiders, crabs, and a number of other insects and lower animals. A final group of instinctive behavior was described as modifiable action patterns (MAPs) and included fixed patterns that could be modified by the environment or by learning. For example, in species of birds, the core of nest-building behavior is fixed, but actual nest building depends on the availability of preferred building materials, which can be altered by location and setting.

With the deciphering of the genetic code during the 1950's, research in instinctive behavior shifted toward the genetic basis of innate behavior. Research has shown that one group of chemicals called neuropeptides are produced by specific genes. Within the brain, these peptides have the ability to govern stereotyped behavior. For example, a specific peptide (angiotensin II), when injected into vertebrates, causes spontaneous drinking activity. Research on neuroactive chemicals that influence behavior patterns is still in its infancy; research on brain functions and neuron pathways has only begun. In the future, biochemists expect to isolate the link between the genetic code and brain function.

There remains one area of stereotyped behavior that has puzzled scientists since the time of Darwin: the question of altruistic behavior. Scientists have wondered how to explain behaviors such as ants drowning themselves in a stream so that others can cross over them or a parent animal risking its life so that offspring can survive. W. D. Hamilton, among others, began to use probability models, which show that cooperative behavior, which may risk the lives of individuals, results in greater survival of the rest of the group. Altruistic behavior not only is "for the good of the species" but also provides the greater probability that large numbers of that group will reproduce and therefore gain an advantage.

The Fieldwork of Ethology

The early students of ethology were often called "bird-watchers" because they began their work by observing the behavior of birds. Fieldwork involves repeated observations of a subject over long periods of time. Eventually, a sequence of behavior emerges, and then it is possible to read the language of the behavior. For example, Lorenz observed that the courtship sequence of the mallard duck involved some ten segmented parts, such as bill-shake, head-flick, tail-shake, and grunt-whistle.

In certain instances, fieldwork with insects and lower animals offers the possibility of direct experimentation. In his attempt to translate the dancing motion of bees, von Frisch made the food source available. Consequently, he was able to vary the distance of the food source, change its location, and alter the quantity of food. Each change in the variables produced some variation in the dance—perhaps a new "phrase" added to the language. In other areas of research, the test subject can be modified for direct experimentation. When William Keeton attempted to explain how pigeons found their way home, he used contact lenses to cover the eyes of the pigeon to block out the position of the sun. He also created secondary magnetic fields around the pigeon to test the subject's sensitivity to the earth's magnetic field.

While all studies of stereotyped behavior begin with observation, either in the field or in controlled settings, further exploration usually requires laboratory research. In Jack Hailman's study of the learning component of sea gull chicks, he constructed models of gull parents and correlated pecking accuracy with growth. He also modified features of the model sea gull to study possible changes in responses from the chicks. As the search for the causes of instinctive behavior moves further into the organism, the methodology follows—into areas of brain function (neuroethology), the chemistry of innate behavior, and the genetic component of behavior. Investigating the source of egg-laying behavior of a species of a large marine snail (*Aplysia*), Richard Scheller and Richard Axel found three genes that produce a number of peptides that govern this behavior.

Instincts and Genes

Instincts are a part of all living organisms, and observable instinctive responses are only a small part of an intricate pattern. The genetic makeup of an organism dictates specific unlearned patterns of responses and variations that, in turn, determine a favorable selection of individuals within a species. Clearly, instincts in sexual selection, reproduction, food gathering, and other basic needs are critical for the survival of members of a species. In higher animals, instinctive activities are often overshadowed (and sometimes disguised) by learned patterns of responses. For example, in dogs, the pulling back of facial muscles and the showing of teeth is a response to fear and attack. In humans, laughter is a similar response to surprise, embarrassment, and uneasiness. Because of social adaptation, however, laughter takes on additional behavioral conventions.

Until the early part of the twentieth century, instincts were thought to be learned responses to specific situations. Consequently, if aggression were learned, then it could be modified, changed, and unlearned. With the establishment of a genetic and biochemical foundation for instincts, research in stereotyped behavior has become part of a heated debate. In 1975, Edward O. Wilson published *Sociobiology: The New Synthesis*. This highly technical work found a surprisingly large audience; in it, Wilson attempted to place all social behavior on a biological basis. Although the work emphasized animal behavior, Wilson implied that all human history was also part of evolutionary biology and that his work would synthesize all the social sciences with biology. Since instincts such as aggression, selection of sexual partners, and care of the young play a prominent part in cultural activities, Wilson seems to suggest that in the future, the study of society will be grounded in neurobiology and sociobiology.

—Victor W. Chen

See also: Altruism; Brain; Communication; Competition; Courtship; Defense mechanisms; Ethology; Habituation and sensitization; Hormones and behavior; Imprinting; Learning; Mating; Migration; Reflexes; Rhythms and behavior; Territoriality and aggression.

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INTELLIGENCE

Types of animal science: Behavior, development
Fields of study: Developmental biology, ethology, evolutionary science

Animals are guided by more than instinct when interacting with their environment, yet the exact measurement of intelligence in various species remains problematic. While scientists devise numerous problem-solving tasks to assess intelligence, anthropomorphism leads to exaggerated claims of intelligence through anecdotal evidence.

Principal Terms

ANTHROPOMORPHISM: attributing human characteristics or states of mind to animals
COGNITION: transformation and elaboration of sensory input
COGNITIVE ETHOLOGY: scientific study of animal intelligence
LEXIGRAMS: symbols associated with objects or places in keyboard communication experiments with primates
PROTOGRAMMAR: word coined to signify the early foundation for grammar development found in primates
RECAPITULATION: stages of human development reappearing in different animal species

Both the general public and scientific community have long been intrigued with questions about how animals think and what are they thinking. Published reports of animal cognition increased dramatically in the last half of the twentieth century. Chimpanzees in the Ivory Coast have demonstrated extensive use of rocks as tools in cracking nuts. These primates have also been reported to hide undesirable expressions from their faces and act as if blind or deaf. Vervets have been found to use an elaborate system of alarm calls that seem to function as words. Parrots can demonstrate the ability to count, and birds exhibit the capacity to make and use tools to gather food. Dolphins apparently understand and follow simple commands. Primates have been trained to use signs in a symbolic fashion, communicating their needs, desires, and thoughts.

Theories of Cognitive Ethology

Cognitive ethology is a relatively new discipline that studies animal intelligence. Donald Griffin is considered to have founded this branch of study through the publication of *Animal Thinking* (1984) and *Animal Minds* (1992). Since the appearance of his books, numerous instances of animal intelligence have been gathered from observation and experimentation.

Traditionally, attitudes about animal intelligence can be sorted into those that place animals on a continuum with humans and those that see animals as distinct from humans. From the former perspective, animal behavior is readily interpreted as a definite sign of various cognitive skills and special abilities along a continuum of development. From a discontinuity perspective, only humans are considered to possess the higher cognitive skill of reasoning. The higher cognitive abilities are considered to be a uniquely human capacity that sets them apart from the lower animals, who are controlled by instinct.

Charles Darwin, in *The Descent of Man* (1871), defended the idea of the intelligence of animals existing on a continuum with humans. Since animals and humans have a common ancestry, animals would have the fundamental capacities for rational choice, reflection, and insight. Darwin concluded that the differences between the minds of humans and animals were of degree rather than of kind. Following Darwin's proclamation, a number of anecdotal studies concerning animal intelligence appeared that suggested extensive cognitive ability in animals. Unfortunately, many of the examples illustrated anthropomorphism. This is the process whereby humanlike characteristics are attributed to animal behavior.

Some interpretations of Darwin's statement created a distorted view about evolution that persisted long into the twentieth century. The idea that life on earth represents a chain of progress from inferior to superior forms began to influence the view of animal intelligence. The theory that ontogeny recapitulates phylogeny also became popular in the early years of the twentieth century. This theory, which does not have any scientific support, suggested that the advancement of life forms corresponded to the stages of development for humans. This stepladder approach to animal intelligence led to a ranking of animals compared to the developmental stages of human infants and children.

This approach to animal intelligence is flawed because it relies on the notion that some animals are more highly evolved than others are. Evolution does not have a single point of greatest evolution. The branches of the evolutionary tree have culminated with many different species occupying special niches. Thus, the "degree" of a species' evolution depends on the extent to which it successfully occupies its niche.

Animals Who Might Think

In addition to this tendency to attribute states of mind to animals that are found in humans, there were a number of cases of labeling trained behavior in animals as signs of reasoning skills. One of the most famous examples was the case of the horse, Clever Hans, in the early 1900's. Wilhelm von Osten owned a horse that demonstrated extensive arithmetic skills. When von Osten presented a written arithmetic problem to Hans, the horse would tap out the answer with his forefoot. Clever Hans also appeared adept at telling time, and answered questions about sociopolitical events by nodding or shaking his head yes or no. The horse's abilities suggested to many individuals the similarity between animal and human minds. Eventually, the Prussian Academy of Sciences discovered that Hans was not answering the

Measuring Arithmetic Skills in Primates

The chimpanzee Sheba was involved in a number of widely reported experiments that purported to demonstrate arithmetic ability in primates. Sheba was taught to associate a tray containing one, two, or three pieces of candy with cards containing the corresponding number of marks. If two candies were present on the tray, Sheba learned to pick the card with two marks. If the correct card was selected, Sheba would be rewarded by being allowed to eat the candy. In the next stage of the experiment, the marks on the cards were replaced by the numerals 1, 2, and 3. Then Sheba had to match the number of candy pieces with the correct number. After Sheba showed success in this phase of the experiment, the candy pieces were replaced with other inedible objects. If Sheba chose the number that matched the number of objects, she was rewarded with the corresponding number of candies. Eventually the numbers were expanded to include 0 and 4. Next Sheba was given the challenge of counting the total number of candies presented on a series of trays. Sheba demonstrated a rudimentary ability for addition showing correct responses 75 percent of the time. Initially the sums were restricted to one, two, or three. Sheba was eventually able to exhibit the skill to add numbers when the candies were replaced with the numerals 1, 2, and 3. Although Sheba was able to show mathematical ability, even the experimenter acknowledged some important limitations. Sheba required extensive training and "heroic" effort on the part of the trainer to accomplish the counting performances. A true mathematical ability should generalize to other situations, yet animals such as Sheba do not demonstrate easy or automatic transfer of numerical performance from one realm to another.

questions by means of any reasoning skills, but was an astute observer of the behavior of his owner and those around him. When questions were posed to Hans, cues were provided unconsciously to the horse about the correct answer. Since horses have evolved to ascertain subtle visual cues from others in their herd, Hans was able to form a number of cued associations which led to a reward. The owner of Clever Hans was not attempting to perpetrate fraud. He believed in the possibility that a horse could have reasoning ability, but von Osten was not sophisticated in how he tested for the skills. The inadvertent cueing of an animal to respond in a certain fashion is one of the major confounding factors found in the investigation of animal intelligence.

The case of Clever Hans illustrates two other problems that confound reports concerning the level of intelligence in animals. First is the problem of anthropomorphism. People develop an emotional bond with animals and interpret behavior in order to enhance the closeness they feel to them. The second problem concerns the methods used to measure intelligence. The classic case of Kohler's chimpanzees illustrates this problem.

In the early part of the twentieth century, Wolfgang Köhler assessed the reasoning ability of chimpanzees to obtain food outside of an enclosure. After a rake was left in the enclosure, food was placed out of reach of the caged chimpanzees. The chimpanzees were able to use the rake to bring food to the cage. Köhler concluded that the animals had insight into the nature of the problem and used reasoning to achieve a solution. A further study, requiring the fitting together of two sticks in order to reach the food, also supported Köhler's conclusions. However, later experimentation has revealed that chimpanzees without a history of playing with sticks could not solve the problem. Apparently, in order to solve the problem, the chimpanzees needed an extensive history of playing with sticks, which enabled them to learn how sticks could be used at a later time. In solving the problem, they were using an instinctual tendency to play with sticks and scraping them over the ground.

Primates and Sign Language

A contemporary example of the problem of measurement can be provided with the case of Washoe, the first chimpanzee to be taught sign language. Because of physical inability to vocalize human speech, chimpanzees were taught sign language as a mode of communication with humans. Soon Washoe and another signing chimpanzee, Nim Chimsky, were reported to have spontaneously created novel sentences through their signing. For example, Washoe was reported to have signed the combination water and bird after seeing a swan. Being a novel combination of signs, the trainers of Washoe explained the behavior as creative insight. Unfortunately, Washoe had also shown repeated signing of meaningless combinations, leading to the conclusion that a significant pairing of signs would eventually appear not because of the primate's cognitive reasoning but as a result of chance. Inevitably, these early attempts to demonstrate animal intelligence were widely discredited as exaggeration or self-delusion on the part of the animal's trainers, and this animal language research from the late 1970's fell into disrepute.

In order avoid the ambiguities of sign language, later researchers used keyboards that related symbols to a variety of objects, people, and places. Much of this research has taken place at the Language Research Center at Georgia State University in Atlanta under the guidance of Dr. Sue Savage-Rumbaugh. In the first experiments, two chimpanzees, Austin and Sherman, were familiarized with a system of symbols or lexigrams. Each was abstract and arbitrarily associated with an object, person, place, or situation. Eventually Austin and Sherman learned to communicate with symbols illustrated on a keyboard. For example, an experiment was devised where one chimpanzee was shown where food was being deposited in a certain container while the other had control of a tool to open the container. With the keyboard present, the chimpanzees were able to communicate with one another to use the tool on the correct container.

Soon a bonobo chimpanzee, Kanzi, became the star pupil of this technique and learned a vocabulary of two hundred symbols. Kanzi eventually showed the capacity to construct rudimentary sentences that were generated spontaneously. The chimpanzees trained using the keyboards appear to be exhibiting a protogrammar. This is a term to indicate the beginnings of grammar, roughly equivalent to the verbal skills seen in a human child about two to three years old.

In the late 1990's, another bonobo chimpanzee, Panbanisha, surpassed the capacities evidenced by Kanzi. Panbanisha has been reported to understand complex sentences and use the keyboard to communicate spontaneously with the outside world. Although the results have been impressive, critics of the Center's activities remain. The question remains whether the chimpanzees are demonstrating extremely effective training or some level of abstract reasoning.

—Frank J. Prerost

See also: Brain; Emotions; Imprinting; Instincts; Language; Learning; Reflexes; Rhythms and behavior; Tool use.

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INVERTEBRATES

Type of animal science: Classification
Fields of study: Anatomy, developmental biology, ecology, entomology, histology, invertebrate biology, marine biology, physiology

Over 98 percent of all known animal species are invertebrates, animals without backbones. At the base of many food webs, invertebrates provide nutrients to a wide range of other animals on land, underground, and in the seas. The diversity within the invertebrates is amazing, ranging from single-celled protozoans to cephalochordates possessing nerve cords, and claiming close relationship to vertebrates.

Principal Terms

COELOM: a true body cavity, lined by mesoderm

COLONY: a cluster of genetically identical individuals formed asexually from a single individual

CYST: a secreted covering that protects small invertebrates from environmental stress

GONOCHORISTIC: having separate sexes; an individual is either male or female

HYDROSTATIC SKELETON: a system in which fluid serves as the support by which muscles interact

MESODERM: a middle layer of embryonic tissue between the ectoderm and endoderm

With the exception of insects, which have extensively colonized terrestrial environments, most invertebrates are aquatic, many of those being marine. Even some of the land dwellers start life as aquatic larvae. Invertebrates follow one of three types of general body plan. Some marine sponges are asymmetrical, lacking an ordered pattern to their structure. Cylindrical organisms, such as sea anemones, are radially symmetric; any cut through the center of the organism divides it in equal halves. Asymmetrical and radially symmetric animals tend to stay in one place; thus their body plan helps them to collect environmental stimuli from every direction. Animals that exhibit bilateral symmetry have right and left halves that are mirror images of each other. They are mobile and usually have a distinct head end. This area of cephalization, concentrated nerve and sensory tissues, is directed forward in their travels, giving them new information about where they are going.

Invertebrate Feeding

Among the protozoans there are a variety of diets and feeding mechanisms. Organisms in the phylum Ciliophora have a cytostome, a cell mouth that can be found anteriorly, laterally, or ventrally, depending on species, on these single-celled creatures. Ciliates feed primarily on bacteria, algae, and other protozoans. Members of the phylum Amoebozoa have a similar diet to the ciliates but, in the absence of mouths, use pseudopodia to wrap around a food item, engulfing it. *Euglena* (phylum Euglenozoa), a flagellate protozoan commonly used in biology laboratories, is a self-feeder (autotroph). It contains chloroplasts and uses light energy to produce sugars, photosynthesized as in plants. It is interesting to note that some euglenids can and do ingest solid food if they are exposed to darkness for too long. Another group of interesting flagellates is the hypermastigotes. Species such as *Trichonympha campanula* live in the guts of termites. *T. campanula* breaks down the high cellulose content present in the termite diet of wood products, something that the termite cannot do for itself. In return these protozoans keep some of the nutrients for themselves.

Sponges, phylum Porifera, do not have any or-

Nematodes Are Everywhere

Members of the phylum Nematoda are typically one to two millimeters in length and tapered at both anterior and posterior ends. It is difficult to tell the head from the tail, externally. Except for the mouth and the genital pore, there are no obvious body openings to the outside. Nematodes do not have eyes, ears, or noses. However, they respond to temperature changes, light, mechanical stimulation, and chemical cues because they do possess special organs located in tiny pits that are sensitive to chemicals, and small papillae that are sensitive to touch. They breathe through their cuticle, skin, which is permeable to water and gases. With such a covering, desiccation (drying out) is a constant threat to their well-being. Thus, nematodes live in moist environments. There are some that are fully aquatic; those that are terrestrial surround themselves in a film of water; and those that are parasitic take advantage of the high moisture levels within the body of the host.

As far as numbers of individuals are concerned, nematodes are regarded as the most abundant multicellular animals alive today. There can be literally millions of these small worms per square meter of soil or shallow water sediment. Free-living nematodes are important for decomposition and nutrient cycling. Of the 40 percent of species that are parasitic, much of the toll of the resulting disease in the host is due to the concentration of individual worms competing with the host for nutrients and blocking vessels or entirely filling the heart. One ounce of undercooked pork can contain one hundred thousand worms, and each female can produce thousands of young in just a few days. Nematodes are prevalent in research labs as well. *Caenorhabidits elegans*, a soil nematode, is a model organism that has been studied to unlock many of the secrets of developmental biology and genetics of humans.

gans, but they do possess specialized cell types. Choanocytes, also termed collar cells, line the inside of the sponge and capture small food particles present in the circulating water. The phylum Cnidaria is well known for quite another specialty. Organisms in this phylum, such as jellyfish, have specialized stinging cells called nematoblasts. One of the functions of cnidae within the nematoblasts is secretion of toxins used to paralyze and kill prey. Cnidarians are patient hunters, lying in wait until their next meal contacts a tentacle or two, triggering the toxic sting.

Tapeworms (phylum Platyhelminthes, class Cestoda) have no mouth or digestive tract. They are highly adapted to a parasitic way of life. Swimming in nutrients that their host, usually a vertebrate, is in the process of digesting, tapeworms absorb nutrients through their outer surface, and return nothing besides waste products to their host.

Many rotifers (phylum Rotifera) are omnivores, meaning they eat anything that will fit into their mouth. After being ingested, prey passing into the muscular pharynx encounters grinding, crushing jaws called trophi. Rotifers have a one-way digestive tract. Wastes pass out the anus rather than being expelled through the mouth, unlike many of the animals discussed thus far.

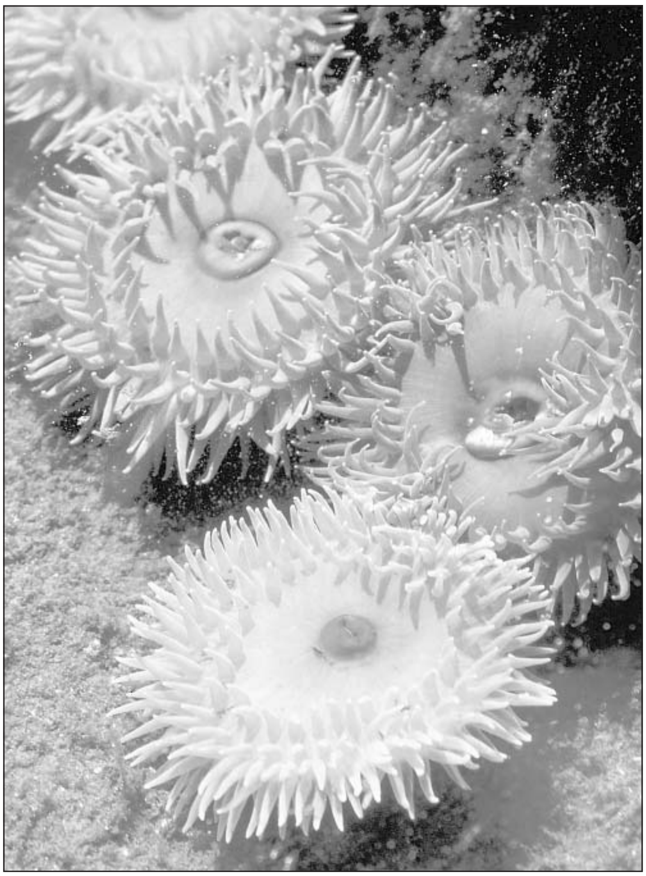
There is a wide range of feeding styles among the mollusks (phylum Mollusca). Some feed on plants; others feed on animals, and others feed on particles suspended in the water or mud that they themselves inhabit. There are also mollusks that are ectoparasites, living on the exterior of their host rather than inside it. An interesting molluscan feeding structure is the radula. The teeth on this tonguelike organ are replaced as they wear down or break.

The phylum Arthropoda is divided into two subphyla based on mouthpart structure. The Chelicerates, including horseshoe crabs, and arachnids (spiders, mites, ticks, and scorpions) have fanglike oral appendages used to grab and shred food items. Conversely, insects and crustaceans generally have mandibles, a pair of jaws for crushing food. This basic plan can be highly modified. The specialized coiled straw proboscis of a butterfly is such an example.

Starfish (phylum Echinodermata) prey on large invertebrates and small fish. These echinoderms have two stomachs and can protrude the cardiac stomach through the mouth and begin to digest prey externally. This is an especially useful maneuver when feeding on particularly large prey or when eating a clam through the small opening between its shells.

Respiration and Circulation

As single cells, protozoans have high body surface to volume ratio. They inhabit wet or at least moist environments and are able to take care of gas exchange through simple diffusion. Even though flatworms, phylum Platyhelminthes, are multicellular, they also posses a large external surface area relative to their internal volume, so they, too, rely on simple diffusion across their body surface area for gas exchange. A highly branched gastrovascular cavity allows most cells to be in contact with the digestive system, which means that nutrients do not have to circulate to remote parts of the body. Metabolic wastes generally diffuse out across the body surface.



Many invertebrates are radially symmetrical marine organisms, such as these sea anemones. (PhotoDisc)

Sponges rely on their body cavity (the spongocoel) for circulation and gas exchange. Seawater with dissolved oxygen is pulled into the spongocoel through pores in the body wall called ostia. Flagella in specialized collar cells lining the spongocoel set up an internal current to provide circulation. Water and waste products then pass out of a larger opening, called an osculum.

Cnidarians also lack specialized respiratory structures. They rely on epidermal and gastrodermal surfaces for gas exchange. The gastrodermis lines the gastrovascular, main body cavity. As its name suggests, the gastrovascular cavity functions in both gastric capacity of digestion and the vascular role of circulation.

Most aquatic mollusks have comblike gills that function in gas exchange and also in filter feeding in some. Both aquatic and terrestrial snails in the subclass Pulmonata have highly vascularized structures that function as modified lungs. Mollusks typically posses a heart or similar pump that circulates fluid through an open circulatory system. In an open circulatory system the conduits, or vessels, are limited, and most organs are bathed directly in the circulatory fluid. Cephalopods, such as squid and octopuses, are mollusks with closed circulatory systems. In a closed circulatory system, blood is contained in vessels. The squid actually has three hearts. The systemic heart receives oxygenated blood from the gills and sends it to the tissues. The two branchial hearts pump deoxygenated blood back to the gills.

Arthropods have open circulatory systems. The circulatory fluid, called hemo-

The Coral Reef Community

Coral reefs are colonies of small invertebrate animals (phylum Cnidaria, class Anthozoa). Some species of coral are solitary; the colonial reef builders are called hermatypic. The reef grows as new members of the colony take up residence on top of the calcium carbonate skeletons of previous generations. In this way, layer by layer, reefs can attain huge dimensions. Australia's Great Barrier Reef is over 2,000 kilometers long and 145 kilometers wide. Coral reefs are very diverse and fragile ecosystems. Reefs consisting of hundreds of species of corals, not to mention the countless species of other organisms, occur only in clear, shallow, tropical marine environments. Corals eat plankton but also rely on photosynthetic symbiotic algae for nutrient provision. Corals provide shelter and feeding grounds for many organisms: sponges, mollusks, echinoderms, tube dwelling worms, and fish, just to name a few reef inhabitants and visitors. Reefs also affect life on land by absorbing wave force, thus mitigating beach erosion.

There are four major types of reef formations. Fringing reefs border the shoreline. A lagoon separates a barrier reef from land. Atolls form on top of submerged volcanoes and platform reefs may form near atolls or be part of a larger barrier reef system. Stresses that threaten reef communities include wide fluctuations in water temperature, sedimentation, coral mining, blast fishing, and souvenir hunting. Natural disturbances, such as storms, can also disrupt life in the reef but may help propagate the reef. The breaking of coral branches during a storm is one way that coral asexually reproduces.

lymph, enters the heart through holes, called ostia. It is then pumped through short arteries and into the body cavity. There are a number of adaptations for gas exchange among the arthropods. Spiders have book lungs consisting of multiple stacked plates, like pages in a book. Insects have trachea, tubes that connect to the outside through holes (spiracles) in the exoskeleton. The trachea transport air directly between body tissues and the environment. Rounding out the arthropods, aquatic crustaceans respire using filamentous gills.

The water vascular system (WVS) is unique to the phylum Echinodermata. This system of canals services thousands of tube feet, in the starfish, for example. These feet extend through the body wall and have many other functions in addition to locomotion. Due to circulating fluid within the WVS, tube feet also are involved in gas exchange, waste excretion, chemoreception, and food collection. Another echinoderm, the sea cucumber, possesses internal rather than external respiratory structures. These respiratory trees attach to the cloaca, the common collection area for the exit of digestive and reproductive systems from the body. Gases are exchanged via the pumping of seawater in and out of the cloaca.

Reproduction and Development

Reproduction among the invertebrates is almost as varied as the animals themselves. Cnidarians and sponges are just two of the many phyla that reproduce asexually, offspring arising by breaking off from the parent organism. Groups such as rotifers and some arthropods alternate between asexual and sexual reproduction, depending upon environmental conditions. The term parthenogenesis is used to describe development of an egg in the absence of fertilization. Parthenogenesis tends to occur during stable, favorable conditions. Sexual reproduction, the mixing of genes from two parents through uniting of egg and sperm, produces individuals with new combinations of genes, which may adapt them for survival under stressful conditions.

There are variations in sexual reproduction as well. Some invertebrates are hermaphrodites. These animals, such as earthworms, possess both male and female reproductive systems. Some can fertilize themselves; others cannot. When hermaphrodites mate with other members of their species, each individual donates and receives sperm, resulting in twice as many offspring per mating. Gonochoristic species have separate sexes, an individual being either male or female. This is the case for most insects.

In marine invertebrates, fertilization may be external. This involves broadcasting sperm and eggs into the surrounding seawater and relying on the ocean currents to bring the two together. Internal fertilization is the rule for freshwater and terrestrial invertebrates. Sperm may be transferred directly into the female's reproductive tract through a copulatory organ such as a penis. An indirect method of sperm transfer involves a package called a spermatophore. This chemical packet commonly provides nutrients for the female and her resultant offspring.

Aquatic larvae are commonly the dispersal stage in the life history of the particular invertebrate. Many times the adults are sedentary or even sessile, anchoring themselves to the ocean floor or remaining in self-constructed burrows. The larvae, on the other hand, are planktonic, relying on the ocean currents for transportation. A similar scenario exists with spiders. The young spin silken parachutes and use the wind currents to disperse away from the web of the mother spider. However, for many terrestrial invertebrates, the young represent the feeding stage. Lepidopteran caterpillars eat voraciously, and some adults, such as the luna moth, do not eat at all, living strictly off food stores acquired as a larva. Especially with the winged insects, it is the adults who colonize new areas.

—*Sarah Vordtriede*

See also: Ants; Arthropods; Bees; Beetles; Butterflies and moths; Circulatory systems of invertebrates; Cockroaches; Cold-blooded animals; Coral; Crustaceans; Echinoderms; Endocrine systems of invertebrates; Exoskeletons; Flatworms; Flies; Grasshoppers; Insects; Jellyfish; Mollusks; Mosquitoes; Muscles in invertebrates; Octopuses and squid; Praying mantis; Protozoa; Roundworms; Snails; Starfish; Tentacles; Termites; Vertebrates; Wasps and hornets; Worms, segmented; Zooplankton.

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ISOLATING MECHANISMS IN EVOLUTION

Type of animal science: Evolution
Fields of study: Ecology, evolutionary science, genetics, population biology, reproduction science, zoology

Isolating mechanisms act to prevent interbreeding and the exchange of genes between species. The establishment of isolating mechanisms between populations is a critical step in the formation of new species.

Principal Terms

ALLOZYME: one of two or more forms of an enzyme determined by different alleles of the same gene; usually analyzed by gel electrophoresis

CHLOROPLAST DEOXYRIBONUCLEIC ACID: a circular DNA molecule found in chloroplasts; chloroplasts are cytoplasmic organelles of green plants and some protists that carry out photosynthesis

FISSION: the division of an organism into two or more essentially identical organisms; an asexual process

HERMAPHRODITE: an individual with both male and female organs; functions as both male and female

HYBRID: a term that in the broad sense can apply to any offspring produced by parents that differ in one or more inheritable characteristics; used to denote offspring produced by a cross between different species

MITOCHONDRIAL DEOXYRIBONUCLEIC ACID (DNA): a circular molecule of DNA found in the mitochondria; mitochondria are cytoplasmic organelles that function in oxidative respiration

NUCLEAR RIBOSOMAL DEOXYRIBONUCLEIC ACID (DNA): nuclear DNA that codes for the ribosomal DNAs; ribosomes are small cytoplasmic particles that function in protein synthesis

Isolating mechanisms (reproductive isolating mechanisms) prevent interbreeding between species. The term, which was first used by Theodosius Dobzhansky in 1937 in his landmark book *Genetics and the Origin of Species*, refers to mechanisms that are genetically influenced and intrinsic. Geographic isolation can prevent interbreeding between populations, but it is an extrinsic factor and therefore does not qualify as an isolating mechanism. Isolating mechanisms function only between sexually reproducing species. They have no applicability to forms that reproduce only by asexual means, as by mitotic fission, stoloniferous or vegetative reproduction, or egg development without fertilization (parthenogenesis in animals). Obligatory self-fertilization in hermaphrodites (rare in animals) is a distortion of the sexual process that produces essentially the same results as asexual reproduction. Many lower animals and protists regularly employ both asexual and sexual means of reproduction, and the significance of isolating mechanisms in such forms is essentially the same as in normal sexual species.

Premating Mechanisms

Reproductive isolating mechanisms are usually classified into two main groups. Premating (prezygotic) mechanisms operate prior to mating, or the release of gametes, and, therefore, do not result in a wastage of the reproductive potential of the individual. Postmating (postzygotic) mechanisms come into play after mating, or the release of gametes, and could result in a loss of the genetic contribution of the individual to the next generation.

This distinction is also important in the theoretical sense in that natural selection should favor genes that promote premating isolation; those that do not presumably would be lost more often through mismatings (assuming that hybrids are not produced, or are sterile or inferior), and this could lead to a reinforcement of premating isolation.

Ethological (behavioral) isolation is the most important category of premating isolation in animals. The selection of a mate and the mating process depends upon the response of both partners to various sensory cues, any one of which may be species-specific. Although one kind of sensory stimulus may be emphasized, different cues may come into play at different stages of the pairing process. Visual signals provided by color, pattern, or method of display are often of particular importance in diurnal animals such as birds, many lizards, certain spiders, and fish. Sounds, as in male mating calls, are often important in nocturnal breeders such as crickets or frogs but are also important in birds. Mate discrimination based on chemical signals or odors (pheromones) is of fundamental importance in many different kinds of animals, especially those where visual cues or sound are not emphasized; chemical cues also are often important in aquatic animals with external fertilization. Tactile stimuli (touch) often play an important role in courtship once contact is established between the sexes. Even electrical signals appear to be utilized in some electrogenic fish.

Ecological (habitat) isolation often plays an important role. Different forms may be adapted to different habitats in the same general area and may meet only infrequently at the time of reproduction. One species of deer mouse, for example, may frequent woods, while another is found in old fields; one fish species spawns in riffles, while another spawns in still pools. This type of isolation, although frequent and widespread, is often incomplete as the different forms may come together in transitional habitats. The importance of ecological isolation, however, is attested by the fact that instances in which hybrid swarms are produced between forms that normally remain distinct have often been found to be the result of disruption of the environment, usually by humans. Mechanical isolation is a less-important type of premating isolation, but it can function in some combinations. Two related animal species, for example, may be mismatched because of differences in size, proportions, or structure of genitalia.

Finally, temporal differences often contribute to premating isolation. The commonest type of temporal isolation is seasonal isolation: Species may reproduce at different times of the year. A species of toad in the eastern United States, for example, breeds in the early spring, while a related species breeds in the late spring, with only a short period of overlap. Differences can also involve the time of day, whereby one species may mate at night and another during the day. Such differences, as in the case of ecological isolation, are often incomplete but may be an important component of premating isolation.

Postmating Mechanisms

If premating mechanisms fail, postmating mechanisms can come into play. If gametes are released, there still may be a failure of fertilization (intersterility). Spermatozoa may fail to penetrate the egg, or even with penetration there may be no fusion of the egg and sperm nucleus. Fertilization failure is almost universal between remotely related species (as from different families or above) and occasionally occurs even between closely related forms.

If fertilization does take place, other postmating mechanisms may operate. The hybrid may be inviable (F1 or zygotic inviability). Embryonic development may be abnormal, and the embryo may die at some stage, or the offspring may be defective. In other cases, development may be essentially normal, but the hybrid may be ill-adapted to survive in any available habitat or cannot compete for a mate (hybrid adaptive inferiority). Even if hybrids are produced, they may be partially to totally sterile (hybrid sterility). Hybrids between closely related forms are more likely to be fertile than those between more distantly related species, but the correlation is an inexact one. The causes for hybrid sterility are complex and can involve genetic factors, differences in gene arrangements on the chromosomes that disrupt normal chromosomal pairing and segregation at meiosis, and incompatibilities between cytoplasmic factors and the chromosomes. If the hybrids are fertile and interbreed or backcross to one of the parental forms, a more subtle phenomenon known as hybrid breakdown sometimes occurs. It takes the form of reduced fertility or reduced viability in the offspring. The basis for hybrid breakdown is poorly understood but may result from an imbalance of gene complexes contributed by the two species.

It should be emphasized that in most cases of reproductive isolation that have been carefully studied, more than one kind of isolating mechanism has been found to be present. Even though one type is clearly of paramount importance, it is usually supplemented by others, and should it fail, others may come into play. In this sense, reproductive isolation can be viewed as a fail-safe system. A striking difference in the overall pattern of reproductive isolation between animals and plants, however, is the much greater importance of premating isolation in animals and the emphasis on postmating mechanisms in plants. Ethological isolation, taken together with other premating mechanisms, is highly effective in animals, and postmating factors usually function only as a last resort.

Field Studies and Experimental Studies

Field studies have often been employed in the investigation of some types of premating isolating mechanisms. Differences in such things as breeding times, factors associated with onset of breeding activity, and differences in habitat distribution or selection of a breeding site are all subject to direct field observation. Comparative studies of courtship behavior in the field or laboratory often provide clues as to the types of sensory signals that may be important in the separation of related species.

Mating discrimination experiments carried on in the laboratory have often been employed to provide more precise information on the role played by different odors, colors, or patterns, courtship rituals, or sounds in mate selection. Certain pheromones, for example, which act as sexual attractants, have been shown to be highly species-specific in some insects. The presence or absence of certain colors or their presentation has been shown experimentally to be important in mate discrimination in vertebrates as diverse as fish, lizards, and birds. Call discrimination experiments, in which a receptive female is given a choice between recorded calls of males of her own and another species, have demonstrated the critical importance of mating call differences in reproductive isolation in frogs and toads. Synthetically generated calls have sometimes been used to pinpoint the precise call component responsible for the difference in response.

Studies on postmating isolating mechanisms have most often involved laboratory crosses in which the degree of intersterility, hybrid sterility, or hybrid inviability can be analyzed under controlled conditions. In instances in which artificial crosses are not feasible, natural hybrids sometimes occur and can be tested. The identification of natural backcross products can attest incomplete postmating, as well as premating isolation. Instances of extensive natural hybridization are of special interest and have often been subjected to particularly close scrutiny. Such cases often throw light on factors that can lead to a breakdown of reproductive isolation. Also, as natural hybridization more often occurs between marginally differentiated forms in earlier stages of speciation, new insights into the process of species formation can sometimes be obtained. Finally, such studies may yield information on the evolutionary role of hybridization, including introgressive hybridization, the leakage of genes from one species into another. Morphological analysis has long been used in such cases, and chromosomal studies are sometimes appropriate. In recent years, allozyme analysis by gel electrophoresis has become a routine tool in estimates of gene exchange, and molecular analysis of nuclear deoxyribonucleic acid (DNA), or mitochondrial DNA, have been useful. As mitochondria are normally passed on only maternally, their DNA can also be used to identify cases in which females of only one of the two species has been involved in the breakdown of reproductive isolation.

Investigations of the role of natural selection in the development and reinforcement of reproductive isolation have employed two different approaches. One has involved the measurement of geographic variation in the degree of difference in some signal character (call, color, or pattern, for example) thought to function in premating isolation between two species that have overlapping ranges. If the difference is consistently greater within the zone of overlap (reproductive character displacement), an argument can be made for the operation of reinforcement. Another approach has involved laboratory simulations, usually with the fruit fly *Drosophila*, in which some type of selective pressure is exerted against offspring produced by crosses between different stocks, and measurement is made of the frequency of mismatings through successive generations. The results of such studies to this time are contradictory, and the role of selection with regard to development of reproductive isolation requires further study.

Enhancing Reproductive Efficiency

The efficiency of reproduction in most animals is enhanced immeasurably by premating isolating mechanisms. Clearly, in animals a random testing of potential mates without regard to type is totally unacceptable for most species in terms of reproductive capacity and time and energy resources. Premating isolation in this sense is a major factor in promoting species diversity in animal communities.

Both premating and postmating isolating mechanisms are also critical to the maintenance of species diversity in that they act to protect the genetic integrity of each form: A species cannot maintain its identity without barriers that prevent the free exchange of genes with other species. Furthermore, a species functions as the primary unit of adaptation. Every species in a community has its own unique combination of adaptive features that enable it to exploit the resources of its environment and to coexist with other species with a minimum of competition. The diversity of different species that can coexist in the same area depends upon the unique "niche" that each occupies; adaptive features that determine that niche are based on the unique genetic constitution of each species, and this genetic constitution is protected through reproductive isolation.

The development of reproductive isolating mechanisms is also critical to the formation of new species (speciation), and ultimately to the development of new organic diversity. The most widely accepted, objective, and theoretically operational concept for a sexual species is the biological species concept. Such a species can be defined as population or group of populations, members of which are potentially capable of interbreeding but which are reproductively isolated from other species. The origin of new species, therefore, depends upon the development of reproductive isolating mechanisms between populations. A major focus of research in evolutionary biology and systematics has been, and continues to be, on the various factors that influence the development of reproductive isolating mechanisms.

—John S. Mecham

See also: Adaptive radiation; Biodiversity; Clines, hybrid zones, and introgression; Convergent and divergent evolution; Ecological niches; Ecosystems; Evolution: Historical perspective; Extinctions and evolutionary explosions; Fauna: Australia; Fauna: Galápagos Islands; Gene flow; Genetics; Hardy-Weinberg law of genetic equilibrium; Mutations; Natural selection; Population analysis; Population genetics; Punctuated equilibrium and continuous evolution; Systematics.

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JAGUARS

Type of animal science: Classification
Fields of study: Anatomy, physiology, wildlife ecology

Jaguars are the largest cats found in North or South America, originally occupying a wide diversity of habitats from the southwestern United States to Patagonia.

Principal Term

VIBRISSAE: stiff hairs, projecting as feelers from nose and head

Among big cats, jaguars, much larger than leopards, are exceeded in size only by lions and tigers. Males weigh from 125 to 250 pounds, are 6 to 9 feet long (including a tail up to 2.5 feet long), and stand twenty-four to thirty inches tall at the shoulder; females tend to be 20 percent smaller. Jaguar heads are massive and rounded; their bodies compact and heavily muscled. Individuals living in densely forested areas of the Amazon basin are significantly smaller than those inhabiting open terrain.

Tawny or yellow, with black rings and spots, jaguar coats resemble those of the leopard; however, jaguar coat rosettes are larger and usually contain black spots in their centers. Examples of melanism occur in Amazon regions, where jaguars are often called black panthers.

Behavior

Jaguar litters usually contain one to four cubs, which remain with their mother for eighteen months to two years while learning how to hunt. Other than during mating periods, adults live solitary lives, patrolling their own distinctly marked territories. Jaguar hunting ranges vary in size from five square miles, where prey is abundant, to two hundred square miles, where it is scarce. Male territories usually overlap the smaller ranges of several females.

Jaguars are crepuscular hunters, preferring dim light in which to stalk and surprise victims by leaping on their backs. The name jaguar comes from the Guarani word *yaguara*, meaning "wild beast that can kill its prey in a single bound." Large eyes and sensitive vibrissae permit jaguars to maneuver in the dark. They are opportunistic hunters, taking armadillos, peccaries, deer, capybaras, anteaters, caimans, turtles, and fish. Jaguars possess the most powerful bite among big cats; large canine teeth easily crush skulls and

Jaguar Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Subclass: Eutheria
Order: Carnivora
Family: Felidae (cats)
Genus and species: Panthera onca
Geographical location: Originally ranged from the southwestern United States to southern Argentina
Habitat: Forests, jungles, and grassy plains
Gestational period: About fourteen weeks
Life span: Ten to twelve years in the wild, over twenty years in captivity
Special anatomy: Large eyes with excellent night vision; jaws adapted to seizing and gripping prey, teeth designed for tearing and slicing flesh

Image Not Available

penetrate armadillo armor or turtle shells. Sharp carnassial teeth and rasplike papillae soon clean their victims' bones.

Relations with Humans

Pre-Columbian Indian societies called the jaguar "Master of Animals," associating it with success in hunting and warfare, invoking it in religious rituals, and assigning it high social status. Jaguar thrones and jaguar skins were power symbols for rulers; hunters and warriors wore necklaces and bracelets of jaguar teeth or claws. Preferred foods of the elite were the meats that jaguars ate: venison, peccary, capybara, and armadillo.

European settlers viewed jaguars as dangerous competitors to be hunted and killed. When Europeans arrived, sixteen subspecies of jaguars inhabited a continuous area stretching from the southwestern United States to Patagonia in Argentina. Before the end of the twentieth century, all subspecies of jaguar were endangered, their territories reduced to a series of disconnected areas lying between southern Mexico and northeast Argentina. In North and Central America, the jaguar lost 67 percent of its range, in South America about 38 percent. Most of the estimated fifteen thousand jaguars remaining exist in a few relatively undisturbed jungle regions of Central America and the Amazon basin.

Hunting, destruction of habitat, and competition with ranchers and farmers all threaten the survival of the jaguar. In 1968, the United States imported 13,5l6 jaguar skins. The number of cats slain declined after the 1975 Convention on International Trade in Endangered Species banned traffic in jaguar pelts. However, illegal trade continues; it is profitable because the beautiful skins are as greatly prized by today's high-status women as they were by Inca monarchs.

Jaguars tend to avoid open areas such as pastures and villages, and rarely cross into fenced fields. However, when ranchers and farmers permit their animals to wander into jaguar hunting territory, they provide an easy meal. Such depredations, along with rare attacks on humans, create demands for the extirpation of the offenders.

Continued destruction of habitat, as forests and jungles are leveled for timber or for farm and ranch land, is the greatest threat to jaguar survival. As remaining territory becomes ever more discontinuous, populations becomes less dense, and reproductive success becomes problematic. Whether jaguars can survive in wild, free-ranging populations, or will be found only in zoos and carefully protected national parks, remains an unanswered question.

—Milton Berman

See also: Carnivores; Cats; Cheetahs; Fauna: Central America; Fauna: South America; Leopards; Lions; Mountain lions; Predation; Tigers.

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JELLYFISH

Type of animal science: Classification
Fields of study: Anatomy, invertebrate biology, marine biology, physiology

Over two hundred species of jellyfish are known; they are abundant, especially in shallow, warm, or subtropical waters. The jellyfish body plan is simple, but they possess unique stinging structures that are used for foraging and defense.

Principal Terms

CILIATED: bearing short, hairlike organelles on the surface of cells, used for motility

CNIDOBLASTS: specialized cells on the body or tentacles of jellyfish that contain nematocysts

MEDUSA: adult umbrella- or bell-shaped forms of jellyfish, with mouth facing downward

MESOGLEA: gelatinous material lying between the inner and outer layers of a jellyfish

NEMATOCYST: stinging structures containing barbs and/or poison

PLANULA: free-swimming, ciliated jellyfish larva

POLYP: immature cylindrical forms of jellyfish with mouth facing upward

The gelatinous jellyfish are widespread in marine environments, although they are most common in tropical and subtropical regions. These ancient animals first appeared on earth over 650 million years ago. The smallest jellyfish are difficult to see without a microscope, while the largest known jellyfish is 2.5 meters in diameter; some jellyfish may have tentacles over 100 feet in length. The body plan of jellyfish is relatively primitive and contains less than 5 percent solid organic matter, the remaining bulk coming from water. They completely lack internal organs. The bell-like jellyfish bodies are composed of an outer layer of epidermis and an inner layer of gastrodermis that lines the gut. The gut has a single oral opening. Between the two layers is the mesoglea, which contains few cells and has a low metabolic rate. Four to eight oral arms are located near the oral opening and are used to transport food that has been captured by the tentacles.

Jellyfish are able to exert minimal control over their movement, being largely at the mercy of ocean currents. Jellyfish do, however, have some regulation over vertical movement. They possess a ring of muscles embedded on the underside of the bell that pulses rhythmically, pushing water out of the hollow bell. Using this jet propulsion, jellyfish can change their position in the water column, moving in response to light and prey.

Feeding Strategy of Jellyfish

Jellyfish are simple but specialized carnivores. Although jellyfish have a low metabolic rate, they have the ability to capture large prey. These two characteristics allow jellyfish to survive in environments where prey are scarce. Jellyfish are equipped with a specialized apparatus, the cnidoblast, for defense and feeding. Cnidoblasts are found by the hundreds or thousands on the tentacles and sometimes on the body surface. Within each cnidoblast is a coiled harpoonlike nematocyst that is discharged by the presence of potential prey. The nematocyst injects poison into the prey as spines on the nematocyst anchor it to the prey. The trapped, paralyzed prey is pulled back by the tentacles and stuffed into the gastrovascular cavity to be digested. Jellyfish do not attack humans, but humans may receive stings if they encounter jellyfish. The effects of jellyfish poison on humans can range from a mild, itchy rash to death.

Jellyfish Facts

Classification:
Kingdom: Animalia
Subkingdom: Eumetazoa
Phylum: Cnidaria
Classes: Scyphozoa (jellyfish), Cubozoa (box jellyfish)
Orders: Stauromedusae (sessile cup-shaped forms), Coronatae (deep-dwelling jellyfish), Semaeostomae (disc jellyfish), Rhizostomae (tentacle-less jellyfish), Chirodropidae and Carybdeidae (box jellyfish)
Geographical location: All the Earth's oceans
Habitat: Almost entirely marine, although a few freshwater species are known
Gestational period: Not well studied, but many species appear to reproduce once a year
Life span: Polyps usually develop over a period lasting a few months but may live for several years producing clones; adult medusa forms live two to six months
Special anatomy: Umbrella-like body; no head or skeleton; composed of outer epithelial layer and inner gastrodermis layer with thick elastic jellylike substance between them; gastrovascular cavity; specialized ring of epitheliomuscular cells that pulses rhythmically to propel the animal through the water; four to eight oral arms; tentacles bearing cnidoblasts containing nematocysts

Jellyfish Reproduction

Most jellyfish proceed through several distinct stages in their life cycles. Male medusae produce sperm that are released from the oral opening into the oral opening of the female. The female then releases fertilized eggs which develop into slipper-shaped, solid masses of ciliated cells called planula which move through the water and even-

The tentacles of jellyfish contain cnidoblasts, organs that shoot harpoonlike, venomous nematocysts into prey; the paralyzed victim is then reeled back to the jellyfish and consumed. (PhotoDisc) tually settle onto a solid surface. From these settled planula develop polyps that have cylindrical stalks attached to the substrate, with tentacles surrounding their mouths. At this stage, the polyps resemble sea anemones. The polyps divide and bud into tiny young jellyfish (ephyra) which are often carried far from the parent polyp by ocean currents. The ephyra develop into mature medusae over several weeks. The medusae normally live three to six months.

—Lisa M. Sardinia

See also: Carnivores; Deep-sea animals; Digestion; Ingestion; Invertebrates; Marine animals; Marine biology; Reproduction.

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KANGAROOS

Type of animal science: Classification
Fields of study: Anatomy, conservation biology, ethology, physiology, reproduction science, wildlife ecology

Kangaroos, comprising six species, are the largest marsupials. They evolved as the major grazing animals in Australia. Alone among large vertebrates, they hop as their preferred form of locomotion.

Principal Terms

DIAPAUSE: an interruption in embryonic development
HERBIVORE: animal solely dependent on plant material for its nutrition
QUADRUPED: animal with four feet

The ancestors of kangaroos differentiated from small, tree-dwelling, possumlike marsupials fifty million years before the present. About thirty million years ago, they came down from the trees of the rain forest that covered most of Australia at the time. Around five million years ago, the continent had started to dry out, and species closely related to modern kangaroos appeared. When the Aborigines first came to Australia forty thousand years ago, the continent included some larger marsupials. The latter apparently were not as fast and mobile as kangaroos, were easier prey, were overhunted, and as a result became extinct. The kangaroos were smaller and swifter, permitting them to survive. The six living species of true, large kangaroos differ in their habitats (temperate woodlands, tropical grasslands, arid outback) and size; the red kangaroo is the largest, with some males weighing two hundred pounds and standing six feet tall; the smallest, the black wallaroo, can weigh sixty pounds. Smaller relatives of kangaroos include wallabies (up to sixty pounds), pademelons (up to fifteen pounds), and rat kangaroos (less than one pound). While kangaroos are only found in Australia, some smaller relatives are also found in New Guinea, which was contiguous with Australia in the distant past.

Physical Characteristics of Kangaroos

Kangaroos stand on large rear legs, using their long tail for added support. They have small front legs, with handlike paws that lack an opposable thumb. Hopping is their most unusual characteristic. Besides kangaroos and their relatives, no vertebrate bigger than ten pounds hops. At slow speeds, kangaroos walk awkwardly and inefficiently, using their front legs and tail. However, at speeds over fifteen miles per hour, they hop upright in a graceful motion that can be more energetically efficient than running by quadrupeds, whose energy use is proportional to their speed. Kangaroos increase their speed by lengthening their stride, while keeping their hop frequency constant, at little increased energy expenditure. They propel themselves by virtue of highly elastic legs which move in unison and use their long tails to provide balance.

As marsupials, kangaroos nurse their young (called joeys) in a pouch. Female kangaroos, half the size of males, have one-month gestations, which can be interrupted if a young is still suckling in the pouch or under adverse nutritional conditions. In these cases, the embryo goes into diapause, a form of "suspended animation," until hormonal signals permit development to resume. The newborn is highly immature, pink and naked, resembles a slug, and weighs less than 0.03 ounces. Using its front legs and a good sense of smell, it crawls from the birth canal into the pouch

The kangaroo's strong tail assists it in maintaining an upright, bipedal posture. It is the only mammal with a weight over ten pounds that hops as its mode of locomotion. (Adobe)

and attaches itself to one of four teats of the mammary gland. Over the next three months, it remains permanently attached to that teat and becomes fully developed. Depending on the species, joeys leave the pouch for the first time at six to ten months, permanently leave the pouch at eight to eleven months, and are weaned at eleven to eighteen months. Females are sexually mature at eighteen months to two years, although some males do not become so until they are four years old.

Kangaroos are herbivores, and all six species are grazing animals. Their teeth are suited to grasses rather than shrubs and trees. They are also very efficient in their use of water, making them suitable for the arid regions of Australia. Some species consume less than 10 percent the water sheep do under the same conditions. When temperatures are moderate, they can get all of their water from the plants that they eat. They are inactive in the heat of the day and cool themselves by panting, sweating, and licking; the latter refers to the fact that they cover their front legs with saliva, which by evaporation cools not only their extremities but also their bodies via a dense network of blood vessels close to the surface. Kangaroos are among the most heat-tolerant of mammals. In addition, they have large, padded feet that compact the soil less than domesticated livestock.

Future of Kangaroos

Totaling over twenty million, the six species of large kangaroos are not presently endangered. This is in contrast with the risk to survival faced by some wallabies and smaller marsupials that are preyed upon by introduced wild animals, such as foxes, or by feral cats. The habitats of most kangaroos have been reduced by human activities, housing, industry, and agriculture, although the range of some of the less arid-tolerant species (eastern gray and western gray) has been increased when water is provided for livestock in remote regions. In addition, areas where sheep are protected from dingoes, as with the patrolled fence that stretches across Australia, have increased numbers of kangaroos. While they do compete with sheep and cattle for food and water, the extent of competition is limited, except during drought. Farming kangaroos for meat and hides remains a possibility but has not been developed. Some extensive preserves would be desirable not only to display these large animals in their natural environment but also to conserve their smaller, endangered relatives.

—James L. Robinson

See also: Embryology; Fauna: Australia; Fertilization; Koalas; Marsupials; Opossums; Pregnancy and prenatal development; Reproduction; Reproductive strategies; Reproductive system of female mammals.

Kangaroo Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Marsupialia
Family: Macropodidae (kangaroos and wallabies)
Genus and species: Macropus, with fourteen species including *M. giganteus* (eastern gray kangaroo), *M. fuliginosus* (western gray kangaroo), *M. rufus* (red kangaroo), *M. robustus* (wallaroo, four subspecies), *M. bernardus* (black wallaroo), *M. antilopinus* (antilopine kangaroo)
Geographical location: Australia
Habitat: Grasslands
Gestational period: One month, followed by six to eleven months in marsupium
Life span: Twelve to eighteen years in the wild; twenty-eight years in captivity
Special anatomy: Hops instead of running, by virtue of elastic legs and large tail for balance; gives birth to highly immature young that nurse and develop in a pouch

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KIDNEYS AND OTHER EXCRETORY STRUCTURES

Type of animal science: Physiology
Fields of study: Anatomy, biochemistry, cell biology

All cells must live in a relatively constant environment. The kidney and other excretory organs play important roles in the regulation of the processes that maintain this necessary homeostasis. Although excretion is often assumed to be the only role of the kidney, it also regulates blood pressure, produces hormones, and affects the body's pH.

Principal Terms

ANTIDIURETIC HORMONE (ADH): a hormone produced in the hypothalamus that controls reabsorption of water in the loop of Henle

CONTRACTILE VACUOLE: the excretory organ of several one-celled organisms

FILTRATION: the process of diffusion of plasma from the blood to the glomerulus and nephron

GLOMERULUS (pl. GLOMERULI): a capsule fitting around capillary blood vessels that receives the filtrate from the blood and passes it into the tubule

LOOP OF HENLE: a slender hairpin turn in the tubule where most adjustment of the water balance of the body occurs

MALPHIGIAN TUBULE: the primitive excretory organ of insects

NEPHRIDIA: the primitive forms of kidneys found in worms and lower organisms

NEPHRON: the basic excretory unit of the kidney

TUBULE: the long, slender part of the nephron that is the location of almost all kidney function

UREA: a substance formed from by-products of protein metabolism and excreted by the kidney

All cells, from the single-celled animals to the highly diversified cells of higher mammals, must maintain a constant internal environment with regard to the kinds and amounts of specific ions, the pH of the protoplasm, the osmotic pressure, the water content of the cells, and the excretion of wastes. The kidney in vertebrates and the varied types of excretory organs found in lower animals perform this function. Although the excretory function is very important, an animal will die more quickly from a disturbance of the composition of the internal environment of the cell than it will from an accumulation of wastes. Fortunately, the kidney performs functions that keep both of these from happening.

Maintaining Fluid Homeostasis

All cells live in a watery environment, which is maintained constant through the processes of homeostasis. Maintaining homeostasis presents different problems for different organisms. For a primate, living in the air, water loss is a constant problem, and water must be conserved. A freshwater fish, on the other hand, takes in large quantities of water that has a lower concentration of salts than its body fluids, and it must excrete the excess. An ocean fish, living in water with a much greater concentration of salts than its body fluids, must obtain water from its environment and still avoid increasing the concentration of salts in the body fluids.

A kidney is able to perform all these functions, although in each of these cases it acts in a different way. The freshwater fish must excrete large quantities of very dilute fluid in order to maintain salt conservation, whereas the saltwater fish must excrete a high concentration of salt in a very concentrated solution. The primate must be able to regulate the output of fluid as a function of water intake. Evolution has adapted the kidney of each animal to its environment.

In addition, animals survive by metabolizing foodstuffs to provide the energy for movement. One of the major metabolic processes is the breakdown of protein to produce energy for the synthesis of other proteins and the rebuilding of body structures. In the breakdown of protein, nitrogen is freed from the organic molecule and must be excreted. One of the resultant nitrogen products is ammonia, which is toxic. The ammonia is converted into a less toxic material, urea (or uric acid, in some animals), before it is excreted by the kidney. In addition, the metabolism of the body usually results in the production of acids, particularly if fat is metabolized. The body functions well only within a narrow range of acidity, so unless the excess acid is removed, serious problems quickly arise. The kidney serves the function of maintaining the pH at a constant value.

The Excretory Organs

The organs of excretion have taken many forms. Simple single-celled organisms such as amoebas are able to form contractile vacuoles, or walled-off spaces within the cell, in which water can be stored and waste products deposited. These vacuoles are periodically transported through the cytoplasm and excreted through the external cell membrane. The size and number of vacuoles are determined by water intake and the organism's need to eliminate water as well as by the accumulation of waste materials.

As animals developed more cell types and the number of cells increased dramatically, the need to provide a constant internal environment around the cells arose. The excretory organs became, of necessity, more complex in nature. In addition to excreting waste products, they developed abilities to retain some ions and excrete others, to retain or excrete water, and to retain or excrete acids or bases to maintain a constant environment.

Many organisms have no obvious means of regulating water and salt balance, and they apparently accomplish this feat through the skin or the gut; others have rudimentary organs of excretion. Many lower animals have nephridia, primitive versions of the kidney that excrete water and wastes and regulate ion concentration. These are simple tubes into which body fluids pass; the fluids are excreted after chemical alteration. In animals such as worms, that have segments, a pair of nephridia may be located in each segment. Some of them open into the body cavity, while others are closed. In some animals, these are well differentiated and are called flame cells. These tubular structures serve to regulate the internal environment of the body. For example, if the sodium concentration in the coelom, or internal cavity, is high, the nephridia excrete sodium; if it is low, they reabsorb it. In the insect, the organ of excretion is the Malphigian tubule, which is able to regulate ion and water exchange. The accumulated fluid is flushed into the gut, where absorption of ions and water takes place.

The Kidney

In vertebrates, the kidney is the organ responsible for eliminating water and waste products. The kidney is a bean-shaped organ that receives a large blood supply from the heart. It has several auxiliary structures: the ureter, which collects fluid or urine from all the tubules; the bladder, which acts as a storage organ; and the urethra, which opens from the bladder to the outside of the body. The kidney consists of more than a million nephrons arranged symmetrically, with the lower part of each nephron pointing toward the hilus (the pole of the kidney where the ureter arises).

The kidney maintains homeostasis of the body through four basic mechanisms: filtration, reabsorption, secretion, and concentration. In filtration, a liquid portion of the blood is transferred to the tubule. There the cells proceed to reabsorb necessary materials, to secrete additional materials into the tubular liquid from the blood, and to concentrate the fluid in the tubule.

The nephron is the fundamental structure of the kidney. The nephron is a long, slender tube with different parts that are capable of secreting or reabsorbing ions, water, and other substances either to remove materials from the blood or to return materials to the blood, depending upon the needs of the body. One process it performs is the elimination of ammonia products and other waste materials.

The nephron consists of two major parts: a glomerulus and a tubule. The process of urine formation begins with filtration. The blood enters the kidney and then the glomeruli, under high pressure from the heart. The pressure forces fluid from the blood into the tubule. The amount is tremendous; in humans, every day some 180 liters (about 40 gallons of fluid) pass from the blood into the nephron. All the blood in the body passes through the nephron about thirty times per day. During this same period, seven hundred liters of blood pass through the kidneys, so only a small portion is actually filtered or transferred to the tubule. Most remarkable of all, only about 1.5 liters of urine are produced each day. The rest of this large volume is reabsorbed by the tubule.

As the fluid passes into the nephron, it enters a section of tubule at the beginning that reabsorbs much of the material needed by the body. Such things as the glucose needed for energy, amino acids for protein building, vitamins, and ions needed to maintain the correct concentration of the blood are removed and transported by the cells of the nephron back into the blood. At the same time, about 85 percent of the water of the filtrate is also transported back into the blood.

The cells of the nephron are able to secrete materials from the blood to the tubular fluid. This process is exactly the opposite of the reabsorption of substances. One of the most readily secreted substances is sodium. The cells of the body are high in potassium and low in sodium; since sodium is a constituent of every diet, the removal of excess sodium is necessary. Sodium is picked up from the blood that circulates around the nephron and is secreted into the tubule. The process of secretion also extends to other materials. The potent antibiotic penicillin was ineffective when it was first used to treat systemic infections, because it was rapidly secreted by the tubules. A high enough concentration could not be accumulated in the blood to destroy bacteria. It became useful only when a derivative that was not secreted could be found.

The Loop of Henle

The tubular fluid that has been adjusted in concentration, volume of fluid, and concentration of ions and other materials now passes into a hairpin-shaped portion of the tubule called the loop of Henle. The loop of Henle adjusts the volume of filtrate. A hormone is produced by the brain (in the hypothalamus) that is capable of altering the permeability of the cells of the loop of Henle to water. The substance, a protein hormone called antidiuretic hormone (ADH), causes the reabsorption of water from the loop. Cells of the hypothalamus respond to the concentration of particles in the blood (its osmotic pressure) and adjust the amount of water that is reabsorbed from the tubule by secreting more or less ADH as necessary to maintain a constant concentration in the blood. The range of adjustment is remarkable. The volume of urine produced can range from about 0.5 liter to more than 30 liters per day, depending upon the need. If water is administered or restricted, the water concentration of the body changes. This causes a change in the production of ADH, which in turn increases or decreases the excretion of water to return the level to normal.

Sweating also causes water loss and thus decreases urine flow. Intake of large amounts of fluid will dilute the body fluids and cause an increased urine output. There is a constant adjustment, because water is lost by breathing, through the skin, and through excretions, and the kidney must make the proper corrections. Losses have been reduced to a minimum in animals such as the kangaroo rat, which lives in the desert and must conserve water. All of its water intake is from seeds and other foods containing some water, and excretion is almost zero. The desert rat is able to concentrate urine to a level about five times that of the human.

As the urine passes from the loop of Henle, it enters upon a final adjustment in the latter portion of the tubule. Volume, concentration of material, and the like are adjusted to maintain homeostasis. Other alterations of the fluid are also made in the passage down the tubule. If the body becomes acidic, the cells of the tubule exchange sodium ions, which are neutral, for acid ions (H+), thus causing the body to lose acid. Conversely, if the body becomes basic (lacks acid or hydrogen ions), the reverse is true.

Studying Kidney Function

The kidney can be studied on many different levels. The output of the kidney, the urine, and the input, the blood, can be analyzed in order to determine function of both kidneys. In some animals, such as the frog, the individual nephrons are visible under a microscope. Through the use of the stop-flow technique, the behavior of an individual portion of the nephron can be studied. In this technique, a very small needle is introduced into one portion of the nephron, and a small drop of oil is injected. Another drop is injected in an adjacent section of the nephron, thus isolating a section between the two drops. The exchanges that occur in that portion of the nephron can then be measured by taking samples of the fluid at intervals.

The whole kidney can be studied by examination of the kidney in relation to a reference substance. For example, the chemical inulin goes through the nephron without any alteration, so its excretion can be compared with other substances: If more of another substance appears in the urine in proportion to the inulin, the substance must have been excreted from the blood into the urine and secreted. If less is present, some material must have been reabsorbed from the tubule into the blood. This is called the clearance technique, and it is widely used to predict kidney function in health and disease. For less sophisticated testing, substances—such as certain dyes—that can be taken orally and are excreted by the kidney can be used to measure the rate of excretion. Radioopaque substances, substances that will appear on X rays, can be used to detect overt kidney malfunction.

—J. H. U. Brown

See also: Circulatory systems of vertebrates; Endocrine systems of vertebrates; Metabolic rates; Osmoregulation; pH maintenance; Water balance in vertebrates.

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KOALAS

Type of animal science: Classification
Fields of study: Anatomy, physiology, zoology

Koalas are solitary animals existing on a low-energy diet of eucalyptus leaves. Since koalas are marsupials, the females have a pouch where their young develop. They are the sole member of the family Phascolarctidae.

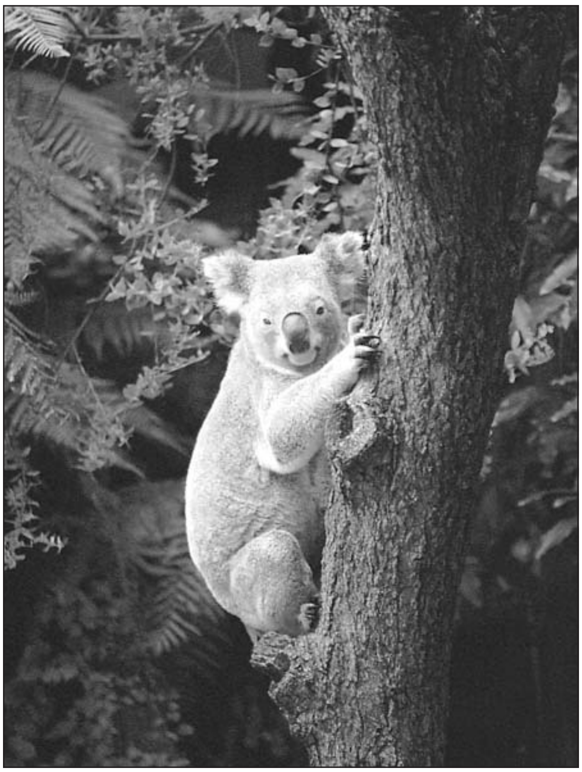
Principal Terms

ARBOREAL: living in trees
BELLOWING: guttural sound used in communication
CAECUM: structure in the digestive tract that aids in digestion and water retention
MARSUPIAL: animals whose young develop in a pouch
NOCTURNAL: active at night

Although they are commonly referred to as "koala bears" because of the resemblance to teddy bears, koalas are not bears. The koalas are marsupials. This is one of the oldest classes of animals, existing since over fifty thousand years ago. Koalas average about twenty-six pounds in weight and thirty-one inches in length. The coat of the koala is the thickest among the marsupials and has a gray to tawny color. White coloration appears on the chin, chest, and forelimbs. The fur is short, soft, densely packed, and springy to the touch. It is the most effective fur insulation among animals. The koalas do not rely on fat beneath the skin for insulation; rather, blood flow to the extremities can be reduced as a means to conserve heat. In the rain, water runs off the koala's fur. Only sick koalas will appear to be wet when it rains.

Koala Life

Koalas are nocturnal and highly arboreal, living solitary lives high up in eucalyptus trees. Koalas are known as phalangers, because they use their hands and hind feet to effectively grip tree trunks and branches when tree climbing and jumping from tree to tree. They walk with a clumsy gait in the following sequence: front right foot then back left foot, front left foot, back right foot. They have a very specialized diet, feeding almost exclusively on the leaves of a few species of eucalyptus. The leaves provide most of their water intake; in fact, the word "koala" means "no drink" in Aboriginal languages. For an average day, a koala will consume about a pound of leaves. They are very fussy



Koalas are extremely specialized feeders, eating primarily the leaves of the eucalyptus trees in which they live. (Digital Stock) eaters, typically being very careful in selecting which leaves from a bough to ingest. The koala uses a set of thirty teeth, comprising incisors, canines, premolars, and molars, to chew the eucalyptus leaves. Each day the koala spends approximately eighteen to twenty-one hours sleeping or resting.

In order to communicate, the koala uses a range of vocalizations. The male koala uses a deep, grunting bellow to communicate its physical and social position. The sound can resemble a far-off rumbling, like a motorcycle or pig snorting. During the mating season, the koala will use the bellowing as a means to locate and accurately pinpoint potential mates. The mating call is a deep, loud, guttural sound that can be heard for long distances. Female koalas do not show the same level of bellowing. Their calls communicate aggression and are part of the mating ritual. Both the male and female koalas share a similar call, sounding like a baby screaming. This is often accompanied by shaking and signals fear. Mother and cubs make soft squeaking noises to one another, as well as humming or murmuring.

Koala Facts

Classification:
Kingdom: Animal
Phylum: Vertibrata
Class: Mammalia
Subclass: Marsupialia
Order: Diprotodontia
Suborder: Vombatiformes
Infraorder: Phascolarctomorphia
Family: Phascolarctidae
Genus and species: Phascolarctos cinereus
Subspecies: P. c. victor (Victoria), *P. c. cinereus* (New South Wales), *P. c. adustus* (Queensland)

Geographical location: Two main groups living out in the wild are in eastern Australia in an area extending from Cooktown in northern Queensland to southwestern Victoria; have been introduced into western and southern Australia

Habitat: Wild eucalyptus forests and woodlands; they are found only in pockets with suitable vegetation of a relatively small number of eucalyptus species that they prefer to ingest

Gestational period: Thirty-five days

Life span: Thirteen to eighteen years

Special anatomy: Females have a pouch that faces the rear and has a drawstring type muscle which can be tightened to close the opening; mammary glands are located along the abdomen within the pouch; females have a duplicate reproductive system with two vaginas; males have dual-pronged, forked penises; each hand has two opposable thumbs, which are crucial for the ability to climb and cling to trees; digestive system includes a caecum, a structure used to digest eucalyptus leaves and assist in water extraction

Koala Reproduction

Females of the species have a pouch in which the young develop. The young are born in nearly embryonic form about the size of a human's little finger. After birth, the infant travels to the mother's pouch, where it attaches to teat. The teat then becomes engorged and forms a seal with the newborn. A single offspring is usually born. It is not until twenty-four weeks after birth that the young is covered with fur and develops teeth. The first six months of life are spent in the mother's pouch. The cub remains with the mother until about twelve months after birth. Mating is a brief event that takes place about once a year. Male koalas are nomadic and play virtually no part in the raising of the young. Extensive chlamydia infection has caused widespread infertility in female koalas and is a major contributing factor in their declining numbers.

—Frank J. Prerost

See also: Embryology; Fauna: Australia; Fertilization; Kangaroos; Marsupials; Opossums; Pregnancy and prenatal development; Reproduction; Reproductive strategies; Reproductive system of female mammals.

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LACTATION

Type of animal science: Reproduction
Fields of study: Biochemistry, developmental biology, embryology, physiology

Lactation is the process by which female mammals produce milk for the nourishment of their offspring. For all species except humans, successful lactation is essential for the survival of the young.

Principal Terms

ALVEOLI: the milk-producing areas within the mammary glands

COLOSTRUM: the precursor to milk that is formed in the mammary gland during pregnancy and immediately after birth of the young

DUCTS: the tubular structures that carry milk from the alveoli to the outside through the nipple or teat

LACTATION: the process of producing and delivering milk to the young; also, the time period during which milk is produced

MAMMARY GLANDS: the milk-producing glands found in all mammals; for example, the cow's udder contains the mammary glands

MILK EJECTION: also known as milk letdown, this is the reflex response of the mammary gland to suckling of the nipple; the hormone oxytocin mediates this reflex

MYOEPITHELIAL CELLS: the specialized cells within the mammary gland that surround the alveoli and contract to force milk into the ducts during milk ejection

NIPPLE: the raised area on the surface of the skin over the mammary gland that contains the duct openings

TEAT: an elongated form of nipple that contains one duct opening

Lactation is the process by which female mammals produce milk to feed their young. The ability to produce milk is one of the defining characteristics of the class Mammalia: All mammals, but no other animals, possess the highly specialized glands necessary for lactation. In evolutionary terms, the appearance of lactation coincides with the tendency of mammals to produce only a few offspring at a time; the provision of milk for these offspring helps to ensure their survival while removing competition between the adults and the young for food.

The Mammary Glands

The mammary glands are the milk-producing organs. The number varies among species from two to about twenty, with a rough correlation between the number of young born and the number of glands present. The glands are located on the ventral surface of the body, either in the thoracic (in humans, for example) or abdominal region (in horses and cows) or in two lines extending almost the length of the body (in dogs and rodents). Both male and female mammals have mammary glands, because in early mammalian development the basic body plan of male and female embryos is identical. The mammary glands of males are nonfunctional, however, since they lack the hormonal stimulation necessary for lactation.

Internally, the mammary glands of all mammals follow the same basic plan, consisting of alveoli that produce milk and ducts that carry the milk to openings on the surface of the skin. The alveoli are surrounded by myoepithelial cells that contract to squeeze the milk into the ducts during suckling by the young.

Externally, considerable variation exists among the mammals in the appearance of the mammary glands and their associated openings. In the spiny anteater and platypus, the many lobes of the mammary glands each open directly to the surface of the abdominal skin through individual ducts, and the young suck the hair-covered skin to obtain the milk. In other mammals, the mammary glands are more obvious as swellings beneath the skin, with a raised area, the nipple or teat, that contains the duct openings. In some four-legged animals (cows, horses, and goats) the mammary glands are located in a baglike structure called the udder, from which are suspended the elongated teats. In humans, the nipple, which contains the openings of fifteen to twenty-five ducts, is surrounded by pigmented skin, the areola. The areola contains glands (tubercles of Montgomery) that secrete a lubricating fluid.

Milk Production

Lactogenesis (milk production) does not begin until a female has produced young. During pregnancy, a complex of hormones prepares the mammary glands for milk production by promoting their growth and internal development. These hormones include prolactin from the mother's anterior pituitary gland, placental lactogen from the placenta within the uterus, and estrogen and progesterone, which are produced in the corpus luteum of the mother's ovary and in the placenta. Other hormones, including cortisol from the adrenal gland, thyroxine from the thyroid gland, and insulin from the pancreatic islets, may also be involved. Progesterone appears to participate in the induction of mammary development, but, paradoxically, it also prevents milk secretion during pregnancy.

Although true milk is not produced during pregnancy, a precursor to milk, colostrum, can be produced in small amounts by the mammary glands of most species. Colostrum is a sticky, yellowish, transparent liquid. Colostrum secretion continues in the first few days after birth of the young; there is then a gradual transition to production of true milk.

Milk contains water, proteins, fats, vitamins, minerals, and a unique sugar, lactose. The exact concentration of the various components varies greatly between species according to the nutritional demands of the young. The milk of seals is high in fat and other solids that contribute to rapid weight gain in the pups, a strategy that appears to be essential for their survival.

Noteworthy among the constituents of milk are antibodies produced by the mother. These antibodies help protect the newborn from disease in the period when the newborn's own immune system is immature and incapable of providing significant defense. The antibody concentration of colostrum is higher than that of true milk, and for this reason the first few days of nursing are considered the most important for immunological protection of the newborn.

The transition in production from colostrum to true milk is brought about by a change in the hormonal status of the mother. At the time of birth, the placenta is expelled from the mother's body, thus removing the source of progesterone, estrogen, placental lactogen, and other hormones. The decrease in progesterone levels is thought to be essential for the onset of lactogenesis. In addition, at the time of birth, there are changes in prolactin secretion that may play a role in initiating milk secretion.

Suckling

Once lactogenesis is established, a set of hormonal reflexes act to match milk production and delivery to the needs of the newborn. Suckling of the nipple involves motions similar to chewing as the infant takes the nipple between the tongue and the palate. This suckling motion stimulates nerve endings in the mother's nipple that relay signals about the stimulation back to the mother's brain. Within thirty to sixty seconds, these signals result in the release of prolactin from the mother's anterior pituitary gland and oxytocin from her posterior pituitary gland. Prolactin causes continued production of milk by the alveolar cells of the mammary glands. Oxytocin acts immediately on the myoepithelial cells of the mammary gland, causing them to contract and push milk from the alveoli into the ducts and thence through the nipple into the infant's mouth. Thus, the infant does not actually remove milk from the mammary gland by suction, but instead is responsible for promoting a hormonal reflex that results in active milk ejection, or letdown, from the mammary gland.

Because of the operation of the prolactin and oxytocin reflexes during suckling, lactation is a biological example of the principle of supply meeting demand. All that is necessary to increase milk production is to increase the suckling stimulus by nursing the young more often. Once established, lactation in some species can be sustained in this manner for years, assuming the nutritional needs of the mother are met. On the other hand, if the mother fails to nurse her offspring, the absence of the suckling stimulus will cause the mammary glands gradually to cease milk production.

The exact composition of the milk is altered as lactation continues to meet the changing nutritional needs of the growing offspring. The most extreme example of the ability of the mammary gland to change the composition of milk is seen in the kangaroo. In this animal, the newborn attaches to a teat in the mother's pouch shortly after birth and remains there for a month or more. A mother kangaroo may nurse offspring of different ages from separate teats, and each teat supplies a milk with the appropriate nutritional composition for that young.

Species vary in time spent suckling the young. The rabbit nurses her litter for only about five minutes once a day, while the rat nurses for about half an hour at a time, at intervals throughout the day. Lactation lasts about ten days in rodents, but it may persist for months in large species such as horses and cows. Continued lactation has a suppressive effect on ovulation that is thought to be attributable to interference by prolactin with the normal hormonal mechanisms that cause ovulation.

The Study of Lactation

Although it has always been clear that milk is expelled from the mammary glands, the realization

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that the glands themselves actually produce the milk is a relatively recent one. Early anatomists erroneously assumed that milk must be a product of the uterus, since the uterus is involved in support and nourishment of the fetus. Thus, much of the early anatomical work attempted to show some sort of connection between the uterus and the mammary glands. It was not until the late 1800's that the light microscope clearly demonstrated that milk is formed within the mammary glands. In the twentieth century, electron microscopy showed that during pregnancy the intracellular organization of the alveoli becomes increasingly more complex as the cells become capable of milk secretion.

Various techniques for labeling compounds with radioactive or fluorescent markers have been used in conjunction with electron microscopy to examine how milk is synthesized in the alveoli. The alveoli cells extract necessary precursors from blood flowing through the mammary gland, assemble the precursors into milk components, and then secrete the constituents of milk into the mammary gland ducts. Specific routes of secretion have been identified for the major components of milk.

More recently, researchers have used cell-free systems to study the biochemical pathways involved in milk synthesis. These systems use isolated fragments of deoxyribonucleic acid (DNA), ribonucleic acid (RNA), and perhaps some cell organelles to examine the intermediate chemical steps in the synthesis of milk components. Using these techniques, researchers have been able to "watch" as complex milk proteins and constituents are assembled step by step. The knowledge of how the components of milk are assembled is leading to a fuller understanding of how the amounts of these substances in milk are hormonally regulated.

Knowledge of the hormones involved in inducing and maintaining lactation has come about through systematic assembly of information from several lines of research. Test animals can be treated with a specific hormone to determine if that hormone causes or suppresses lactation. The test animals may be males or immature females, with the goal being the duplication of the specific mix of hormones that cause lactation in the adult female. The opposite approach may also be taken: An endocrine gland can be removed from a lactating female to determine if the hormonal products of that gland are necessary for lactation. Another approach is to make careful measurements of the levels of hormones circulating in the blood as the lactational state changes; any hormone that shows a correlated change may be a good candidate for further investigation by treatment or removal from test animals. These methods have led to an understanding of the importance of prolactin, placental lactogen, oxytocin, estrogen, and progesterone in promoting lactation, but researchers still do not understand how the system is fine-tuned. For example, considerable variation exists in the volume and quality of milk produced by different individuals—or by the same individual at different times—but these differences cannot currently be explained by any known change in hormone levels. Research is focusing not only on describing changes in circulating levels of hormones but also on elucidating the exact effects of these hormones on the biosynthetic pathways within the mammary gland.

—Marcia Watson-Whitmyre

See also: Birth; Digestion; Endocrine systems of vertebrates; Hormones in mammals; Ingestion; Mammals; Nutrient requirements; Offspring care; Placental mammals; Pregnancy and prenatal development; Reproductive system of female mammals; Sexual development.

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LAKES AND RIVERS

Types of animal science: Classification, ecology, reproduction
Fields of study: Anatomy, ecology, zoology

Lakes and rivers are large bodies of water produced by the hydrologic cycle. Lakes are stable bodies of water surrounded by land, while rivers are moving bodies of water flowing downhill toward oceans. They comprise important, animal-rich ecosystems.

Principal Terms

CARNIVORE: any animal that eats only the flesh of other animals

COURSE: the pathway of a river from its source to its entry into an ocean

ECOSYSTEM: an ecological community, which together with its environment is perceived as a unit

EROSION: the processes, including weathering, dissolution, and abrasion, by which earth or rock is removed from a part of earth's surface

ESTUARY: part of river's lower course, near entry to an ocean, where slow river flow and tidal action forms mud flats and sand banks

HYDROLOGIC CYCLE: earth's cycle of evaporation and condensation of water, which produces rain and maintains oceans, rivers, and lakes

LAKE: a large area of water surrounded by land

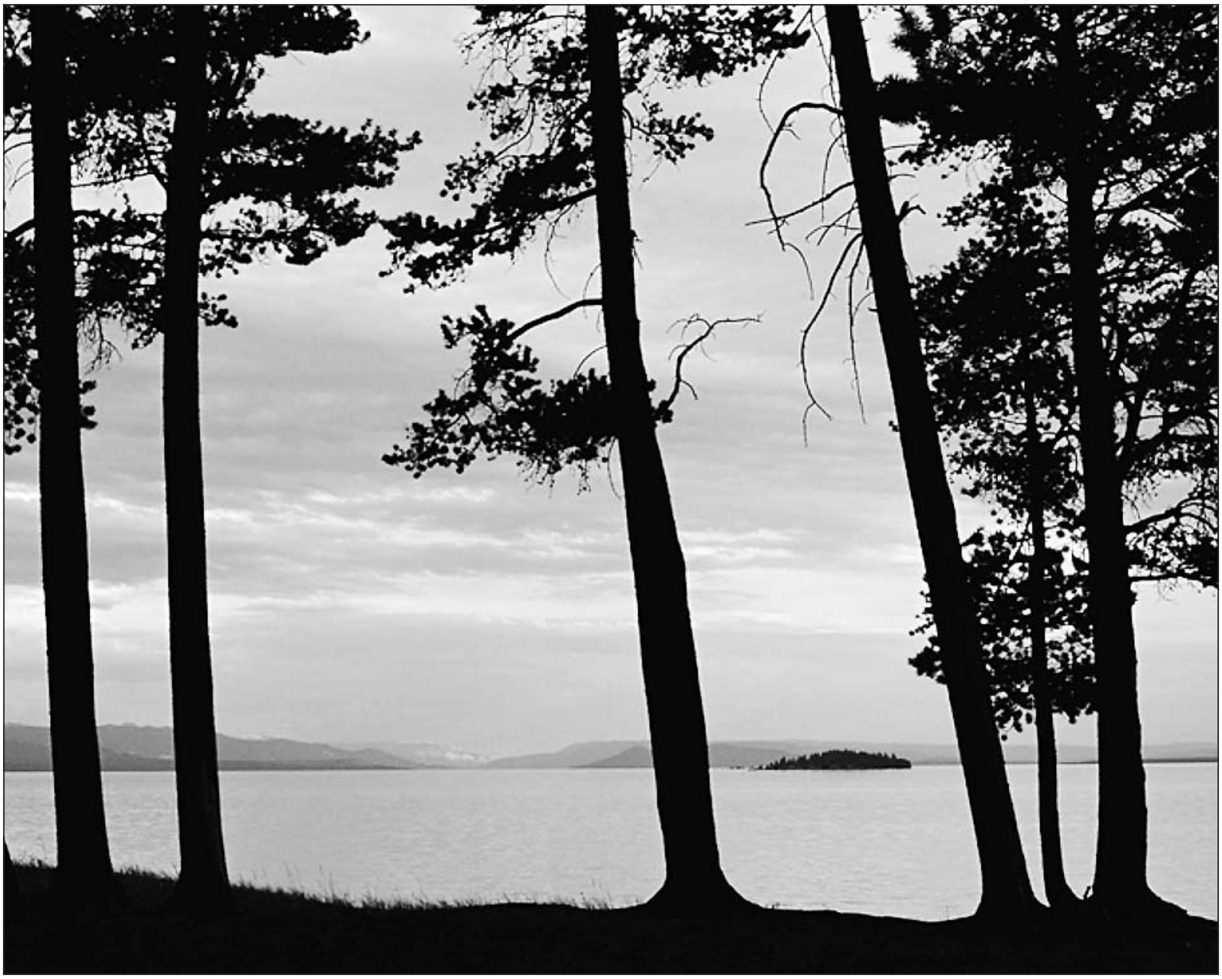
A lake is a large body of water surrounded by land. Lake waters move, partly due to rivers that enter and leave them. In addition, lake water circulates vertically, especially near its surface, where sunlight heats the water and lowers its density. Seasonal warming and cooling of water, evaporation, and other factors contribute to annual cycles of vertical lake water movement.

Most lakes form in hollows dug out of the ground by glaciers. Some huge lakes are really inland seas (such as the North American Great Lakes). Lake water is supplied by rivers and accumulated from rain draining off nearby land. River water contains minerals obtained by running over rocks, and rain holds airborne chemicals. Continued water flow through a lake keeps it fresh, enabling animal and plant survival. When water does not flow out of a lake, minerals are trapped and concentrated, as solar heat evaporates water. In time, salt accumulation turns such lakes into bodies of salt water (such as the Dead Sea, ten times saltier than the oceans) in which few organisms can live.

Animals Found in Lakes

Lakes provide rich habitats for many kinds of wildlife. They are also excellent examples of ecosystems, self-contained ecological units wherein all plants and animals present depend on each other for survival. Removing or damaging one plant or animal species can cause a chain of events that affect, even ruin the ecosystem.

Land beside a lake is usually marshy. Rushes, reeds, willow, and alder trees, as well as water lilies, grow in the shallows around a lake edge. The plant roots prevent lakeshore erosion. Farther from shore are submerged and floating plants which produce oxygen and provide food for small underwater animals such as insects, insect larvae, snails, shellfish, and worms. These small animals are eaten by fish, which are then eaten



Lakes offer rich habitats for complex ecosystems comprising organisms that live on both land and water. (Digital Stock)

by birds. Land mammals, such as martens and bears, also eat the fish. Overall, lake plants and animals make up a food chain that supports the lake ecosystem.

A great number of animals inhabits lakes and live around them. Animals present vary greatly depending on the lake's geographic location. For example, birds, which usually eat fish and aquatic insects, inhabit lakes throughout the world. Lake-dwelling bird species range from ducks, geese, and loons in Canada's cold lakes, to ducks, kingfishers, and herons throughout the United States, to the flamingos of the southern United States, Central and South America, and Africa. Marabou storks and other carrion eaters also inhabit African lakes.

Flamingos may be among the most dramatic of lake-dwelling birds. There are six species of these gorgeous water birds, which have long legs for wading, webbed feet, swanlike necks, and red, flame-colored, pink, or white feathers. Their bills bend abruptly in the middle and the upper mandible fits tightly into the lower one. Flamingos dip their heads upside down under water and scoop backward to feed. Their bill edges have ridges, and when the tongue pushes against the inner bill, the water runs out, leaving behind shellfish or other food. Flamingos live along lakes in nests made of mud, hollow on top, and able to hold one egg. The largest species, the greater flamingo, has two subspecies, one bright red, the other pale red. Males reach five feet tall. The smallest, most abundant species is the lesser flamingo.

Reptiles such as snakes and salamanders, amphibians such as frogs, and many turtle species are also present in lakes. Depending on size, they eat insects or each other, and are themselves eaten by birds. Many different fish species are also present, from minnow to sunfish to trout. They are parts of food chains, eating insects, plants, small reptiles, and each other, depending on size.

River Animals

Only animals adapted to cold, fast-flowing water survive in the upper courses of rivers, which are fine habitats, clean and full of oxygen. Some plants survive, but limpets, snails, and hardy water insects are preponderant. They become foods for the carnivorous fish, such as trout and salmon, found in rivers' upper courses.

The current slows along a river's middle course, and sediment settles to the river bed as earth and rock particles holding minerals on which plants thrive. These plants, from microscopic algae up, are used as food by wildlife inhabiting river banks, such as otters, martens, and raccoons, as well as fish and other animals which live in river waters. Small fish and insects, such as water striders, dragonflies, and aquatic beetles, are plentiful in the water. Reeds and trees are also homes and nests for birds of many kinds, as well as small to medium-sized mammals, such as rodents and skunks, snakes such as water moccasins, and other reptiles.

Depending on location, the size and danger associated with middle course river-animal life varies. However, food chains in rivers also assure continuation of the balance of nature, as small plants and animals are eaten by medium-sized animals and those creatures are, in turn, eaten by bigger animals. The largest, most dangerous river animals are found in the hot southwestern United States, Central and South America, Africa, and Asia.

Crocodiles, alligators, and caimans are among the most dangerous river animals. They are all crocodilians, differing in size, position of the fourth mandibular tooth, and snout shape. Crocodiles have lizardlike bodies up to twenty-five feet

Rivers

Roughly 70 percent of Earth's surface is covered with water. About 97 percent of this water is salt water in oceans, and 2 percent is freshwater in glaciers and groundwater. Only 1 percent is freshwater in rivers, lakes, and water vapor. Freshwater is recycled again and again by evaporation and condensation in a hydrologic cycle which creates and maintains rivers and lakes.

When water vapor condenses and falls as rain, it seeps into the ground, filling pores in soil and rocks. After all pores fill, excess water pools on the surface, flowing downhill due to gravity. Then it becomes streams that coalesce into rivers. Each river is a large body of water, regenerated over and over by the hydrologic cycle, flowing through low ground areas that become channels (river courses) and valleys. Because Earth's oceans are lower than the land, rivers flow down into them.

A river and the composition of its banks change as movement toward the ocean both creates and destroys land. A river's course has upper, middle, and lower parts. The upper course, near the river's source, flows downhill and carves deep valleys, as well as waterfalls wherever tough rock resists erosion. Next, the river flows onto plains in its middle course, and the gently sloping land slows it, leading to sideways erosion and snakelike bends. The last part of a river, its lower course, near entry to an ocean, is often an estuary. Here, the slow flow of the river across virtually flat land causes settling of sediment, forming mud flats and sandbanks.

long, with short limbs, long, thick tails that facilitate swimming, huge teeth, eyes atop their heads, and short, broad snouts in which the fourth mandibular teeth are visible. They are cold-blooded and inhabit salty, brackish, and fresh water in Africa, Australia, Asia, the Indies, and the Americas. They are carnivores, eating birds, amphibians, fish, mollusks, crustaceans, small mammals, and large mammals ambushed while drinking. Crocodiles mate in the water. After two-month gestation periods, females lay eggs on land. The eggs hatch in three months. Crocodiles can live for up to one hundred years.

Alligators, physically and reproductively similar to crocodiles, are only up to sixteen feet long. Their fourth mandibular teeth are hidden by their upper lips, they are more comfortable on land than crocodiles, and they have short, broad snouts. During the day, alligators sun themselves on river banks in the southeastern United States, China, and Central and South America. Caimans of Central and South America are small alligators, only up to eight feet long (although the black caiman can be twice as large). They inhabit rivers and swamps. Alligators and caimans live for forty-five to sixty-five years.

The largest river mammal is the herbivorous African hippopotamus, which can reach lengths of fifteen feet and body weights of four tons. All sorts of fish live in rivers, including minnows, catfish, sunfish, bass, trout, and river dolphins. Most such fish are not very dangerous to organisms other than their specific prey. However, the carnivorous piranha of South American rivers eat any animals that stray into their territory.

Many wild animals found in a river's middle course are even more plentiful downriver in its lower course, where the current is quite slow. However, in estuaries, which are salty due to the admixture of ocean water with the river's freshwater, few plants and animals can survive. There, worms, crustaceans, and gastropods such as snails inhabit mud banks and provide food for birds such as herons, gulls, and kingfishers.

River Ecosystems

Rivers contain series of ecosystems whose compositions vary with conditions in a given portion of the upper, middle, or lower course. In river ecosystems, like those in and around lakes, all plants and animals depend on each other for survival, and removing or harming one species can ruin the ecosystem. Beyond this, existence of multiple ecosystems on land and their connection to aquatic ecosystems points out that damage to any living organism or its local ecosystem will have ripple effects, which can spread out to damage much wider areas than at first perceived. Hence, reasonable actions of humans toward all other living organisms should be attempted and achieved.

—Sanford S. Singer

See also: Ecosystems; Food chains and food webs; Forests, coniferous; Forests, deciduous; Habitats and biomes; Marine biology; Rain forests; Tidepools and beaches.

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LAMPREYS AND HAGFISH

Type of animal science: Classification
Fields of study: Anatomy, evolutionary science, physiology, systematics (taxonomy), zoology

Jawless vertebrates, or Agnatha, are represented today by the lamprey and hagfish. These organisms are of great interest as the survivors of a once-flourishing group of Paleozoic vertebrates that includes the earliest vertebrates in the fossil record.

Principal Terms

AGNATHA: a class of vertebrates that includes all forms in which jaws are not developed; the group to which the earliest vertebrates belong

AMMOCOETE: the larval form of lamprey, which lives in river silts

CLADISTICS: a method of determining relationships in which shared derived (advanced) characters exhibited by the organism are used

CYCLOSTOMES: the modern agnathans, comprising lampreys and hagfish

GNATHOSTOMATA: all vertebrates in which jaws are developed

NASOHYPOPHYSIAL OPENING: an opening in the head of modern agnathans leading to a sac that aids in olfaction

OSTRACODERMS: armored fossil agnathans that flourished during the Paleozoic

PALEOZOIC ERA: time period from 570 to 245 million years ago, which comprises the Cambrian, Ordovician, Silurian, Devonian, Carboniferous, and Permian periods

The vertebrates are normally divided into two groups based on the presence or absence of jaws. The vast majority possess jaws and are termed Gnathostomata; jawless forms are termed Agnatha. The Agnatha are represented today by the lampreys and hagfish, organisms of little economic importance but of great interest to biologists as the sole survivors of an extensive group of Paleozoic (245 to 570 million-year-old) agnathans, which includes the earliest known vertebrates. The extant forms are often referred to as the cyclostomes, the fossil forms as ostracoderms; however, these do not constitute monophyletic groups (groups including the common ancestor and all descendants), and some fossil Agnatha are closely related to cyclostomes.

The Physiology of Jawless Fishes

Lampreys and hagfish are similar in general appearance despite far-reaching differences in internal organization. Both are elongated fish, without paired fins, that swim with an eel-like motion and reach lengths of one meter and weights of up to one kilogram. They possess an entirely cartilaginous skeleton; however, the organization of the body conforms to the basic vertebrate pattern. The lamprey has more active life habits and, therefore, has a more developed median fin. The propulsive section of the tail is longer than that of the hagfish. The lamprey's mouth is surrounded by a sucker-like oral disc covered by small teeth on its internal surface. This rasping organ allows the lamprey to attach itself to prey, on which it feeds by rasping away surface tissues and ingesting blood. Above and behind the oral disc is the nasohypophysial opening, which leads into an olfactory pouch and ends blindly in a dilated sac above the anterior gill pouches. Lampreys have seven gill pouches opening through seven gill ports.

In hagfish, the mouth is ventral and overhung

Image Not Available

by a rostrum, and it contains a dental plate that can be rapidly retracted, enabling the animal to bite off fragments of tissue from the dead and decaying fish on which it feeds. The nasohypophysial duct passes backward below the brain to join the pharynx, and the respiratory current passes along it. Hagfish are quite variable in their number of gill pouches and openings. Pacific hagfish have twelve pouches with separate openings (this number may vary up to fifteen), while Atlantic hagfish have five pouches with one common opening. The eye is vestigial and covered by surface tissue, so it is not normally visible.

Lampreys

There are about thirty-five species of lampreys, and all breed in freshwater and spend the major part of their life cycle in a freshwater larval stage before transformation to an adult stage. The eggs develop into a blind larval form, the ammocoete, which burrows into silt banks and remains for several years filtering microscopic particles from the water. The ammocoete is very unlike the adult, as no suctorial disc is present; a ciliated groove on the floor of the pharynx, together with a tubular endostyle, forms the feeding apparatus. After metamorphosis, three different types of adult lamprey are known: nonparasitic brook lampreys; freshwater parasitic forms; and anadromous forms (living in marine conditions but ascending rivers to spawn). The nonparasitic forms, which constitute about half the known genera, have the mechanisms for parasitic feeding but do not use them. The gonads mature immediately after metamorphosis, the intestine atrophies, and the foregut remains as a solid rod. These nonparasitic forms remain dwarf as they cannot feed, and six to nine months after metamorphosis they reach sexual maturity, spawn, and die.

The parasitic freshwater forms live entirely in river systems, where they feed on fish. The anadromous forms move downstream to the estuary or sea after metamorphosis. There, they feed voraciously and grow rapidly, eventually returning to the river on an upstream spawning migration after one to three years. As in all lampreys, death follows shortly after spawning. In some cases, it appears that populations of originally anadromous lampreys may have become landlocked and are now entirely freshwater. That is what appears to have happened with the lampreys (*Petromyzon marinus*) that now inhabit the Great Lakes. They are capable of causing significant damage to fish populations and almost eradicated trout and whitefish from the Great Lakes between 1950 and 1960, when they peaked in that system, resulting in the collapse of a flourishing fishery.

Hagfish

Hagfish are purely marine fish, in contrast, and as they are benthonic (live on the bottom) and often inhabit deep water, little is known of their reproductive biology beyond the fact that eggs may be laid at any time of year and there appears to be no larval stage. They remain buried in mud during the day, emerging at night to feed. It appears that they normally attack only dead or dying fish, lacking the suction apparatus that makes the lamprey so successful in its attacks on living organisms; however, they will consume small invertebrates if they are available. When feeding, they may show "knotting behavior," during which the flexible body ties into a knot in order to gain a better purchase for the tearing off of food fragments. One characteristic of all twenty species of hagfish is the development of mucus pores along the body. If roughly handled or irritated, these pores produce copious quantities of mucus, resulting in the name "slime eels" for these animals. Neither hagfish nor lampreys are of more than local economic importance.

The Fossil Record

The fossil record of hagfish and lampreys is sparse, presumably because of the lack of an ossified endoskeleton. Both are known only from the Pennsylvanian period (280 million years ago) of Illinois and show close similarity to modern forms. These sediments also include two other agnathans of unknown affinities, indicating a wide diversity of forms of this type. There is, however, an extensive record of armored agnathans (ostracoderms) from rocks of Ordovician to Devonian age (360 to 470 million years old). These have been divided into two main groups, the Osteostraci and the Heterostraci, together with some smaller groups.

The Osteostraci were a group of fish that lived in the Silurian and Devonian periods (370 to 425 million years ago) and were characterized by the presence of an armored head-shield, the rest of the body being covered by large bony scales. The large eyes were dorsally placed, and between them were the pineal foramen (an opening for a light-sensitive organ) and the nasohypophysial opening. Located laterally on the head-shield were sensory fields that probably were sensitive to pressure waves in the surrounding water. The ventrally placed mouth and dorsoventrally flattened head indicate that the Osteostraci were benthonic fish, possibly feeding by sucking organic debris or small organisms into the mouth. Paired pectoral fins may have acted to move the animals by rhythmic undulations. Because the head-shield surrounded the brain, a considerable amount of detail of brain structure and cranial nerve pattern has been preserved. It has shown that the general pattern was very similar to that of the lamprey, implying a close relationship.

The Heterostraci were a long-ranging group whose earliest representatives occurred in the Middle Ordovician period (470 million years ago) and represent the first known record of vertebrates. Typical Heterostraci were armored over the anterior part of the body by variable numbers of bony plates and were further characterized by having only one pair of external gill openings. They were common in shallow marine and freshwater environments during the Upper Silurian and Devonian periods (360 to 425 million years ago) but became extinct at the end of the Devonian. They seem to have been adapted to a variety of modes of life, from benthonic detritus feeding to cropping algae and filter feeding. The Ordovician forms are known from rocks in North and South America and Australia and are united with later Heterostraci by the presence of the same type of acellular bone, aspidin, in the armor. Their exact position is uncertain, however, as they do not appear to have a series of branchial (gill) openings on each side.

Although it is clear that the Osteostraci were closely related to modern lampreys, no relationship has been determined yet between hagfish and any ostracoderm group. The relationship of the fossil and modern agnathans to gnathostomes is also still the subject of considerable debate, though in broad terms it is accepted that lampreys are the sister group of gnathostomes and hagfish the sister group of lampreys and gnathostomes. Much further information is needed before the details of their phylogeny can be elucidated, and continuing work on these organisms will aid understanding of both the origin of vertebrates and the early development of major vertebrate groups.

The Ichthyology of Jawless Fishes

Fish are generally excellent subjects for study and for the demonstration of anatomy, physiology, ecology, evolution, and other aspects of science. The detailed anatomy of the cyclostomes has been known for many years, and knowledge in this area is dependent on careful dissection of specimens. General knowledge of the life cycle, ecology, and feeding habits of the modern forms is based on observation either in the natural habitat or in aquariums. As lampreys spend most of their life cycle in freshwater, understanding of their development is fairly complete. Hagfish, however, are marine benthonic fish that move and feed mostly at night, and hence the ability to observe them is somewhat limited and understanding of their life cycle is incomplete. Sophisticated laboratory techniques now make it possible to analyze the biochemistry and physiology of these organisms and compare them to other chordates. Studies have also been made of their swimming methods, using high-speed cameras and electromyography, a technique that allows the tracing of the electrical changes that take place in muscles when they are active.

Fossil Agnatha cannot be studied as completely, because only the hard parts are preserved in the sediments. Techniques for studying these remains have changed very little in the past one hundred years. The bones are removed from the rock by chipping or dissolving the surrounding sediment away. Bone is composed of calcium phosphate and thus will resist some acids that can break down carbonate rocks. The acids most commonly used are acetic acid and formic acid, and the specimen to be dissolved out is often backed with plastic so that it does not disintegrate when the supporting matrix (surrounding sediment) is removed. The bone from these ancient agnathans is often so well preserved that thin ground sections can be made and viewed through a microscope using transmitted light.

The characters determined by these means are used to determine relationships. Studies on the relationships of the fossil and recent Agnatha have relied in recent years on the methodology termed "phylogenetic systematics," or "cladistics." Cladistics is distinguished from other taxonomic methods (taxonomy is the study of interrelationships) by the fact that it is a rigorous system in which only shared advanced characters are used to show relationships. These relationships are expressed as branching diagrams termed cladograms (from the Greek *klados*, "branch"), hence the name cladistics. Although studies using this methodology have improved understanding of the relationship between modern Agnatha and the gnathostomes, the relationships of the fossil forms are still poorly understood.

Modern Jawless Fishes

Modern Agnatha, or cyclostomes, are relatively rare and unimportant organisms, although they are representatives of a group that was important in the early history of vertebrate evolution. For example, hagfish can be a nuisance to fishermen, attacking and destroying bait and even the catch itself. Lampreys, because of their active parasitic mode of life, can be a serious menace to fisheries, as evidenced by the sea lamprey depredations in the Great Lakes. The construction of a canal bypassing Niagara Falls unfortunately allowed lampreys to enter the upper Great Lakes from Lake Ontario, where they had been established. Once in the upper lakes, they underwent a population explosion, probably as a result of the abundance of prey fishes, lack of predators, and suitability of the system for spawning and maintenance of larvae. The establishment of the lamprey resulted in a serious decline of a number of fish species and the collapse of a flourishing commercial fishery that has only been reversed by the establishment of control measures and the use of larvicides.

The fossil Agnatha, or ostracoderms, are generally poorly known as a result of their incomplete preservation. Yet they do throw some light on the earliest stages of vertebrate evolution, indicating that, as far back as 470 million years ago, humankind's earliest ancestors were small, rather tadpolelike fish with an external armor of bony plates. Although they appear in the fossil record before the earliest jawed vertebrates, or gnathostomes, it appears that the separation into jawed and jawless forms had already occurred. Many gaps remain, but it is to be hoped that further discoveries will enable humankind to develop a clearer picture of its earliest vertebrate ancestry.

—David K. Elliott

See also: Amphibians; Chordates, lower; Evolution: Historical perspective; Extinction; Fish; Gill, trachea, and lung anatomy; Invertebrates; Marine animals; Marine biology; Reptiles; Symbiosis; Systematics.

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LANGUAGE

Type of animal science: Behavior
Fields of study: Evolutionary science, human origins

The origins of human language and animals' communicative abilities help to achieve an understanding of humans' position in the natural order of evolution.

Principal Terms

CLOSED-CLASS VOCABULARY: typically including the structural and functional words, such as prepositions, determiners, quantifiers, and morphological markers, closed in the sense of resisting the introduction of new members

DISPLACEMENT: language's power to refer to or describe things and events beyond the constraints of the here and now

GRAMMAR: the structure of a language, consisting of systematic rules to specify word formation, such as inflection, derivation, and compound words (morphology), and systematic rules to specify how words should be ordered in combination to form phrases and sentences (syntax)

OPEN-CLASS VOCABULARY: content words such as nouns, verbs, and adjectives, open in the sense of its readiness to admit new members

PRODUCTIVITY OR GENERATIVITY: language's power to produce or generate an infinite number of understandable words and sentences from a finite number of symbols and rules

SEMANTICITY: meaning in language

SYMBOL: something that stands for something else, the connection between symbol and object being arbitrary in nature

One way to understand humans' position in the natural order of evolution is to locate the origins of language. Some scholars think that language is probably the product of the "mental mutation" of the large brain of *Homo sapiens*, because human language is the only animal communicative system that possesses all of the fundamental characteristics of arbitrary symbols, semanticity, grammar, productivity, duality of patterning, and displacement. Furthermore, human children are able to become effective users of such complex symbolic systems without formal teaching and within a fairly short period of time, in striking contrast to the limited expressions of animals, even after lengthy and extensive training. Linguist Noam Chomsky, for example, has proposed that human beings have a unique language forming capacity and human babies are innately equipped with a "Language Acquisition Device," which resides somewhere in the brain.

Many others, however, disagree with this discontinuity theory of the human language origins. Instead, they argue for an evolutionary ground (neuroanatomical, behavioral, cognitive, social, and cultural) to cultivate language formation. They believe that language is no exception from the governing of the law of evolution. For example, Philip Lieberman rejects the existence of linguistic genes or a language organ in the human brain. Rather, language had its first sprout at the intersection of the evolutionary products of neural mechanisms, communication, and cognition. These are the two main theories of language origins. The first line builds on the protolanguage theory, the second on the notion of behavior determinism in evolution.

Protolanguage Theory

"Protolanguage" means that utterances are not yet full language, although they serve symbolic referential and other communicative functions. The telegraphic speech of toddlers (such as "Mommy cookie!") has been used as an example. A "baby talk" was formed first, only to be shaped and refined later into a full language. It was hypothesized that modern speech could have been possible about 100,000 years ago, when the earliest *Homo sapiens* started to migrate from Africa to other places. John McCrone reasons that toolmaking and tool use, moving in troops to other regions, and collective hunting called for more group actions, which in turn promoted social interaction. These activities required joint attention and intentional communication. Using eye contact and gesture to direct attention as a means beyond reflexive behaviors to achieve joint attention might thus have been a major step toward human speech. The prolonged period for taking care of dependent human infants, a consequence of brain growth, afforded opportunities to cultivate the intimacy between mother and child. Meanwhile, social ties in a colony began to form. All these changes might have encouraged what could be called personalized noises. To meet their communicative needs, early *Homo* species were pressured to refine and stabilize their coarse communicative noises into protowords. These protowords were then passed down to the next generations. Practice of such vocalizations in turn further promoted vocal structure refinement.

The evolutionary principle of economy and efficiency was at work, so that concept categories (words) and combinatorial rules (grammar) were naturally selected, because words and grammar are far more cognitively economic and efficiently generative than mechanical one-to-one referential associations. Martin Nowak and David Krakauer, based on their mathematical and computational modeling using computer simulations, have contended that protolanguages can evolve in a nonlinguistic society. At first, signal-object associations were established, and later, combinations of sounds to form words and combinations of words to form sentences evolved into semantic and syntactic systems through natural selection to reduce mistakes in communication.

In addition to the supportive results of computer simulations, other empirical evidence came from studies involving primates and human children. In Leavens and Hopkins's study, 115 chimpanzees (*Pan troglodytes*) in captivity (aged three to fifty-six years), without any explicit training whatsoever, commonly employed gaze alterations and a pointing gesture in face-to-face communicative interactions with humans and among themselves. This demonstrated the presence of communicative intent and gestural precursors of language among humans' closest relatives, chimpanzees. The bonobo (*Pan paniscus*) Kanzi understands spoken English sentences and knows how to use human-designated lexigrams to announce his intention, all through laissez-faire learning without explicit teaching. The chimpanzee Washoe spontaneously taught her acquired American Sign Language (ASL) to her adopted son Loulis. Human babies are like chimpanzees in many ways. As McCrone describes it, human infants are born with the standard ape vocal plan—it is after six months that the voice box descends down into the throat. Human infants first play with vowels (coo) and then babble (combining vowels with consonants)—so vocalization comes before producing true words. They also employ gaze alterations and gestures to communicate before they say words. In the second year, they produce telegraphic speech, typically composed of two to three content words, which happens to be the mode of expression in the utterances of language-trained chimps (such as "Shirt hide" by Kanzi).

Behavior Determinism

William Noble and Iain Davidson do not think that a protolanguage existed in evolution. They have also cautioned people against accepting the performance of animals in captivity and human interaction experiences as evidence to back up evolutionary arguments, because these environments are drastically different from the ecologies of the *Homo* ancestors millions of years ago. These environments are not the same as those of the free-living primates, either. Language-trained animals' performance is like language emergence in human infants, who learn through interaction with other humans who already have language, a learning process quite different from the prehistoric origins of symbols and language from scratch.

Noble and Davidson agree that natural selection favored bipedalism, leading to neuroanatomical changes including larger brains. They do not believe, however, in biological determination of behaviors. Instead, they believe the opposite. The behavior of standing upright led to larger brains that needed to consume more energy. Meat as a good energy source had already been increased in the diet of *Homo erectus*. As meat-eaters, hominids had to run fast (either to catch prey or to escape predators). Running brought about better control of the breathing system (necessary for speaking) and adjustments to the thermoregulatory system (leading to the selection of the feature "hairlessness," which could have fostered face-to-face adult-infant interaction). In addition, hunting for meat facilitated coordinated group actions as well as tool creation. To expand food sources hominids began migrating, which further promoted groups and interaction. Thus the social context was present for the emergence of language.

In their discussion, Noble and Davidson have emphasized one important behavior responsible for the emergence of language: stone throwing. To be effective, manual control and timing control had to be achieved. As the timing control behaviors were bettered, the neuroanatomical structures improved too. These positive adjustments, together with other contextual changes, led hominids on an increasingly divergent behavioral path from their chimpanzee relatives. Better control of the forearm could develop into a pointing form. Hairlessness made it easy to carry an infant hominid in front, increasing the likelihood of adult-baby mutual observation and imitation. One such likely behavior could be arm extensions for referring. Later, better-controlled movements of forearms and fingers developed into a pointing form. Any vocalizations in company with manual gestures were first associated with the referred objects, and later became symbols, once it was realized that the sounds alone could stand for the targets themselves, even when they were out of sight.

There is consensus that the human vocal structure is a necessary condition for human speech. It has been noticed that animal vocalizations are graded in nature. A graded system contains only variations of vowel sounds but no consonants. Variations of vowels, although functional in communication, lack distinctive boundaries to mark different categories. Sue Savage-Rumbaugh and Roger Lewin have concluded that language is unlikely to emerge unless an organism can produce consonants, no matter how large its brain. How the human vocal tract acquired the ability to pronounce consonants unfortunately remains a mystery.

The evolution of language must have benefited the *Homo* species tremendously. Noble and Davidson have speculated how language could have contributed to human mentality. For example, colonization in different places would cause isolated groups to have trouble in understanding each other. Such failures and misunderstandings could contribute to the awareness of "us" vs. "them." This appreciation would lead to the realization of the possibility for a group to use their own symbolic system as a means for social control. Thus, human mentality, with language in use, is itself an evolving feature of the natural world. It is only logical that, with language available, mental representation of the world became possible, which eventually made abstract, imaginary, retrospective, hypothetical, and metacognitive thinking a reality. No wonder these modes of thinking reflect themselves in the characteristics of human language.

Animal Communication

Animals do communicate, at least in a broad sense. Animals use vocalizations, facial expressions, gestures, body postures and movements, and even odors, to warn peers, to attract attention, to find food, to care for the young, to mark territories, and to maintain social structures. However, animal communicative systems are typically not recognized as language because of they lack the key features of a true language. Many have argued that animal communication, even among chimpanzees, is in essence instinctive and reflexive. McCrone says that these behaviors are not under conscious control, and are triggered only by an event in the immediate environment, with both parties present. Hence, chimpanzees have no true arbitrary symbols or displacement. In addition, animal communicative systems are "closed," with no combinatorial rules to create new meanings; hence they lack duality of patterning, syntax, and productivity. Edward Kako has pointed out that no animals so far, including the language-trained ones, have demonstrated the ability to understand closed-class lexical items. Despite the criticisms, animals' language-learning achievements have been acknowledged.

Talking Animals

The most famous talking parrot is Alex, an African gray parrot (*Psittacus erithacus*) trained by Irene Pepperberg. Alex is able to speak many words and phrases referring to objects, materials, actions, colors, shapes, numbers, and locations. He can answer questions that require labeling objects, classifying objects (color and substance), comparing objects ("bigger than" or "same as/

American Sign Language Among Primates

Primates are members of the mammalian order Primates, which includes prosimians, or lower primates, and anthropoids (monkeys, apes, and humans). Apes are any primates of the subfamily Hominoidea, including the small apes and the great apes. The gorilla (*Gorilla gorilla*) is the largest of the great apes. Another great ape is the chimpanzee. The larger member of the chimpanzee family is the common chimpanzee (*Pan troglodytes*), and the smaller member is the bonobo (*Pan paniscus*) or the pygmy chimpanzee.

To obtain an understanding of their evolutionary roots, human beings have turned to the great apes, especially chimpanzees, because they are humans' closest living relatives, sharing as much as 98 percent of identical genetic material. Many attempts have been made to teach apes to learn language. Early attempts to raise apes along with human babies in the hope that these human-reared apes would learn to speak human language ended in failure, but researchers came to realize that apes do not have the vocal structure necessary for producing human speech sounds. Enlightened by the Braille system of writing for the blind and sign language for the deaf, researchers began to employ nonverbal symbolic systems, including plastic chips (David Premack's chimp Sarah), computer lexigrams (Duane Rumbaugh's chimp Lana), and American Sign Language (ASL). This line of research has yielded interesting results. Allen and Beatrice Gardner's chimp Washoe acquired ASL, and, moreover, she began to combine words and taught her adopted son, Loulis, to use ASL. Twelve percent of the ASL utterances produced by Herbert Terrace's chimp Nim were spontaneous. Francine Patterson's gorilla Koko mastered six hundred ASL words. Through natural observation and social interaction, Sue Savage-Rumbaugh's bonobo Kanzi understands spoken English and uses sign language and computer buttons in communication.

Language research with primates creates a path for humans to search for their links to animals. There are many potential research areas, such as body language, cultural transmission of learned language over generations, and the impact of language-trained chimpanzees living with naïve peers in their natural environment, just to mention a few. On the other hand, scientists are concerned about the well-being and the rights of the primates, especially in the areas of early separation from the mother, or lab controls. Many questions have no answers yet, but one thing is certain—scientific inquiry will go on, and it will be done with good ethical concerns.

—Ling-Yi Zhou

different from”), and counting (from one to six).

Two Hawaii bottle-nosed dolphins (*Tursiops truncatus*), trained by Louis Herman and his colleagues, are Phoenix, with an acoustic language, and Akekamai (Ake), with a gesture-based language. They can correctly carry out commands in varied word orders (syntax) with different meanings. They have further demonstrated their semantic and grammatical knowledge by either not executing grammatically incorrect and semantically nonexecutable orders or by extracting an executable segment from an anomalous string and then completing the task according to the meaning provided in that specific syntactic structure.

Sue Savage-Rumbaugh’s bonobo Kanzi is an exciting language star. Kanzi understands spoken English and uses hand signals as well as geometric symbols, and moreover, he has learned all that without explicit instruction but by mere social observation and interaction, just as a human baby learns a language. This natural learning process was successfully replicated with Kanzi’s sister, Mulika.

Comparative Language Research

Research methodology in the comparative language field has been improved greatly over the years. Designation of “language” takes into consideration the biological constraints of the species involved. Social interaction in a natural way is underscored. Possible experimenters’ and trainers’ biases are controlled through blind techniques such as blindfolding the eyes of the person who gives commands, using one-way mirrors and remote cameras, or separating the person who does recording and interpretation from the one who gives the command. Recent data are thus more scientifically sound than before. Yet some people are not happy with the fact that humans have imposed their dialogue on the animals. These people are now using the playback technique to decode the meaning of the signals in animals’ own communicative systems. Many species have been studied in their natural ecological niches, including vervet monkeys, tigers, humpback whales, orcas or killer whales, and elephants. These animals’ wild calls in nature are recorded, and then are played back to the animals to see their differentiated reactions, thus making the message decoding possible. The playback studies are very encouraging in confirming the symbolic nature of animals’ natural “languages” in the wild.

It is very important to study the animal’s own “language” for its own sake, for without such knowledge, commenting on nonhuman species’ linguistic abilities in the frame of human language is at least prejudiced. As primatologist and psychologist Roger Foutes put it: “The best approach to science is a humble one. We are humble enough to take the animals we are studying on their own terms and allow them to tell us about themselves. Too often science takes an arrogant approach.” According to him, “Someday we’ll realize that the human voice is not a lone violin but part of an orchestra. We’re not playing a solo; instead it’s a symphony.”

—Ling-Yi Zhou

See also: Apes to hominids; Chimpanzees; Communication; Communities; Displays; Emotions; Ethology; Gorillas; Groups; Hominids; *Homo sapiens* and human diversification; Human evolution analysis; Insect societies; Intelligence; Learning; Mammalian social systems; Neanderthals; Pheromones; Tool use; Vocalizations.

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LEARNING

Type of animal science: Behavior
Fields of study: Ethology, neurobiology

Learning is any change or modification in behavior that involves the nervous system and cannot be attributed to the effects of development, maturation, or fatigue. Learning takes a number of forms, including habituation, sensitization, associative learning, perceptual learning, and insight.

Principal Terms

ADAPTATION: any heritable characteristic that increases the probability that an animal will survive and reproduce in its natural environment

CONDITIONING: the behavioral association that results from the reinforcement of a response with a stimulus

INNATE: any inborn characteristic or behavior that is determined and controlled largely by the genes

INSTINCT: any behavior that is completely functional the first time it is performed

NATURAL SELECTION: the process of differential survival and reproduction that leads to heritable characteristics that are best suited for a particular environment

STIMULUS: any environmental cue that is detected by a sensory receptor and can potentially modify an animal's behavior

Learning, as defined by ethologists, is simply any change or modification in behavior that is directed by previous experience and involves the nervous system but cannot be attributed to the effects of development, maturation, fatigue, or injury. These latter phenomena contribute to changes in behavior that generally do not constitute learning. Learning takes a number of forms, including habituation, sensitization, associative learning, perceptual or programmed learning, and insight. Each type has its own basic characteristics and adaptive significance. Habituation and sensitization are the simplest and most widespread forms of learning, and insight is the most complex and least understood form. Insight involves the ability to put two previous experiences together to solve an unrelated problem.

Habituation and Sensitization

Habituation and sensitization are considered the simplest forms of learning. Habituation involves a decrease in a behavioral response that results from repeated presentation of a stimulus. A young, naïve duck, for example, will exhibit an innate startle response when any hawk-shaped object is passed overhead. With repeated presentation of the hawk model, however, the intensity of the bird's reflex declines as the animal becomes habituated, or learns that the stimulus has no immediate significance. Habituation learning is common throughout the animal kingdom and has tremendous adaptive significance in that it prevents repeated response to irrelevant stimuli that could otherwise overwhelm the animal's senses and prevent it from accomplishing other critical tasks. One of the common characteristics of habituation is that after a short period, usually defined by the particular species and the stimulus in question, the animal will completely recover from the habituation experience and will again exhibit a full response to the stimulus. This, too, has important survival implications, especially for species that rely on stereotypic alarm responses for avoiding predation.

In contrast to habituation, sensitization is the increase in intensity of a response that results from the repeated presentation of a stimulus. A good example is the heightened sensitivity to even relatively soft sounds that results from the initial presentation of a loud, startling noise, such as a gunshot. Sensitization differs from habituation in important ways. First, the specific stimulus that elicits a sensitization response is different from the stimulus to which the animal becomes sensitized. Second, the underlying physiological mechanisms that control these two processes are fundamentally different.

The third and broadest category of learning is associative learning. In this type of learning, an animal makes a connection between some primary environmental stimulus (that involves either a reward or punishment) and a novel or neutral stimulus that is paired with the first stimulus.

Classical and Operant Conditioning

The simplest form of associative learning is classical conditioning, first studied by Ivan Pavlov. Pavlov observed that when a dog is presented with food, the dog will begin to salivate. He referred to the food in this case as an unconditioned stimulus (US), and to the salivation reflex as the unconditioned response (UCR). When the unconditioned response is effectively paired with a second, novel stimulus, such as a light or bell (called the conditioned stimulus, or CS), the dog will, after several trials, associate this second stimulus (CS) with the US and begin to salivate whenever the CS is presented. The salivation reflex that occurs following presentation of the CS is termed the conditioned response (CR).

Although classically conditioned learning is often associated with the controlled experiments of psychologists, it undoubtedly occurs throughout the animal kingdom, and it may be one of the most common ways by which animals learn about their immediate environment. A good example of this is the phenomenon of taste-aversion learning. Taste-aversion learning occurs when an animal associates a specific odor or visual stimulus with an unpleasant experience resulting from the consumption of an unpalatable or poisonous food item. After even a single experience with the distasteful food, the animal will subsequently avoid ingestion, even if it means starvation. Taste-aversion learning is especially important for nonspecialist feeders that forage on a variety of foods and must periodically sample unfamiliar food items. This learning phenomenon also serves as the basis for the evolution of many warning signals in animals.

Through natural selection, many distasteful prey have evolved distinctive marks, colorations, odors, or behavioral characteristics that serve as a reminder (a CS) to predators that it is distasteful or harmful. After one negative experience with this prey, the predator learns to associate these characteristics with the sight or smell of the animal. Such characteristics have obvious survival benefits for the prey. Taste-aversion learning differs from classical conditioning in that the critical time between the CS and the US is usually much longer and in that only one trial is necessary for the learning to occur. This latter effect has important implications for animals that rely on aversion learning to avoid poisoning. Many animals, such as blue jays and rats, wait a specific length of time after ingesting a novel food item to determine whether they will become ill.

A second major form of associative learning is operant, or instrumental, conditioning. Unlike classic conditioning, in which the animal is passively involved in the learning experience, in operant conditioning the animal learns by manipulating some part of its environment. In traditional operant learning experiments the animal, for example, presses a lever or rings a bell in order to receive some reward. Because this kind of learning usually improves with practice, it is often referred to as trial-and-error learning. This kind of learning has obvious adaptive significance under natural conditions. Perhaps the best example of this is the reinforced trial-and-error learning that is necessary for many young vertebrates to perfect their feeding techniques. The naïve young of many mammals and birds greatly enhance their feeding efficiency when repeatedly allowed to manipulate their food. Similarly, many animals, including insects, use this reinforced practice to learn their way around in their habitat, home range, or territory, much the way a rat learns its way around in a maze.

Programmed Learning

In addition to associative learning, there are a number of types of learning that seem to involve mechanisms more complex than simple association. The most common examples include song learning (in birds) and imprinting. Ethologists often refer to these types of learning as programmed learning, since they only take place at certain times and under very restricted circumstances.

Imprinting is the process whereby a young animal develops a behavioral attachment to some other animal or object. Animals have been observed to imprint naturally on their parents, individuals of the opposite sex, food items, preferred habitats, and home streams (in the case of salmon). All such types of imprinting have two general features in common. First, the imprinting must occur during some critical period. The most familiar type of critical period is that which occurs in parental imprinting, a specific imprinting routine whereby a newborn becomes behaviorally fixed on a parent. First described by Konrad Lorenz, this type of learning requires a critical period shortly after birth, in which the young learns to recognize and follow the parent. Outside this period the learning simply cannot occur. The second characteristic common to all types of imprinting is that the young animal must be actively involved in the learning process. In fact, the strength of the imprinting seems to depend largely on the degree of this involvement.

Song learning in birds is fundamentally quite similar to imprinting in that it too requires a specific learning period. White-crowned sparrows, for example, learn their song from their fathers, usually from one to six weeks after birth. During this critical period, these young birds learn to imitate the song that is specific to their species as well as the variations and dialect characteristic of their population. When young birds are raised in isolation and prevented from hearing their own species' song, they develop an abnormal vocalization. If given the opportunity to hear a recording of a normal adult song of its species during the critical learning period, the young bird will learn to sing normally. If, on the other hand, the animal is exposed to the song of some other closely related species, the animal will not develop a normal song. This suggests that birds are somehow innately programmed to learn their species-specific songs. Thus, it seems that both imprinting and song learning are in many ways quite similar and may be controlled by the same underlying mechanisms. The tendency to classify these as complex behaviors, however, may be attributable in part to ethologists' lack of understanding of these mechanisms.

Insight

Perhaps the most advanced and least understood form of learning is insight. Insight is said to differ from other forms of learning in that it is characterized by a modification in behavior that is not contingent on some particular recent experience. Instead, insight behavior involves the ability to put two independent ideas together to solve a third, unrelated, problem. Wolfgang Köhler's classic observations on learning in chimpanzees illustrate the phenomenon of insight. He observed that when a preferred food item (such as a banana) was placed out of reach of a caged chimpanzee, the animal quickly learned to use a pole as an extension of its arm to pull in the food; when the food was hung overhead, the animal would learn to stack boxes to reach the food. Examples of tool use by chimpanzees observed under natural field conditions include the use of sticks as probes for gathering insects and the use of small branches for warding off potential predators.

Although this type of problem-solving behavior seems fundamentally more complex than any other type of learning, it has been suggested that many of the specific behaviors cited as examples of insight may be nothing more than extensions of associative learning. Pigeons, for example, can be conditioned to perform certain activities that they use later in solving more complex problems. A pigeon conditioned at one time to push a box across its cage floor and at another time to climb on a box and peck at a food lever will later push and position a box under a lever so that it can peck at the lever and receive a reward. While this seems to reflect some type of problem-solving ability, it is interesting that birds that are not previously conditioned cannot solve the problem. Thus, insight may build on some form of associative learning.

Insight learning has also been invoked to explain the origin of many types of cultural learning. Cultural learning occurs when one animal in a group discovers a unique or novel behavior and the other members learn to copy the behavior through the process of observational learning. One of the classic examples of this kind of learning was observed in the blue tit, a small European bird that was observed to strip the caps off milk bottles in order to drink the cream that surfaced at the top. In relatively little time, the behavior spread and was exhibited by this species all across Western Europe. Although there is little doubt that such cultural transmission involves nothing more than the simple imitation of another animal's behavior, it is not clear whether the origin of such behaviors reflects some form of innovation.

Ethological and Psychological Approaches

The study of behavior and learning has long been characterized by two very different methodological and philosophical approaches: those of ethology and psychology.

Ethology, the study of animal behavior, is built on several very specific assumptions and principles that clearly distinguish it from the field of psychology. First, the study of ethology involves objective, nonanthropomorphic (that is, not biased by human expectations or interpretations) descriptions and experiments of the learning process within a natural context. Konrad Lorenz, one of the founders of the field, insisted that the only way to study behavior and learning was to make objective observations under completely natural field conditions. Building on Lorenz's purely descriptive approach, Nikolaas Tinbergen conducted rigorous field experiments, similar to those that now characterize modern ethology. The classic work of early ethologists helped demonstrate how an animal's sensory limitations and capabilities can shape its ability to learn. For example, in a series of classic learning experiments, Karl von Frisch convincingly documented the unusual visual capabilities of the honeybee. He first trained honeybees to forage at small glass dishes of sugar water and then, by attaching different visual cues to each dish, provided the animals with an opportunity to learn where to forage through the simple process of association. From these elegant (but simplistic) experiments, von Frisch found that bees locate and remember foraging sites by the use of specific colors, ultraviolet cues, and polarized light, a discovery that revolutionized how scientists view the sensory capabilities of animals.

A second important feature of ethology is that it is built on the assumption that learning depends not only on environmental experience but also on a variety of underlying physiological, developmental, and genetic factors. The work of countless neurobiologists, for example, clearly demonstrates how behavioral changes are linked to modifications in the function of nerves and neuronal pathways. By observing the response of individual nerves, neurobiologists can observe changes that occur in the nerves when an animal modifies its behavior in response to some stimulus. In a similar way, they can show how learning and behavior are affected when specific nerve fibers are experimentally cut or removed. Unfortunately, however, neurobiologists' understanding of the physiological control of learning is limited to simpler kinds of learning such as habituation and sensitization.

Like the neurobiologists, behavioral geneticists have shown that much of learning, and behavior in general, is intimately tied to internal mechanisms. The results of hybridization experiments and artificial breeding programs clearly demonstrate a strong genetic influence in learned behaviors. In fact, it has been well documented that many animals (including both invertebrates and vertebrates) are genetically programmed (or at least have a genetic predisposition) to learn only specific kinds of behaviors. Finally, the most important characteristic of ethology is that it places tremendous importance on the evolutionary history of an organism. It assumes that an animal's ability to learn is shaped largely by its evolutionary background, and it emphasizes the adaptive significance of the various types of learning.

In comparison with ethology, the field of psychology emphasizes the importance of rigorously controlled laboratory experiments in the study of learning. The most widely used methods in this field are those of classic and operant conditioning. The primary objective in these approaches is to eliminate and control as many variables as possible and thereby to remove any doubt as to the factors responsible for the behavioral changes. These approaches have met with considerable success at identifying specific external mechanisms responsible for learning. These techniques, however, tend to focus only on the input (stimulus) and output (response) of an experiment and, as a result, de-emphasize the importance of proximate mechanisms, such as physiology and genetics. In addition, these approaches generally ignore the evolutionary considerations that ethologists consider so fundamental to the study of behavior.

Understanding the Learning Process

Although the approaches used to study learning vary tremendously, nearly all such studies are directed at two goals: to understand the adaptive value of learning in the animal kingdom and to understand the physiological, genetic, and psychological mechanisms that control learning. For any animal, the adaptive advantages of learning result primarily from the increase in behavioral plasticity that learning provides. This plasticity (ability to be flexible) provides the animal with a greater repertoire of responses to a given stimulus and thereby increases the chances that the animal will survive, reproduce, and pass the genes that control the learning process on to the next generation. In comparison, the value of an innate behavior lies primarily in its ability to provide a nearly stereotypic response to a stimulus on the very first occasion on which it is encountered. Innate reflexes are especially important in situations in which there may not be a second chance for the animal to learn an appropriate response. The best examples are basic feeding responses (for example, the sucking reflex in newborn mammals) and predator-escape behaviors

Image Not Available

(alarm calls in young birds). It is a common misconception, however, that a learned behavior is attributable entirely to the animal's environment, whereas instinct is completely controlled by the genes. Many studies have demonstrated that numerous animals are genetically programmed to learn only certain behaviors. In contrast, it has been shown that instinct need not be completely fixed, but can be modified with experience. Thus, learning and instinct should not be considered two mutually exclusive events.

In addition to its evolutionary implications, the study of learning has provided considerable insight into the internal mechanisms that control and regulate behavior. These mechanisms are the cellular and physiological factors that provide the hardware necessary for learning to occur. As neurobiologists and geneticists learn more about these types of control, it is becoming increasingly evident that learning, at nearly all levels, may involve the same basic mechanisms and processes. In other words, the only difference between simple and complex behaviors may be the extent to which the learning is physically constrained by the biology of the animal. Thus, many invertebrates, by virtue of their simple body plan and specific sensory capabilities, are limited to simple learning experiences. Vertebrates, on the other hand, live longer and are not as rigorously programmed for specific kinds of behavior.

—Michael Steele

See also: Brain; Ethology; Habituation and sensitization; Imprinting; Instincts; Language; Primates; Reflexes.

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ANIMAL LIFE

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LEMURS

Types of animal science: Anatomy, behavior, classification, ecology, evolution
Fields of study: Conservation biology, ecology, ethology, zoology

Over fifty species of lemurs have been identified and classified in the superfamily Lermuroidea in the Primate order. They have evolved separately from East African and other primates for at least forty million years.

Principal Terms

DENTAL COMB: forward projecting lower incisors and canines that are used for grooming and feeding

DENTAL FORMULA: denotes the types of teeth in one quarter of the mouth: incisors, canines, premolars, molars

POLYGYNY: males compete for access to several females

PRIMITIVE: a feature that reflects an ancestral condition rather than those that represent more recent evolutionary changes (derived)

SEXUAL DIMORPHISM: behavioral and anatomical differences between the sexes

SUBLINGUA: fleshy plate under the tongue used to clean the dental comb

Lemurs are primitive monkeys that originally inhabited parts of North America, Eurasia, and Africa, but competition with monkeys and apes resulted in their present distribution, restricted to Madagascar. Humans arrived on Madagascar about two thousand years ago, contributing to extinctions of one third of the island's species through habitat destruction, hunting, climate change, and perhaps new diseases. Most lemurs are highly endangered.

Most lemurs are arboreal (tree-dwelling), although ring-tailed lemurs spend more time on the ground. Lemurs subsist primarily on three to four food species, consisting of a mix of leaves, fruit, buds, bark, and shoots, but favored foods can vary monthly or seasonally. The golden bamboo lemur tolerates high levels of cyanide in the bamboo shoots. The smaller, nocturnal lemurs and the aye-aye eat more insects. Several species are cathemeral (active during parts of day and night), and there are also diurnal (day-active) forms, such as ring-tailed lemurs or indris. The diurnal species may have a nocturnal past, because they share certain features with nocturnal lemurs, including seasonal breeding, female dominance, and reliance on scent for communication.

Unique Primates

Lemurs exhibit many types of social organization. They are solitary in smaller nocturnal forms, while larger diurnal or cathemeral forms live in pairs that sometimes congregate in larger groups, usually with 1:1 sex ratios. Lemurs lack sexual dimorphism, and if there is a difference, females are larger than males. In social species, females largely dominate males, to the extent that males signal submissiveness to all females independent of context. This unusual primate pattern may be due either to seasonally low food productivity and the resulting reproductive costs, or may be partly a function of extinctions of raptors that preyed on primates.

Lemurs range in size from the pygmy mouse lemur at thirty-one grams (about one ounce) to the indri at seven kilograms (sixteen pounds), although many extinct forms were larger. All lemurs have longer posterior than anterior limbs, and their anatomy reflects their ability to practice vertical clinging and leaping. This is most developed in the sifakas and indris, which generally position themselves vertically while in the trees, leap from tree to tree, and exhibit a leaping, kangaroo-like gait when on the ground.

Cheirogaleidae include the fat-tailed and greater dwarf lemurs, primates that hibernate for up to six months during the dry season. Many of the females in Cheirogaleidae, Megaladapidae, and Lemuridae carry offspring in their mouths and sometimes park them on branches when active.

The aye-aye has a high brain-to-body ratio and also has incisors that grow throughout its life (as in rodents) resulting in a dental formula of 1-0-0-3. The teeth are used to gnaw on dead wood during searches for grubs that are then removed with a lengthy third finger.

—Joan C. Stevenson

See also: Apes to hominids; Baboons; Cannibalism; Chimpanzees; Communication; Communities; Evolution: Animal life; Evolution: Historical perspective; Fauna: Madagascar; Gorillas; Groups; Hominids; *Homo sapiens* and human diversification; Human evolution analysis; Infanticide; Learning; Mammalian social systems; Monkeys; Orangutans; Primates.

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Most lemurs live an arboreal lifestyle. (PhotoDisc)

Lemur Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Primates
Suborders: Prosimians (lemurs, lorises, and tarsiers) or Strepsirhini (lemurs and lorises only)
Superfamily: Lemuroidea
Families: Lemuridae (brown, black, crowned, red-bellied lemurs, bamboo lemurs, ring-tailed lemurs, mongoose lemurs, ruffed lemurs); Megaladapidae (sportive lemurs); Cheirogaleidae (dwarf lemurs, mouse lemurs, fork-marked lemurs); Indriidae (avahi or woolly lemurs, indris, sifakas); Daubentoniidae (aye-ayes)

Geographical location: Madagascar and adjacent Comoro Islands

Habitat: Forests (primary or secondary, dry, humid, or rain forests, evergreen or bamboo forests); sometimes also bush, scrub, or savanna edges of humid forests, spiny deserts, and tree plantations

Gestational period: From 65 days in the dwarf lemur to 175 days in the larger sifaka, indri, and aye-aye

Life span: Ranges from about nine years in the greater dwarf lemur to twenty-five to thirty years in ring-tailed, brown, and black lemurs

Special anatomy: A long snout with a sensitive, moist pad (rhinarium); incompletely fused bony eye socket; reflecting retina (tapetum); ancestral dental formula of 2:1:3:3; dental comb in the lower jaw and sublingua; unfused lower jaw and frontal bone; multiple pairs of breasts; two-section uterus; grooming claw on second toe of foot

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LEOPARDS

Type of animal science: Classification
Fields of study: Anatomy, physiology, wildlife ecology

Large cats widely distributed over Africa and Asia, leopards have the greatest geographic range of any wild cat, but face severe pressure from humans within many of their natural habitats.

Principal Terms

CANINES: four pointed, elongated teeth that grasp and kill prey
CARNASSIALS: pairs of large, cross-shearing teeth on each side of jaw
CREPUSCULAR: active at twilight or before sunset
MELANISTIC: having dark coloration of skin and hair
PAPILLAE: sharp, curved projections on tongue

Male leopards vary in length from five to eight feet, including a twenty-eight to thirty-seven inch tail. They stand eighteen to thirty-two inches high at the shoulder and weigh from fifty-five to two hundred pounds, depending on subspecies and geographic area. The largest leopards tend to inhabit mountainous terrain and colder regions. On average, females are 40 percent smaller than males. Leopard coats are short and sleek in the tropics and densely furred in colder areas. Their base color varies from yellow cream in desert areas, to golden yellow in grasslands, becoming deep gold in mountains and forests. All leopards are spotted, with black spots arranged in rosettes along the back and sides. Unlike jaguars, leopard rosettes do not have a spot in the center. Leopards in dark, moist tropical forests of Asia are often melanistic and are called black panthers; dark coats may be advantageous in areas of dim light.

The name leopard is also given to two other species: the snow leopard (*Panthera uncia*), displaying cream-colored fur and grayish rosettes, that inhabits mountainous Central Asia, and the clouded leopard (*Neofelis nebulosa*) of Southeast Asia, carrying grayish fur with cloudlike blotches on its sides. Both are endangered by overhunting for their beautiful fur.

Leopard Behavior

Leopard litters average two cubs; weaned at about three months, they soon begin to accompany their mother on hunts. Cubs remain with their mothers eighteen to twenty-four months before leaving to establish their own territories. Adult leopards are solitary hunters. Males sometimes hunt with females shortly after mating but play no role in raising the young.

Leopards are stealthy nocturnal or crepuscular hunters, preferring to stalk prey in the dark or half-light. They pursue a wide variety of targets as opportunity offers, including reptiles, rodents, birds, fish, and hoofed animals. Leopards kill by biting their victims' necks, strangling them, or severing their spinal cords with canine teeth. Scissoring carnassial teeth and rasplike papillae soon clean all bones of meat. Where their habitat abuts human settlements, leopards hunt close to houses, sometimes eating pets or livestock, but rarely attacking humans. Leopards are agile climbers; in areas where they face competition from lions or hyenas, leopards carry prey twice their body weight high into trees to discourage scavengers.

Relations with Humans

Leopard populations have been decimated by intensive hunting for their prized fur and through destruction of their habitat by expanding human populations. Originally, leopards had the widest east-west range and greatest habitat tolerance of any feline species. Their range included all of Africa outside the Sahara, as well as the Middle East, India, Indonesia, China, Korea, and eastern Siberia. Leopards are now endangered in much of Asia and virtually extinct in North Africa, the Middle East, China, and Korea. The 114 Amur leopards (*Panthera pardus orientalis*) currently held in zoos greatly exceed the estimated thirty or fewer still inhabiting the wild.

International traffic in leopard skins, though banned by the Convention on International Trade in Endangered Species, continues to be a problem, yet the leopard is showing greater survival success than its feline competitors in Africa, the lion and the cheetah. Leopards persist in substantial numbers in sub-Saharan Africa, where they are protected. Perhaps 100,000 or more roam the African plains, a number greater than the estimated total population of all other great cats—lions, tigers, jaguars, and mountain lions—combined. However, even where they are valued and guarded

Leopard Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Subclass: Eutheria
Order: Carnivora
Family: Felidae (cats)
Genus and species: Panthera pardus
Geographical location: Found over most of Africa south of the Sahara, in the Middle East and India, north to central Asia, and south to Indonesia
Habitat: Grasslands, forests, mountains, and jungles
Gestational period: 3 to 3.5 months
Life span: About fifteen years in the wild, twenty to twenty-five years in captivity
Special anatomy: Large eyes with excellent night vision; jaws adapted to seizing and gripping prey, teeth designed for tearing and slicing flesh

Leopards are very agile climbers and usually haul their prey into trees to keep it away from scavengers. (Digital Stock) as tourist attractions in national parks, illegal hunters continue killing them and farmers on the edge of parks spread poison to protect their cattle and sheep from wandering predators.

Wherever human populations press on leopard habitat, often exaggerated stories of man-eaters arise. One such narrative describes the "Man-Eating Leopard of Rudyaprayag," who was accused of stalking and killing 115 pilgrims en route to a religious shrine in northern India, over a period of eight years, before being hunted down and killed.

—*Milton Berman*

See also: Carnivores; Cats; Cheetahs; Fauna: Africa; Fauna: Asia; Jaguars; Lions; Mountain lions; Predation; Tigers.

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LIFE SPANS

Types of animal science: Development, reproduction
Fields of study: Biochemistry, cell biology, developmental biology, genetics, population biology

An animal's life span, the time lapsing between its birth and death, differs greatly from species to species because of differing environmental pressures, chance variations in physical conditions, and heredity.

Principal Terms

LIFE CYCLE: the sequence of development beginning with a certain event in an organism's life (such as the fertilization of a gamete), and ending with the same event in the next generation

LIFE EXPECTANCY: the probable length of life remaining to an organism based upon the average life span of the population to which it belongs

LIFE SPAN: the maximum time between birth and death for the members of a species

METABOLISM: the biochemical action by which energy is stored and used in the body to maintain life

MORTALITY RATE: the percentage of a population dying in a year

Life span has two common meanings, often confused. Popularly, the term can refer to the longevity of an individual, but in biology it is more abstract, a characteristic of the entire species rather than individual members. In this sense, life span is the maximum time an individual can live, given its environment and heredity, and life expectancy is the amount of time remaining it at any point during its life span.

The great variety within the animal kingdom complicates the definition of life span. For some species, life span is essentially the same as its life cycle, the return to the same developmental stage from one generation to the next. Salmon, for instance, hatch from eggs in small streams, migrate to the sea where they reach maturity, then struggle up rivers to return to the site of their hatching in order to produce more eggs. After completing the reproduction cycle, both males and females die. For most animal species, however, an individual may produce several generations of offspring before dying. In the case of humans, individuals can live long after their fertility ends.

It is often difficult to measure the life span for specific species, and in fact, a time period is seldom definitive for all species members. Rather, scientists recognize that mortality, the percentage of individuals that die each year (or each day in some cases), increases for a population of organisms until at some age it reaches 100 percent, and all individuals in a generation are dead. Finding the life span of laboratory animals is fairly simple: A population is given the best possible living conditions, and observers wait for the last individual to die. That, presumably, is the optimal life span for the species. Much the same procedure can determine the life spans of pets and animals in zoos, except that the population to be observed is much smaller, sometimes only a single individual. Likewise, the records of thoroughbred domestic animals, born and raised in captivity, provide evidence for the maximum species life span. Most animals live in the wild, however, where investigations face a great variety of conditions and anecdotal evidence can be misleading. For example, biologists long thought that bowhead whales lived only about fifty or sixty years, but in the late 1990's, various new kinds of historical and biochemical evidence identified bowheads that lived well into their second century. Moreover, species

Image Not Available

whose members can, if need be, go into dormancy show a large variation in individuals' apparent longevity, even when all members pass through a single life cycle.

In general, however, the life span variation among species falls into a fairly narrow range of time. The shortest life spans, which last a single life cycle, can be a matter of days, while the longest last more than two hundred years. Humans enjoy the greatest longevity among primates; scientists estimate the theoretical maximum human life span to be from 130 to 150 years, more than double that of the species with the next greatest endurance, gorillas and chimpanzees. However, several kinds of invertebrates live more than two centuries.

Life Span Limiters and Extenders

While each species has a theoretical maximum life span, few if any individual animals reach it. Three general influences limit longevity: environmental pressures, variations in physiological processes, and heredity.

Most domesticated species have longer life spans, frequently two times longer, than their wild relatives, and wild animals in captivity often live longer than in their natural habitat. The gray squirrel, for example, lives for three to six years in the wild, but from fifteen to twenty years in a zoo. The reason is clearly the safer, healthier, less stressful environment. Predators are one of the biggest threats in the wild, as are fluctuations in climate that affect the availability of food and shelter. Natural calamities such as hurricanes, wild fires, and earthquakes also take their toll.

Disease and chance injury also kill off many organisms, but even if disease is absent, many physiological processes in the body appear to degenerate or stop with age. Biochemists find that individual cells age and die. Cross-connections among connective tissue, such as ligaments and cartilage, gradually reduce the body's flexibility and inhibit motion. Chemical plaques build up in brain tissue, hindering the electrochemical connection among neurons. Highly reactive oxidants, the ionized molecular byproducts of cellular metabolism, also build up with age and degrade the operation of cells' mitochondria, the generators of chemical energy, as well as other cellular organelles. Moreover, laboratory tests reveal that cells can divide only a certain number of times—about fifty for some human cells—and then they die, a limit called the Hayflick finite doubling potential phenomenon. In connection with this finding, geneticists discovered that the lengths of deoxyribonucleic acid (DNA) at the tips of chromosomes, called telomeres, shorten with age and appear to play a role in cell dysfunction and death.

Other genetic factors help determine the age limit of cells and the entire organism. Research in the late 1990's with mice and roundworms uncovered genes that regulate cell life, including one kind that causes cells to suicide if their DNA or internal structure is too damaged to function properly or if the cells turn cancerous. Loss of function by genes damaged during cell division (mitosis) or by environmental toxins can impair a cell's ability to maintain metabolism, or set loose functionless or even outrightly harmful proteins and enzymes into the blood stream and lymph system—all of which can bring on illness. Organisms that escape such effects still may face genetic disease. Most human populations, for instance, now have a longer life expectancy than ever before; because of it, neurodegenerative diseases (such as Alzheimer's disease), cardiovascular dysfunction, and immunological disorders, caused or made possible by genes, grow ever more common. Because many of these life-shortening maladies were rare or nonexistent before the twentieth century, natural selection has not had a chance to cull them from the human genome. Similar diseases crop up in domestic animals and wild animals in captivity.

Late twentieth century research also identified several ways to extend life. A sharply reduced diet extends the lives of mice and fruit flies beyond their normal life span (although for the brown trout, a richer diet is life-extending), and lower than normal temperature has the same effect on fruit flies, fish, and lizards. Discovery of the relation of telomere length to cell death and isolation of genes that order cells to suicide allowed scientists to bioengineer animals with cells whose DNA self-repaired the telomeres and genes that failed to trigger cell-suicide; the result was individuals that in some cases had life spans twice the normal length or more. However, the most pervasive life-extending method is the development of social life—colonies, herds, packs—in which individuals work together to protect, shelter, and feed themselves and rear their offspring. In the case of humans (and perhaps some whales), culture and intelligence permit the species to pass on recently acquired information from one generation to the next and even to alter the environment to lengthen collective and individual life spans.

Size and Life Span

Biologists noted long ago that large animals live longer than small animals, but why this should be true was a mystery. In 1883, Max Rubner proposed that the relation had to do with metabolism. Large animals have a smaller skin surface to body mass ratio than smaller animals; accordingly, large animals lose heat more slowly and so can maintain body functions with less energy burned per unit of mass; in other words, a slower metabolism. Scientists since found that individuals of different animal species all use about the same amount of chemical energy during their lives, twenty-five to forty million calories per pound per lifetime. (There are significant exceptions: Humans consume about eighty million calories per pound.) Because small animals must burn energy at a higher rate, the argument holds, they physically wear out faster.

In 1932, Max Kleiber derived a mathematical relationship for Rubner's proposal. According to Kleiber's law, also known as the quarter-power scaling law, as mass rises, pulse rate decreases by the one-fourth power. So elephants, which have 104 times the mass of chickens, have a pulse rate one tenth as fast. Scientists suggest that the relation results from the geometry of circulatory systems and point out that the quarter-power scaling law is pervasive in nature, but the underlying reason for it remains unknown. In any case, plenty of exceptions to the mass-life span correlation exist. With a life span of about one hundred years, box turtles outlive fellow reptiles, for example, and humans outlive all mammals (with the possible exception of some whale species) regardless of size. Exceptions also occur among domestic species living sheltered lives: Cats have longer life spans than dogs.

Theories of Life Span

A 1995 review of data from earlier animal studies suggested that heredity accounts for about 35 percent of the variation in life spans among invertebrates and mammals; 65 percent comes from unshared environmental influences. Nonetheless, theorists in the life sciences continue to debate the relative influence of genetic and other biochemical factors on the one hand and environment fac-

The Big, the Old, and the Immortal

In some species, the older an animal gets, the larger it grows. Big sharks are old sharks, as are big crocodiles and snakes. In 1912, a reticulated python was found that measured thirty-two feet, ten inches in length, the longest ever, but no one knows how old it was. The age record for snakes goes to Popeye, a boa constrictor at the Philadelphia Zoo that died in 1977 at the great age of forty years and three months. Even for reptiles, however, Popeye's life span was modest. One Madagascar radiated turtle lived 188 years.

Most species, including humans, grow to a maximum size and then stop. The longest attested life span for a person is 122 years, achieved by France's Jeanne Louise Calment, who died in 1997, followed by Japan's Shigechiyo Izumi, who died just short of 121 years in 1986. Despite theories relating large body mass to long life span, some big and small animals in the wild have about the same life expectancy at birth: fifty years for both golden eagles and most whales, for instance, or twenty-four years for rhesus monkeys compared with twenty-five years for lions.

There is some disagreement over which animal species has the longest life span. The tubeworms growing on the ocean floor near hydrocarbon-seep sites in the Gulf of Mexico are thought to be as much as 250 years old, and so have been called the longest-lived noncolonial animals without backbones. However, some mollusks of the class Lamellibranchia, such as quahogs, a variety of clam, have also been called the longest-lived animal. They, too, can lie snug in their ocean bed for 250 years.

Whether classified as animals or not, bacteria hold the record for life span. If they are not eaten by predators or killed by environmental change, these single-cell creatures are theoretically immortal. Furthermore, they do not get larger with age: They divide.

tors on the other hand. The debate derives from the premise that life spans are the product of the natural selection that ensured species' reproductive success. The proposals fall into three categories: random damage (stochastic) theory, programmed self-destruction theory, and ecological theory.

Random damage theories emphasize the wear and tear on the body that accumulates with metabolic action. It is the source of damage that differs from one theory to another. One holds that the buildup of metabolically produced antioxidants is the key factor, a spinoff of the long-standing conjecture that the faster an animal's metabolism is, the shorter its life span. A second theory focuses on proteins that change over time until their effect on the body alters for the worse, especially when the proteins are involved in cellular repair. There is, for example, the altered connective tissue that causes the cross-connections stiffening tendons and ligaments. Another such change is the glycosylation of proteins or nucleic acids, in which a carbohydrate is added. Glycosylation is involved in such age-related disorders as cataracts, vascular degeneration among diabetics, and possibly atherosclerosis A third theory points to the buildup of toxins inside cells, and a fourth concerns the potential problems that come from errors in metabolism or viral infection which slowly impair or kill cells. Fifth, the somatic mutations theory proposes that chance mutations accumulate in a person's nuclear or mitochondrial genome and induce cell death or produce proteins and enzymes that have aging effects.

Programmed death theories hold, as the name suggests, that a species' genetic heritage includes a built-in timer or damage sensor. Telomeres shorten as DNA ages until the genes at the end of chromosomes are unprotected and subject to deterioration during the splitting and gene crossover of mitosis. The genes then lose their ability to produce essential biochemicals, whose absence harms the body or leaves it defenseless against damage from infection or injury. Damage sensors can include the genes that instruct cancerous or malfunctioning cells to die. Although such genes clearly are a means to check the spread of disease, their cumulative effect may be harmful. Furthermore, scientists discovered genes that produce much more of, or less of, their metabolic products as cells age, which also contributes to the overall aging of the body.

The ecological theory draws conclusions about life span from a species' role in its environment. Small animals have faster metabolisms and live shorter lives, it is argued, because they are not likely to escape predators for very long. Therefore, they evolved to mature and reproduce rapidly. Large animals typically have more defenses against predators and can afford to take life slowly. Moreover, animals that evolve defensive armor, spines, or poison also avoid predation and live longer than related species that do not. Finally, species that evolve mechanisms to withstand environmental stress, as from extreme temperatures or food scarcity, also have long life spans.

The theories assume that the life span for individuals within a species serves the survival of the entire species. Yet even a species' days on earth are numbered. Environmental change can slowly squeeze them from their habitats, a catastrophe may wipe them out indiscriminately, or they may evolve into a new species. Scientists estimate that the average life span for a multicellular species lasts from one to fifteen million years. That average is stretched by several notable exceptions in the animal kingdom—such living fossils as crocodiles (140 million years old), horseshoe crabs (200 million), cockroaches (250 million), coelacanths (a type of fish, 400 million), and certain mollusks of the genus *Neopilina* (500 million).

—*Roger Smith*

See also: Aging; Birth; Death and dying; Demographics; Extinction; Extinction and evolutionary explosions; Genetics; Growth; Heterochrony; Mark, release, and recapture methods; Metabolic rates; Migration; Offspring care; Population analysis; Population fluctuations; Population genetics; Population growth; Predation; Reproduction; Reproductive strategies; Veterinary medicine; Wildlife management; Zoology; Zoos.

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LIONS

Type of animal science: Classification
Fields of study: Anatomy, wildlife ecology

Lions, celebrated in myth as the King of Beasts, are the second largest of the big cats and the only members of the Felidae family to live and hunt in groups in the wild.

Principal Terms

CANINES: four elongated, pointed teeth that grasp and kill prey
CARNASSIALS: pairs of large, cross-shearing teeth on each side of jaw
CREPUSCULAR: active after sunset and in early morning
DIMORPHISM: existence of two distinct forms within a species
PAPILLAE: sharp, curved projections on tongue

Surpassed in size only by tigers, African male lions range in weight from 330 to 420 pounds, stand about forty-eight inches tall at the shoulder, and average 8 to 9.5 feet in length, including the tail. Females are smaller, weighing from 260 to 350 pounds, stand about forty inches tall, and average seven to eight feet in length. The Asian lion subspecies (*Panthera leo persica*) is similar in size, but somewhat shorter and stockier in build.

Among cats, lions are the only species to show sexual dimorphism—mature males display a distinctive mane encircling their head and shoulders; it darkens with age, giving the lion a majestic look. Coat color is normally tawny yellow to reddish brown in both sexes, with black accents on ears, tail tips, and manes. Cubs are born spotted, but by three months of age begin showing the uniform coat color of their parents.

Lion Behavior

Unlike other wild cat species, lions live and hunt in groups, called prides. (Domestic cats exhibit some similarities in group behavior.) The pride's core consists of two to twelve closely related lionesses, who assist each other in raising their cubs. Female offspring usually remain members of the group, but males are driven off before becoming sexually mature. Two to four unrelated males live with the pride, fathering the cubs, protecting the pride, and proclaiming their territory with scent marks and loud roars that can be heard for five miles. Males rarely control a pride more than three or four years before being replaced by younger, more powerful challengers.

Lions are crepuscular hunters, preferring to rest in the shade during the heat of the day; they emerge at sunset or in the early morning to pursue their prey. Lionesses do most of the killing, cooperating when stalking and ambushing victims. The preferred targets are medium to large hoofed animals such as antelopes, zebras, and wildebeests. Males rarely participate in chases unless their weight is needed to bring down large bull buffaloes; however, males claim first place at the pride's feasts. Lions are also opportunistic scavengers, stealing prey from leopards, cheetahs, and hyenas. Similar to other big cats, lions kill by biting their victims' necks, strangling them, or severing their spinal cords with sharp canine teeth. Scissoring carnassials and rasplike papillae leave little of their victims other than bones and skin.

Lions and Humans

Throughout history, lions have been called "King of Beasts" and used to symbolize royal authority. Rulers, often described as lions, wore lion skins to

Lionesses do most of the hunting for the pride. (Digital Stock)

impress subjects with their majesty and power. Hunters demonstrated bravery and prowess by killing lions. Lions have been celebrated in myth and legend from antiquity to the present; in astrology, Leo Major reigns as the fifth house of the Zodiac.

Originally, lions existed throughout southern Europe, all of Africa, the Near East, and from southwest Asia to India. As human population and agriculture expanded, hunting and habitat destruction greatly reduced lion numbers. By 100 C.E., lions had been eliminated from Europe, by the time of the Crusades they were extinct in the Near East, and before 1900 had vanished from North Africa and most of Asia. When the Nawab of Junagadh established the Gir Forest Lion Sanctuary in Gujarat, India, in 1965, less than 100 Asian lions remained in the world; a 1990 study estimated that the population had rebounded to about 250 individuals.

Estimates of the African lion population south of the Sahara Desert run as high as fifty thousand. The overwhelming majority live in national parks and reserves, where wild animals are protected as valuable national assets, attracting tourists and significant income. In the parks, lions have become so accustomed to humans that they sometimes rest in the shade of tour buses to avoid the afternoon sun. As human populations continue expanding, governments face pressure to reduce the preserves and permit agriculture and grazing to increase the food supply. However, most naturalists believe the monetary value of wild animals in producing foreign exchange will ensure the long-term survival of the African lion, even if reduced in numbers.

—*Milton Berman*

See also: Carnivores; Cats; Cheetahs; Fauna: Africa; Fauna: Asia; Groups; Jaguars; Leopards; Mountain lions; Predation; Tigers.

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Lion Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Subclass: Eutheria
Order: Carnivora
Family: Felidae (cats)
Genus and species: Panthera leo

Geographical location: Once common to many areas of Europe, Africa, and Asia; now found only within protected areas in Africa south of the Sahara and in one wildlife refuge in India

Habitat: Grassy plains, savannas, and open woodlands

Gestational period: 3 to 3.5 months

Life span: About twelve to fifteen years in the wild, twenty years or more in captivity

Special anatomy: Large eyes with excellent night vision; jaws adapted to seizing and gripping prey; teeth designed for tearing and slicing flesh

Brakefield, Tom. *Kingdom of Might: The World's Big Cats*. Stillwater, Minn.: Voyageur Press, 1993. Documents habits, natural history, biology, and challenges that change in population and habitat pose for lions. Extensive bibliography.

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LIZARDS

Types of animal science: Behavior, classification, ecology, evolution, reproduction
Fields of study: Anatomy, conservation biology, herpetology, physiology, systematics (taxonomy), zoology

More than six thousand species of reptiles have been identified and named. They are classified in the order Squamata, of which slightly more than four thousand are lizards. The remainder are snakes. Technically, snakes comprise one group of limbless lizards. Squamata is the largest order of extant reptiles.

Principal Terms

ACTIVE OR WIDE FORAGING: moving about in search of prey

AUTOTOMY: loss of the tail by controlled muscle contractions resulting in breakage at intervertebral sutures

BEHAVIORAL THERMOREGULATION: maintaining relatively constant body temperature by shuttling between warm and cool microhabitats

ECDYSIS: sloughing off of old skin, which is replaced by new skin from underneath

LECITHOTROPHY: nutrition of developing offspring from yolk reserves within the egg

MATROTROPHY: nutrition of developing offspring directly from the mother; in the case of lizards, via a placenta

OVIPARITY: production of shelled eggs by females

PARTHENOGENESIS: reproduction in which unfertilized eggs develop into females genetically identical to their mothers

SIT-AND-WAIT FORAGING: sitting in one place, waiting, and attacking prey as they move

SPECTACLE: transparent scale covering the eye as a replacement for the eyelid; occurs in some lizards and all snakes

VIVIPARITY: production of live young by females

Lizards belong to the order Squamata, along with snakes. There are approximately four thousand lizard species.

Lizard Reproduction

Most lizards reproduce sexually, although some are parthenogenetic. Most lizards are polygynous, with males mating with more than a single female, although a few, such as Australian sleepy lizards (*Trachydosaurus rugosus*), are monogamous. Mating occurs after complex social behavior often involving prolonged courtship. Fertilization is internal. Males have paired intromittant organs called hemipenes, one of which is inserted in the female's cloaca during mating. Once eggs are fertilized, the female carries eggs or embryos for various periods of time. The weight of unborn offspring usually reduces the female's ability to run fast, thus affecting her ability to escape predators. Many females change their behavior while gravid to reduce the costs of reproduction. Costs of reproduction are not confined to increased predation risk; energy required for locomotion increases as well due to the added weight that females carry around while gravid.

Most lizards produce eggs (oviparity) but many produce live young (viviparity) following extended gestation periods. Females of oviparous species deposit eggs in places that are moist but not wet, such as inside rotted logs or in the ground, often under rocks. Most lizard eggs have pliable, leathery-shelled eggs, but a few, such as geckos, have hard, calcified eggshells. Lizard eggs

Lizard Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Vertebrata
Subphylum: Tetrapoda
Class: Reptilia
Subclass: Diapsida
Superorder: Lepidosauria
Order: Squamata
Suborders: Iguania (iguanids, chamaeleonids, and agamids); Scleroglossa (all other lizards and snakes); Gekkota (gekkonids, eublepharids, diplodactylids, and pygopodids); Autarchoglossa (teiids, gymnophthalmids, lacertids, xantusiids, dibamids, amphisbaenids, trogonophids, rhineurids, bipedids, scincids, gerrhosaurids, cordylids, anguids, xenosaurids, helodermatids, lanthanotids, varanids, and "snakes")
Geographical location: Every continent except Antarctica
Habitat: A vast majority live on land or in trees in all habitats (desert, savanna, temperate and tropical forest); a few are semiaquatic; one, the Galápagos iguana, dives into the ocean and feeds on algae
Gestational period: Highly variable; eggs of *Anolis* lizards hatch in several weeks, while embryos of some skinks (*Mabuya*) require a year
Life span: Variable; some small skinks and geckos live one year or less, whereas Gila monsters (*Heloderma*) and large monitors (*Varanus*) live thirty years or more
Special anatomy: All lizards have scales (like other reptiles), paired copulatory organs in males (hemipenes), and claws on their feet; most have four legs, an elongate tail, eyelids, and external ear openings; some lizards in several families have lost two or all four legs as adaptations for life underground, some have their ear openings completely covered by scales, some have short tails, and some have their eyes covered by a transparent scale (spectacle); some subterranean lizards, such as the strange worm lizards, have eyes reduced to an eyespot covered by scales

in the nest are vulnerable to predation by many animals because they cannot move. Eggs contain yolk, which is high in energy and thus a good food source for snakes, mammals, and even some other lizards. Consequently, mortality of lizard eggs in nests is high. A vast majority of oviparous lizards do not provide parental care to eggs, but females of a few, such as five-lined skinks and glass lizards, remain with the eggs, brooding them until they hatch. Hatchlings cut slices in their eggshells with a specialized scale on the front of their jaw, called the egg tooth. Parental care ends once offspring exit the eggs. Hatchlings are fully formed, resembling miniature adults. Females of viviparous species often provide some parental care to neonates (newborns). Most help neonates free themselves from embryonic membranes, often eating the membranes. A few, such as the large Australian sleepy lizard, engage in extended parental attention, but it does not involve feeding or grooming the young, as in birds and mammals.

A number of lizard species in several different families reproduce by parthenogenesis, a process in which females produce daughters that are genetically similar to their mothers without the involvement of males. In such species, potential population growth is extremely high because no energy is wasted on males and every individual produces offspring.

Although sex determination in most lizards is chromosomal, as in humans, some species of lizards lack sex chromosomes and have environmental sex determination. Eggs incubated at one set of temperatures produce all males, whereas eggs incubated at another set of temperatures produce all females.

The juvenile stage of most lizards is also a high mortality stage. Juvenile lizards are relatively small in body size, and, as a consequence, many predators can easily eat them. Because juveniles do not reproduce, all energy taken in is devoted to growth and maintenance. When lizards reach sexual maturity, growth slows and most energy is directed into reproduction and maintenance. Males use energy in reproductive related behaviors such as territorial defense and courtship, whereas females use energy for production of eggs.

Evolution of Sensing Systems

One of the most fascinating aspects of the natural history of lizards is the variation in relative importance of sensory systems and its consequences. Most lizards in the suborder Iguania are visually oriented, sit-and-wait predators. They capture prey by a process known as tongue prehension; basically, they stick their tongues out and carry insects into the mouth on their tongues. They are colored for camouflage, move very little, and attack moving prey from perches, to which they usually return. Their social systems usually involve territoriality, the defense of a specific area against intruders of the same species. In most instances, territorial behavior is directed toward other males.

Lizards in the suborder Scleroglossa use a combination of visual and chemical cues to locate and discriminate prey. They have well-developed vomeronasal systems; they pick up chemicals from the external environment with their tongues and bring them into the mouth, where they are passed over the vomeronasal organ (also called the Jacobson's organ) in the roof of their mouth. This organ transfers information directly to the lizard's brain, allowing it to discriminate prey on the basis of chemicals much like mammals' sense of smell. These lizards capture prey by grasping prey between their jaws. The tongue may be used to help manipulate prey within the mouth but is not used to capture prey. Most of these are active foragers; they travel around, searching for prey, many of which are not moving.

Venomous and Dangerous Lizards

Most lizards will bite in self-defense, and, because all lizards have teeth, some will break the skin. Only two lizard species in the world are venomous, the Gila monster and its close relative, the Mexican beaded lizard. Both have powerful jaws and are difficult to remove should they bite. They do not have fangs like poisonous snakes; rather, they have grooved teeth with venom glands located in the rear of the mouth. Venom moves along the grooved teeth as the lizards grind their jaws while biting. Bites are only rarely fatal. Large monitor lizards are nonvenomous, but their mouths contain high levels of bacteria, which can cause dangerous infections following bites. Some of the larger monitors, such as the Komodo dragon of the Lesser Sunda Islands, have sharp, serrated teeth and can bite completely through the

Iguanas are sit-and-wait predators that catch passing insects with their long tongues. (Digital Stock)

Some Types of Lizards

Anoles (genus *Anolis*) are highly diverse, with more than three hundred species, all in the New World. Most are arboreal, and females produce only a single egg in each clutch.

Chameleons (family Chamaeleonidae), restricted to the Old World, have prehensile tails and long protrusible tongues that they use to capture insects.

Chuckwallas (genus *Sauromalus*) are herbivorous lizards of the American Southwest desert that hide in rock crevices, where they inflate their bodies, making it very difficult to remove them.

Flying lizards (genus *Draco*) of Southeast Asia have large flaps of skin along the sides of their bodies that become parachutes when erected by their ribs, allowing them to glide through the air after jumping from tree surfaces.

Geckos (family Gekkonidae) include many species with adhesive toe pads, which allow them to climb smooth, vertical surfaces.

Glass lizards (genus *Ophisaurus*) have no legs and superficially resemble snakes. Their long tails are easily broken and often break into several pieces, each of which moves around violently, distracting predators while the lizard slowly escapes.

Iguanas (*Iguana iguana*) are large tropical lizards that feed exclusively on plants. They have microorganisms in their digestive tracts that break down cellulose, allowing them to digest leaves.

Monitors (genus *Varanus*) are large, intelligent lizards living in the Old World and Australia. The largest monitor is the Komodo dragon, which reaches nearly twelve feet in total length.

Night lizards (genus *Xantusia*) are secretive lizards that live in rock crevices and under branches of fallen Joshua trees in the desert southwest of North America. Even though they are very small in size, they are long-lived.

Tegu lizards (genus *Tupinambis*) live in open habitats in South America and reach more than 3.5 feet in total length.

Whiptail lizards (genus *Cnemidophorus*) are unusual New World lizards in that many species are parthenogenetic, reproducing without males and producing only female clones.

leg muscles of large vertebrates. As a result, their bites are potentially life-threatening even though they rarely attack humans.

—Laurie J. Vitt

See also: Chameleons; Cold-blooded animals; Reptiles; Salamanders and newts; Smell; Snakes; Turtles and tortoises.

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LOCOMOTION

Type of animal science: Physiology
Fields of study: Anatomy, biochemistry, physiology, zoology

Locomotion, the ability to move from one place to another as needed, is widespread. It is seen in unicellular animals, which move via cilia, flagella, or like amoebas. The locomotion of multicellular animals includes crawling, walking and running, swimming, gliding, and flying.

Principal Terms

AIRFOIL: the wing of a flying animal or airplane that the provides lift and/or thrust needed for flight

ANGLE OF ATTACK: the angle at which an airfoil meets the air passing it

EUKARYOTE: a higher organism, whose cells have their genetic material in a membrane-bound nucleus and possess other membrane-bound organelles

LIFT: the force enabling flight; it occurs when an airfoil makes air passing it move so as to lower air pressure above the airfoil to values below that beneath the airfoil

LOCOMOTION: the ability of an organism to move from one place to another as needed

MITOCHONDRION: a subcellular organelle that converts foods to carbon dioxide, water, and energy

SESSILE: an organism that is not capable of moving from its point of origin

STRIATED MUSCLE: voluntary or skeletal muscle, capable of conscious enervation

Being a sessile animal, unable to move from place to place, makes life difficult for a wide variety of reasons. For example, if food is not available in a very limited area, death may come very quickly. As a result, a great many living animals, from unicellular microbes to the multicellular higher organisms, have developed the ability to move from one place to another as needed. This ability for self-directed movement is called locomotion.

Locomotion is under conscious (or voluntary) control. In essence, it serves to allow living creatures to move in chosen directions, toward food, away from danger, toward mates, and so on. Locomotion is essential for the optimization of the lives of animals. This can be seen in two ways: Most living animals are capable of locomotion; it is particularly well developed in large, higher organisms.

The Physiology of Locomotion

Many unicellular animals, such as protozoa, carry out locomotion via hairlike organelles called cilia and flagella, or by amoeba-like motion. Their movement is not complex. Multicellular animals, crawl, walk, run, swim, glide, or fly. The basis for these much more complex activities is cooperative operation of their skeletons and muscles, along with other processes needed to suit each organism to its environment. In addition, nerve impulse transmission coordinates locomotion.

The skeleton and the muscles act as the levers that can move to produce body motion in chosen directions and as the machines that produce the motive ability required for locomotion. Skeletons are of two types. The external, bony, jointed exoskeletons of arthropods (insects and crustaceans) surround them like medieval suits of armor. This design limits the dexterity of arthropods and the complexity of the motion possible for them. In contrast, the bony endoskeletons of vertebrates are much more complex and produce the ability for much more complicated and dexterous locomotion.

The muscle involved in locomotion can be exemplified by vertebrate striated skeletal muscle. This type of muscle is called striated because its fibers appear to be banded when viewed under light microscopes. Such muscle is under the conscious (voluntary) control of any higher organism containing it and wishing to move toward a desired place. Striated muscle is either red or white. Red striated muscle has a very good blood supply—the basis for its color—and obtains energy in the course of oxidizing foods into carbon dioxide and water. This occurs in its many mitochondria, subcellular organelles that carry out oxidative, energy-getting processes. White striated muscle has less of a blood supply and less mitochondria. It obtains most of its energy by converting food to lactic acid, without much use of oxidation or mitochondria.

All locomotion uses the contraction and relaxation of muscle or related systems, which can be thought of as muscle waves. In the unicellular eukaryotes (such as protozoa), cilia and flagella are used. These structures are cell organelles that are whiplike and identical in their makeup. However, their size and number per cell differ. One protozoan type may have on its surface hundreds of cilia, each ten to twenty microns long. Another species can have one or two flagella up to 250 microns long.

Both cilia and flagella cause movement by producing a wavelike motion transmitted all through the organelle, outward from its base. Their action uses organized protein microtubules in a network, interconnected by arms and spokes reminiscent of fibrils, and crosslinks of striated muscle. The mechanism of their action also uses a sliding mechanism initiated by a protein called dynein. Cilia and flagella are also found in multicellular eukaryotes, including humans. For example, flagella propel human sperm and are found in human lungs, where they mediate the removal of dust and dirt from the airways.

Amoeboid motion also occurs in protozoa. Here, their protoplasm flows in the direction of

Cheetahs are the fastest animals on earth, running at speeds of up to seventy miles per hour. They increase the distance covered in each step by leaping as well as running. (Corbis)

Muscle and Bone

Light microscopy of striated muscle fibers reveals a regular pattern of alternating light and dark bands that is repeated every few microns along the fibers. This banding pattern has been found to explain muscle contraction. The process operates due to the presence in the muscle of two kinds of filaments, thick filaments and thin filaments, which run lengthwise along each muscle fiber. Thick filaments are made mostly of a protein called myosin and have projecting cross-bridges. Thin filaments contain mostly the protein called actin and have no cross-bridges. When a muscle contracts, due to energy input, the cross-bridges of the thick filaments attach to the thin filaments surrounding them, pulling them so that they slide between thick filaments. This sliding action shortens the muscle fibers, and as the shortening proceeds, cross-bridges detach and reattach after walking to positions further along the thin filaments.

If a vertebrate animal is to walk, run, swim, or fly, a system of levers is required to turn its muscle contractions into locomotion. This is provided by its endoskeleton, which pulls the levers inside the body, joined to muscles. The skeletons of vertebrates are made of bones, which meet at joints that allow bending and twisting due to the action of muscles attached to the bones. A joint which only allows bending to occur (such as an elbow or knee) has flexor muscles to bend them and antagonistic extensor muscles to straighten them. Joints, such as those in the fingers, have the ability for much more freedom of movement. This is because they are moved by a larger number of muscles. Some muscles attach directly to the bones of the skeleton, but others join the bones via tendons.

desired motion, forming pseudopods, followed by forward locomotion of the cell. This type of locomotion seems to depend on cytoplasm transitioning between fluid endoplasm and gel-like ectoplasm. Pseudopod formation occurs due to the action of microfilaments of actin, one of the contractile proteins also found in striated muscle. Thus, the contraction mechanism may be similar to that in striated muscle.

The various forms of locomotion include crawling, walking and running, swimming, gliding, and flying. These locomotive processes all use muscle waves based on actin and myosin fibrils. However, the complete systems involved become more and more complex due to increases of the needs of locomotion, crawling on earth's surface, walking or running on land, swimming in lakes and oceans, and gliding or flying in the air. The increases in complexity are mostly due to the need for the involvement of more and more muscles.

Crawling, Walking, and Running

Crawling is movement on land without legs, produced by waves of muscular activity traveling along the crawler's body. Two crawling creatures are snakes and snails. When a snake crawls, it curves its body into bends around stones and ground irregularities. These bends travel backward along the snake's body in muscle waves. The waves push against the stones and irregularities and propel the snake forward. Snails, in contrast, usually crawl on a long foot covered with mucus, using waves of muscle contraction that travel along the foot. Snail locomotion depends on their interesting mucus, which resists gentle pressure as if it were a solid, but when pressed hard behaves like a liquid. The muscle waves of snail feet are designed so that foot portions moving forward exert pressure enough to liquefy the mucus, while parts that move backward do not.

All living organisms capable of walking or running have skeletons because the processes are intricate and require the use of a relatively large number of muscles in a complex fashion. Walking is locomotion at a slow pace, when there is no need for speedy movement. Running enables organisms to move much more quickly. It is done when predators threaten, or if there is an unthreatening reason to travel more quickly than usual, for instance, to obtain some choice food or a mate.

The complexity of walking and running is made clear by the coordination required. For example, when four-footed animals walk, at least one forefoot and one hind foot are kept on the ground at all times. In walking bipeds, at least one foot is on the ground at all times, and at intervals, both feet are on the ground. In running, there are times when both feet leave the ground simultaneously. Four-footed mammals walk slowly, but often attain higher speeds by trotting, cantering, or galloping. In each of these gaits, there are differences in the operation of the legs. For example, in a gallop, both forefeet are set down at one instant and both hind feet are set down at the next instant. This is not due to chance; rather, it allows the back muscles to contribute to the work done and spread the overall effort through the body.

Another aspect of the differences between walking and running is the interaction of the feet with the ground. Some animals, including humans, walk or run with the entire bottom of the foot on the ground; this is known as plantigrade locomotion. In contrast, most quadrupeds carry out these actions with only their toes on the ground, known as digitigrade locomotion. Such differences in ways in which vertebrates walk and run add to the complexity of the processes and the number of muscles used. The rate at which an animal moves also depends on its foot size. The larger the foot area that touches the ground while walking or running, the slower the animal. The complexity of running activity adds to total speed. For example, cheetahs can run at a speed of sixty-five to seventy miles per hour, partly by adding to their gait a series of leaps at chosen intervals. The added leaps help to produce the ability to move three times as fast as exceptional human athletes can run one hundred meter dashes.

Flying, Thrust, Drag, and Lift

Heavier-than-air craft, whether birds, bats, or airplanes, must conquer gravity to enter the air in controlled flight. In the case of animals who fly—as well as of airplanes—three different forces are involved. The first, called thrust, is empowered in animals by wing flapping. Thrust enables forward horizontal movement, as long it exceeds the second force, drag, caused by air viscosity.

The third aerodynamic force, lift, is the key to flight. It enables upward rise into the air, at a right angle to the direction of the forward motion. Lift in living creatures is supplied by the wings of flying animals. These wings (airfoils) are moved so the angle at which they meet air passing them (the angle of attack) makes the air flow much more rapidly past the upper airfoil surface than past its lower surface. This drops the air pressure above the airfoil to values below the air pressure under it and engenders lift needed to fly. In flying animals, the angle of attack (as in birds) is altered by wing motion adjustments.

The importance of the angle of attack of airfoils is clarified by its use and misuse by human pilots during flight. Angles of attack of up to fifteen degrees increase lift, enabling fast climbs but slowing airspeed. When the angle of attack is too steep, air currents atop airfoils decrease lift and cause aircraft to drop toward the ground in stalls. When pilot misjudgment produces a stall, the craft crashes unless the pilot quickly decreases the angle of attack. Birds do this instinctively, and so effortlessly that crashes due to bird stalls do not occur.

Swimming, Gliding, and Flying

Organisms that swim in water range from tiny ciliated or flagellate microbes to blue whales that are over one hundred feet long. Their locomotive operations are complex and use oarlike rowing, hydrofoil motion of propellers, body undulation, and jet propulsion. Oar and propeller actions have some similarities, but oars push in the direction of a desired movement, while propellers work at right angles to blade motion. Propeller action is due to lift, caused by hydrofoil action in the water. Propeller-mediated animal locomotion is more complex than walking or running, especially in the case of whale flukes. These hydrofoils, in addition to complex motion, must be tilted at angles which provide more lift than drag, under widely varying conditions.

In animals that swim by undulation, movements are made like the crawling of a snake. Here, the resistance to motion of poorly compressible water makes it easier for the swimmer to slide forward along its long axis than sideways along its short axis. The squid exemplifies those organisms that move by jet propulsion. A squid does this by drawing water into its mantle and squirting it out forcefully from an organ called a funnel. The squirt is aimed forward when a squid wants to swim backward, or backward when it seeks to swim forward.

One of the problems associated with locomotion by swimming is that most tissues in swimming organisms are more dense than water. Such organisms would sink, lacking ways to raise body buoyancy. These needs add to the complexity associated with swimming, compared with walking or running on land. Ways in which to counter sinking include swimming with all fins extended like airplane wings, as sharks do, to add buoyancy by increasing the surface area of the body. Also, swimming animals, such as the bony fish, adjust their densities to match that of the water via gas-filled swim bladders in their body cavities.

Only insects, birds, and bats are capable of locomotion by true flight. However, some other animals glide for short distances. Best known are flying squirrels, which glide from tree to tree. Also, flying fish use their large pectorals as wings of a sort. They leap out of the oceans with the fins spread and glide through the air for up to half a minute. As is the case with whale flukes in water, a glider supported by lift on its wings is slowed and pulled down by drag. Thus, most gliding organisms do not stay in the air for long Their time suspended aloft depends upon maintaining the appropriate angle of attack of their wings. They can adjust glide speed by changing these angles of attack. Increasing this angle slows them and decreasing it allows them to speed up.

Soaring, or gliding for long distances, is possible only for animals aloft in quickly rising air. Few animals other than birds and butterflies have wings capable of sustained gliding. The needed air currents are found mostly over hillsides or coastal cliffs and in thermals, which are currents of hot air rising from ground heated by the Sun. Vultures soaring to scan for carrion can travel for distances up to fifty miles. Butterflies, gulls, and albatrosses also soar for long distances. Long-distance soaring is very often used on migration trips, to conserve energy for other activities.

Ways to increase glide or soar distance include tilting the body to suit different angles of attack and moving wings forward or backward. These actions provide streamlining and move the center of gravity of the body. Gliding and soaring animals make turns by giving one wing a higher angle of attack than the other. Furthermore, gliding is usually done with legs retracted, to increase streamlining. The legs are lowered like the landing gear of airplanes when a braking effect is required. Clearly, locomotion in the air is even more difficult than swimming, involving much more complex interactions of the muscles and the skeleton.

Power, needed for most sustained flight, is obtained when flying animals flap their wings. There are two main animal flight types, high-speed flight and hovering flight. In the high-speed flight of birds, bats, and insects, the body moves forward at the same speed as the wings. The wings beat up and down as the animal moves forward through the air. Each down stroke produces lift and propels the flying animal forward and supports it in the air. The angle of attack of the upstroke is increased, so as to produce very little lift. This is because lift, acting upward at right angles to the wing's path, would slow high-speed flight.

In hovering flight, the body is stationary and the wings move very quickly, as when hummingbirds feed. Animals use two hovering techniques. Most often, their wings are kept horizontal and beat straight backward and straight forward. They turn upside down for each backstroke, adjusting the angle of attack so lift is obtained. The hum of hummingbirds is due to the frequencies with which their wings beat (twenty-five to fifty-five cycles per second). Insects buzz, whine, or drone, according to the sound produced by the higher frequencies at which their wings beat. In some cases, as in pigeons, hovering is accomplished when the wings clap together at the end of an upstroke. The clap enhances airflow into the space formed as they separate and so enhances lift. Initial wing-clap hovering in pigeons causes the sound first made when a flock flies away together.

—Sanford S. Singer

See also: Endoskeletons; Exoskeletons; Flight; Muscles in invertebrates; Muscles in vertebrates; Physiology; Respiration in birds; Wings.

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LUNGFISH

Type of animal science: Classification
Fields of study: Anatomy, evolutionary science, paleontology, systematics (taxonomy)

Lungfish are freshwater members of the subclass Sarcopterygii, the fleshy- or lobed-finned fishes. As their name indicates, lungfish have lungs evolved from the swim bladder and can breathe air. Because they are among the fishes most closely related to the tetrapods, they play a crucial if controversial role in the study of vertebrate evolution.

Principal Terms

CONTINENTAL DRIFT: theory that the continents have moved slowly apart from an early landmass, explaining why many species appear to be closely related while separated by wide expanses of ocean

ESTIVATION: similar to hibernation; period of reduced activity or dormancy triggered by dry and/or hot environmental conditions

METAMORPHOSIS: pronounced developmental change in form or structure of an animal after birth or hatching, as in the transformation of tadpoles into frogs

SWIM BLADDER (AIR BLADDER): an internal organ evolved from the gut that allows a fish to regulate its vertical position in the water column (maintain its balance)

TETRAPODS: four-legged vertebrates (amphibians, reptiles, birds, and mammals)

Lungfish fossils first appear at the beginning of the Devonian period, about 400 million years ago. Once distributed around the world, lungfish now occur in only three areas (South America, Africa, and Australia) that were once adjacent but have since separated due to continental drift. South American and African lungfish are more closely related to one another. They have reduced gills and two lungs and are true air breathers, while Australian lungfish have one lung and rely mostly upon their gills for respiration, gulping air at the water surface to breathe only when dissolved oxygen is in short supply.

African and South American Lungfish

There are two related families in this order. The African family, Protopteridae, has one genus (*Protopterus*) and four species (*P. annectens*, *P. aethiopicus*, *P. dolloi*, and *P. amphibius*). They live in the rivers, lakes, and swamps of East and Central Africa and grow to 2 meters (6.5 feet) in length. The South American family, Lepidosirenidae, has only one species, *Lepidosiren paradoxa*. It lives in swampy areas of the Amazon and Paraná river basins and in the swamps of the Chaco region and grows to 1.2 meters (4 feet) in length.

During spawning season, males dig holes for the eggs and guard both eggs and young after they hatch. The South American male develops branched, gill-like structures on his pelvic fins that may supply extra oxygen to himself as he incubates and to his offspring. Juveniles hatch with adhering organs to attach to plants. They have external gills like salamander young and undergo metamorphosis. Adults live on crustaceans, mollusks, and small fishes. They survive the dry season by resting quietly in moist burrows dug in the mud. If it becomes too arid, they seal their burrows with mud, secrete a protective covering of mucus, and estivate, sometimes for several months. During estivation, metabolism slows down to conserve energy and air. Once the rainy season begins, water enters the burrow and awakens the estivating fish.

Australian Lungfish

The Australian lungfish was first discovered in 1870. This lungfish closely resembles fossil lungfishes except that its skull contains fewer, larger bones. It has remained unchanged for 100 million years or more, longer than any other vertebrate known. There is now only one living species of this order, *Neoceratodus forsteri*, and it occurs naturally in only two locations, the Burnett and Mary rivers in Queensland, Australia, although it is being introduced into other rivers in an effort to ensure its survival. During the summer, the rivers dry up, and the lungfish survive in small pools. They cannot estivate.

Spawning takes place after the rainy season starts. The eggs are laid in masses of fifty to one hundred on aquatic plants. The young breathe through the gills and skin. They do not have adhering organs or external gills and do not undergo metamorphosis. They develop pectoral fins at about fourteen days and pelvic fins at about ten weeks, gradually assuming the adult shape. They feed on algae, but adults feed on small fishes, mollusks, crustaceans, insect larvae, and some plants and grow to a size of about 1.8 meters (6 feet) and forty-five kilograms (one hundred pounds). They have broad, flat heads with the mouth underneath, small eyes, and pointed tails. The body is olive green or brown above and pinkish below.

—Sue Tarjan

See also: Fauna: Africa; Fauna: Australia; Fauna: South America; Fish; Lungs, gills, and tracheas.

Lungfish Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Superclass: Gnathostomata
Class: Osteichthyes
Subclass: Sarcopterygii
Order: Dipnomorpha or Dipnoi
Families: Lepidosirenidae (African and South American lungfish); Dipnorhynchidae, Dipteridae, Phaneropleuridae, Ctenodontidae, Conchopomidae, Sagenodontidae, Ceratodiae (Australian lungfish)

Geographical location: Africa, Australia, and South America

Habitat: Freshwater only (rivers, lakes, swamps, and marshes)

Gestational period: Australian lungfish, twenty-one to thirty days; African and South American lungfish, eleven to fifteen days

Life span: Unknown; larger fish may live to be many years old

Special anatomy: Elongated bodies, continuous rear fins composed of connected dorsal, caudal, and anal fins; Australian lungfish—laterally compressed body, large scales, two pairs of flipperlike pectoral and pelvic fins, one lung; African and South American lungfish—eel-like body with small scales, two pairs of long, thin pectoral and pelvic fins, paired lungs

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LUNGS, GILLS, AND TRACHEAS

Type of animal science: Anatomy
Fields of study: Anatomy, histology

Gills, tracheas, and lungs are respiratory organs that are the primary sites of gas exchange in certain groups of animals. Gills are present in water-breathing animals, and tracheas and lungs are found in animals that breathe air. The structure and design of these organs are related to the particular manner of their function.

Principal Terms

BRONCHUS (pl. BRONCHI): an individual tube that is part of a lung and leads to one of the smaller lung parts

DIFFUSION: the passive movement of molecules from an area of high concentration (or pressure) to an area of lower concentration, often across a distance or a barrier

EPITHELIUM: a thin membrane that lines or coats a surface; in respiratory organs, the layer of cells that covers or lines the surface is called the respiratory epithelium

GILL: an extension or outpocketing of the body wall of an animal that creates a limblike structure, much as the fingers of a glove extend from the palm; gills are found almost exclusively in animals that breathe water

LAMELLA (pl. LAMELLAE): lamella means "platelike," and an individual lamella can be any one of several structures in the context of gas-exchange organs; these are usually found in gills

LUNG: a concave inpocketing of the body wall of an animal (in contrast to a gill); lungs occur in air-breathing animals

TRACHEA (pl. TRACHEAS): a tubular inpocketing of the body found mostly in insects and the spiders (arachnids), both of which are air breathers

The anatomy of a respiratory organ—gills, tracheas, or lungs—determines the way in which the organ functions. The design of the organ is specifically related to the way in which the animal functions in the world. Design refers to whether the structure is internal or external, large or small, and concerns some aspects of how it works. In order to understand the function of most organs and organ systems, it is necessary to know the structure.

The structure, or anatomy, can be considered from several different levels of organization. Gross structure is the size, shape, and position of the whole organ within the animal. Fine structure, on the other hand, refers to the microscopic level of organization. The microscopic structure includes the type and thickness of cells, the number of cells, and a description of the cell surface.

Common Features of Respiratory Organs

There are a few common features among gills, tracheas, and lungs in terms of both the gross structure and the fine structure. All three are organs of gas exchange and are therefore designed to permit oxygen and carbon dioxide gas to diffuse passively across this specific part of the body wall. Because one of the factors that directly affects diffusion is the total surface area, respiratory surfaces are greatly increased in order to maximize the movement of gas. Thus, the largest part of the total surface of an animal is the respiratory surface, no matter whether it is a lung, gill, or trachea. All three types of respiratory organs have openings to permit air or water to flow in (and out), tubes for conducting air or water to the exchange surface, the exchange surface itself, and the necessary support to hold the surface in place. The exceptions are those animals that have external gills with no enclosing cover.

The commonality of gas exchange function also imparts similar features to the microscopic level of structure. The epithelia of all three types of organs are thin and made of cells that are individually thin, providing less of a barrier to gas movement (although there is an exception to this in gill structure).

Gills

Gills are the most diverse and varied of all respiratory organs. Gills are found in aquatic animals, both vertebrate (animals with internal skeletons) and invertebrate (animals with external skeletons or no hard skeleton). With few exceptions, all animals with gills live in and breathe water, even if the volume of water is small and only one life stage of the animal breathes water. Most people are familiar with several types of animals that breathe water and use gills: fish, crabs, lobster, shrimp, crayfish, clams, aquatic insects, many worms (but not all), and numerous other animals. The form and function of gills have been variously modified in different animals through the process of natural selection.

The gills of many marine worms and of the marine sea hare and sea slug (both are related to snails) are thin, blind-ending tubules representing extensions of the body wall that form an elaborate treelike structure. For the most part, these are not complicated either in the pattern of blood flowing through them on the inside or in the way water is passed over them on the outside. Worms and sea slugs usually extend the gills into the water above and let the water's own movement bring the oxygen-filled water to the gills. Sea hares, however, cover the gills with a flap of skin, an extension of the body wall, and pump water over the gills by the beating action of numerous tiny cilia.

The gills of crabs are formed from a central structure, called an arch, and platelike extensions of the gill arch, called lamellae. Each lamella has a thin layer of epithelium, but because it is formed as an extension of the outside layer of the body, the epithelium is covered with a very thin layer of shell, called chitin. This is true of crabs, lobster, shrimp, and all the crustaceans. Nevertheless, the layer still permits the exchange of gases between the blood on the inside and water on the outside.

Each lamella is exposed to the water on both sides and has numerous supporting cells on the inside that keep the two sides apart so that blood may flow between. These support cells are called pillar cells, and if an observer could look down between the sides, the inside would look something like a forest. Blood comes into each lamella from a single channel, an artery, located at the top, and flows out through a vein located at the bottom of the lamella.

Not all lamella are alike even in the same crab, much less in crabs from habitats as different as the deep ocean and a tropical forest. One of the major differences is that some epithelia are specialized to transport salts actively across the gill in much the same way as the kidney does in a mammal. These gill lamella are thicker, with cells that are modified to transport sodium and chloride. Blue crabs, land crabs, and crayfish (which have podia instead of lamellae) are examples of animals with this type of specialization.

Not all crustaceans have gills that are lamellar in form; the crayfish and lobster have fingerlike projections of the gill arch. These projections are called podia and are more like the blind-ending tubules found in some worms than they are like the lamellae of crabs. The inside of the podia is divided, however, so that blood flows to the tip of the tube on one side and back to the animal on the other side of the podia.

Fish gills are not unlike those of a crab in many ways, but those of fish are more complex. Both are composed of flattened extensions of a trunklike support structure that contains the blood vessels. Gills of most teleost fish (bony fish, such as perch and bass) have further, or secondary, extensions from these, which are oriented perpendicular to the main lamella. The result is that the primary lamellae form a flat surface in a horizontal plane, and the secondary lamellae form the largest surface area, extending in a vertical plane. Some primitive fish, or those with adaptations to special conditions, have reduced secondary lamellae.

Some of the major differences between vertebrate and invertebrate gills are that fish gills are thinner, so that the layer separating the blood from the water is not as thick in fish. Fish-gill epithelia are usually about 20 percent as thick as those of the invertebrates described. Many fish have two different types of lamellae on the gill arch: primary and secondary lamellae. Many fish gills also contain specialized cells to transport salts across the border between the animal and the water, as happens in blue crabs.

Tracheas

Tracheas, found in insects, spiders, and related invertebrates, are long, thin tubes that extend from the outside of an animal to the inside, similar to the way a trachea leads to the lung in humans. The tracheal system, however, is made up entirely of branching tubules, each somewhat smaller than the one leading to it. The major tubes are called tracheas and the smaller ones are tracheoles; the smallest ones are as thin as hairs and reach within a very short distance of the cells inside the body. The outside opening to each trachea is controlled by a special structure, a spiracle, that can open and close the trachea.

Lungs

Lungs are actually the simplest type of respiratory system to describe in terms of animal type, distribution, and variations on the common form. Lungs are found only in air-breathing vertebrates, are always internalized, and have a single opening through which air flows both in and out. A single tube, the trachea, is the conducting passage for inspired and expired air. This tube branches into two smaller tubes, the bronchi, that lead to each of the individual sides, or lobes, of the lung. Tracheas and bronchi are usually, if not always, reinforced with cartilage rings for structural support to prevent collapse. Thus, animals with lungs actually have two, one on each side.

Tracheas and bronchi are not designed for gas exchange but are conducting tubes that also serve to "condition" the air before it reaches the lungs. Both tubes are lined with special cells that have hairlike projections called cilia on the surface. The cilia continually sweep small particles (such as dust) toward the outside to protect the lungs. Other cells in tracheas and bronchi secrete mucus to keep the surface moist and maintain high humidity so that air will be 100 percent humid when it reaches the alveoli.

At the end of the tubes of the lungs are the sac structures that form the gas-exchange surface. These very thin structures are the alveoli and are the site of gas movement into and out of the body. On the inside of each alveolus is an entire network of tiny blood vessels, capillaries, that supply the blood which is the source of the carbon dioxide that is exhaled and is the sink for the oxygen taken up at the alveoli.

Studying Respiratory Organs

The anatomy of gas-exchange organs is studied in whole living animals, in preserved specimens, and in sections prepared for microscopic examination. Both light microscopy and electron microscopy are used to study these organs. Light microscopy is simply the use of a microscope that requires standard lighting with the type of lens systems that have been used for decades; there are also some much more sophisticated systems that use specialized optics and lighting techniques. Electron microscopy uses beams of electrons to enable magnification of more than 100,000 times and the visualization of cells and their component parts. In some cases, miniaturized laser optics are used to examine the relatively large organs, such as lungs, while they are functioning. This application is often used in health-related studies and diagnosis of disease.

Studying the gross morphology of gills, tracheas, and lungs involves the dissection of a whole animal, either preserved or freshly deceased. Each option offers advantages, and both methods will be employed in a complete examination. Part of the dissection will be to determine qualitative features such as attachment points, spatial relations, and general appearance. A thorough study of the anatomy of an organ also includes measurements of features such as surface areas, number of parts, distances, and volumes. These are the quantitative measures, and they are applicable to all the organs. These numerical values are absolutely necessary in order to quantify the functions.

In the case of small animals, including shrews, insects, and fish the size of minnows, a dissection of the whole animal may have to be carried out with additional magnification, using a microscope designed for such work. These microscopes are called dissection microscopes and have enough distance between the lens and the object to allow dissection with small instruments by hand. In a few cases, the material is so small that microdissecting techniques developed by neurobiologists must be used. Traditional histological examination of respiratory organs has also revealed much about the design and nature of these structures. Histological examination (examining tissue structure, usually under a microscope) reveals the thickness of the epithelium, the number of layers, and some information about the nature of the material in the layers.

One of the purposes for studying the anatomy of all respiratory structures, and lungs in particular, is to improve medical applications. In veterinary medicine, knowledge of the general structure of lungs is crucial in treating diseased lungs and other respiratory problems. The use of animals in research has always been a controversial topic, but if such research is to be conducted properly, then accurate knowledge of the anatomy of the experimental animals is necessary. In this way, the animals can be kept healthy and monitored properly so that the intended purpose of the research may be realized.

Comparing Respiratory Structures

Evolutionary and taxonomic relationships are revealed in comparisons of respiratory structures in some groups of animals. Other relationships are evident in making comparisons between very different groups. There are only subtle differences in lung structure among the air-breathing vertebrates with lungs: amphibians, reptiles, and mammals. These differences occur more in the gross structure than at the cellular level, indicating how evolutionary pressures create successful adaptations.

The differences in the gill structures of crabs, worms, and fish from various habitats give valuable insight into evolutionary changes. Land crabs and air-breathing fish have fewer gills, fewer lamellae with thicker surfaces, and special structures to hold them in position. These latter are needed in air because without the support offered by water the gill lamellae would otherwise adhere to one another and not function. Similarly, some fish that live in water that contains too little oxygen must depend on air breathing and show these same adaptations.

One of the most widely studied aspects of comparing respiratory structures in different animals is the evolutionary transition from breathing water to breathing air. The transition from water to land has always interested scientists, and this level of anatomy is part of that interest. Biologists have examined the differences between air and water breathers in many groups of animals generally, and in groups that have both, such as the crabs and the amphibians, in particular. The features of interest include the surface area, thickness, position in the body, and pattern of circulation.

Few groups of animals display such a clear example of the evolution of structure and function in the tracheal system as do insects. Insects have a respiratory system, the tracheas, that reaches nearly to the cells themselves, bringing them oxygen-laden air and removing the carbon dioxide produced by the cells. It would seem, then, that there would be little need for a circulatory system to serve that function, and indeed there is but a rudimentary one in insects.

Anatomy of respiratory structures is also studied in relation to other functions and organ systems. The circulatory system provides the blood that exchanges gases with the water or air on the outside of the animal. Thus, the anatomy of the blood vessels is an important part of the anatomy. Similarly, the control of the flow of blood to the lungs or gills is critical for respiratory system function.

The fine structure of several types of respiratory systems, but primarily gills, is part of the study of other, nonrespiratory functions. The gills of some aquatic animals play an important role in regulating the animal's salt balance. In these animals, the fine structure of the gills shows where this process takes place and what special modifications are needed.

—Peter L. deFur

See also: Adaptations and their mechanisms; Anatomy; Cell types; Circulatory systems of vertebrates; Gas exchange; Histology; Osmoregulation; Physiology; Respiration and low oxygen; Respiration in birds; Respiratory system.

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MAMMALIAN SOCIAL SYSTEMS

Type of animal science: Behavior
Fields of study: Anthropology, ecology, ethology, zoology

Social organization in mammals ranges from solitary species, which come together only to breed, to large and intricately organized societies. Understanding the social systems of mammals is essential for effective conservation of species.

Principal Terms

BROWSER: an organism that feeds primarily on leaves and twigs of trees and shrubs rather than on grasses

CARNIVORE: a member of the meat-eating order Carnivora, which includes dogs, cats, weasels, bears, and their relatives

EUSOCIAL: a social system with a single breeding female; other members of the colony are organized into specialized classes (exemplified by bees, ants, and termites)

GRAZER: an organism that feeds primarily on grasses

PRIMATES: members of the order Primates—monkeys, apes, and their relatives

RODENT: a member of the order Rodentia—squirrels, rats, mice, and their relatives

SAVANNA: a grassland with scattered trees; some ecologists restrict the term to tropical regions

TERRITORY: an area that an animal defends against other members of the species and that often contains food, shelter, and other requirements for the individual or group

UNGULATE: a hoofed mammal from the order Artiodactyla (pigs, cattle, antelope, and their relatives) or from the order Perissodactyla (horses, rhinoceroses, tapirs, and their relatives)

All levels of social organization occur in mammals. There are solitary species, such as the mountain lion (*Felis concolor*), in which the male and female adults come together only to mate, and the female remains with her young only until they are capable of living independently. At the other numerical extreme are some of the hoofed mammals, which form herds of thousands of individuals. Other extremes might be considered in terms of specialization for social life. The most socially specialized mammal is probably the naked mole rat (*Heterocephalus glaber*) of Africa, which has a eusocial colony structure similar to that of ants, bees, and termites. Between these extremes, there are many variations. No current theory accounts for the diversity of mammalian social systems, but two broad generalizations are consistently employed to explain mammalian species' social organization. These are the environmental context in which the species exists and the mammalian mode of reproduction.

More than any other group of animals, mammals are required to form groups for at least part of their lives. Although in all sexually reproducing animals the sexes must come together to mate, mammals have an additional required association between mother and young: All species of mammal feed their young with milk from the mother's mammary glands. This group, a female and her young, is the basis for the development of mammalian social groups. In some species, the social group includes several females and their young and may involve one or more males as well.

The particular social organization adopted by a mammalian species is a response to the environmental conditions under which the species lives. The species' food supply and the distribution of that food supply are often the predominant determinants, but predators on the species are also important in determining the form of its social organization. The best way to see the effects of these factors on mammalian social structure is by example.

Primate Social Organization

The primates are the most social group of mammals. Monkeys demonstrate the importance of food supply and its distribution in determining social structure. The olive baboon (*Papio anubis*) occupies savannas, where it exists in large groups of several adult males, several adult females, and their young. Finding fifty or more animals in a group is not uncommon. Individual males do not guard or try to control specific females except when the females are sexually receptive. The group's food supply is in scattered patches, but each patch contains an abundance of food. The advantage of having many individuals searching for the scattered food is obvious: If any member finds a food-rich patch, there is plenty for all.

Predation probably also plays a role in the olive baboon's social organization. The savannas they roam have many predators and few refuges for escape. A large group is one defense against predators if hiding or climbing out of reach is not practical. Having many observers increases the chance of early detection, giving the prey time to elude

Primates, such as these chacma baboons, are the most social of mammal orders. Social structures offer increased safety from predators, efficient use of food resources, and a wider range of learning opportunities for the young. (Corbis) the predator. A large group can also mount a more effective defense against a predator. Large groups of baboons use both of these tactics.

The hamadryas baboon (*Papio hamadryas*), on the other hand, lives in deserts in which the food supply is not only scattered but also often found in small patches. The hamadryas baboon's social structure contrasts with that of the olive baboon, perhaps because the small patches do not supply enough food to support large groups. A single adult male, one or a few adult females, and their young make up the basic group of fewer than twenty individuals. Several of these family groups travel together under certain conditions, forming a band of up to sixty animals. Within the band, however, the family groups remain intact. The male of each group herds his females, punishing them if they do not follow him. The bands are probably formed in defense against predators. They break up into family units if predators are absent. At night, hamadryas baboons sleep on cliffs, where they are less accessible to predators. Because suitable cliffs are limited, many family groups gather at these sites. Hundreds of animals may be in the sleeping troop, probably affording further protection against predators.

Though there are exceptions, forest primates consistently live in smaller groups. In many species, fewer than twenty individuals make up the social group at all times. These consist of one or a few mature males, one or a few mature females, and their offspring. The groups are more evenly distributed throughout their habitat than are groups of savanna or desert primates. In forests, the food supply is more abundant and more evenly distributed. Escape from predators is also more readily accomplished—by climbing trees or hiding in the dense cover. Under these conditions, the advantages of large groups are minimal and their disadvantages become apparent. For example, in small groups the competition for mates and food is less.

Ungulate Social Organization

The ungulates have all levels of social organization. African antelope demonstrate social organizations that, in some ways, parallel those of the primates. Forest antelope such as the dik-dik (*Madoqua*) and duiker (*Cephalophus*) are solitary or form small family groups, and they are evenly spaced through their environment. Many hold permanent territories containing the needs of the individual or group. They escape predators by hiding and are browsers, feeding on the leaves and twigs of trees.

Many grassland and savanna antelope, such as wildebeest (*Connochaetes*), on the other hand, occur in large herds. They outrun or present a group defense to predators and are grazers, eating the abundant grasses of their habitat. In many cases, they are also migratory, following the rains about the grasslands to find sufficient food. The social unit is a group of related females and their young. Males leave the group of females and young as they mature. They join a bachelor herd until fully mature, at which time they become solitary, and some establish territories. The large migratory herds are composed of many female/young groups, bachelor herds, and mature males. The social units are maintained in the herd. Though it may seem strange to speak of solitary males in a herd of thousands, that is their social condition. The male territories are permanent in areas that have a reliable food supply year-round, but they cannot be in regions in which the species is migratory. Under these conditions, the males set up temporary breeding territories wherever the herd is located during the breeding season.

There are parallels with primate social patterns. Large groups are formed in grasslands, and these roam widely in search of suitable food. The groups are effective as protection against predators in habitats with few hiding places. Smaller groups are found in forests, where food is more evenly dispersed and places to hide from predators are more readily found.

Rodent Social Organization

Rodents also have all kinds of social organizations. The best known, and one of the most complex, is the social system of the black-tailed prairie dog (*Cynomys ludovicianus*). The coterie is the family unit in this case, and it consists of an adult male, several adult females, and their young. Members maintain a group territory defended against members of other coteries. Coterie members maintain and share a burrow system. Elaborate greeting rituals have developed to allow the prairie dogs of a coterie to recognize one another. Hundreds of these coteries occur together in a town. The members of these towns keep the vegetation clipped—as a result, predators can be seen from a distance. Prairie dogs warn one another with a "bark" when they observe a predator, and the burrow system affords a refuge from most predators.

The only vertebrate known to be eusocial is the naked mole rat. It occurs in hot, dry regions of Africa. The colony has a single reproductive female, a group of workers, and a group of males whose only function is to breed with the reproductive female. The workers cooperate in an energetically efficient burrowing chain when enlarging the burrow system. In this way, they are able to extend the burrow system quickly during the brief wet season. Digging is very difficult at other times of the year. The entire social system is thought to be an adaptation to a harsh environment and a sparse food supply.

Carnivore Social Organization

Most carnivores are not particularly social, but some do have elaborate social organizations. Many of these are based on the efficiency of group hunting in the pursuit of large prey or on the ability of a group to defend a large food supply from scavengers. The gray wolf (*Canis lupus*) and African hunting dog (*Lycaon pictus*) are examples. In both cases, the social group, or pack, consists of a male and female pair and their offspring of several years. There are exceptions, solitary carnivores and carnivores that form temporary family units during the breeding season, such as the red fox (*Vulpes vulpes*), which hunt prey smaller than themselves. The coyote (*Canis latrans*) can switch social systems to use the food available most efficiently. It forms packs similar to those of the gray wolf when its main prey is large or when it can scavenge large animals and is solitary when the primary available prey is small.

These examples and many others show that the social groups of mammals are based on the family group. The particular social organization employed by a species is determined by the ecological situation in which it occurs. The specific aspects of the environment that seem to be most important include food abundance, food distribution, food type, and protection from predators.

Fieldwork and Laboratory Studies

Observation has been a very important method of studying mammal societies. One of the reasons that primate and ungulate societies are so well known is that they are large and active during the day, and so are easily observable. The observer must take great pains to be inconspicuous or, in some cases, to become a part of the subject's environment. Small mammals (and sometimes larger mammals) have been kept in enclosures and observed to learn more about their social lives. The observer maps movements, records activities and interactions, and analyzes the data that result.

Simple observation is enhanced by manipulating the subjects in various ways. Individual animals can be marked, or in some cases they can be identified by natural color patterns, scars, or other marks. These marked individuals can be followed, and their behavior and interactions with other individuals observed. Radios and radioactive tracer elements are sometimes implanted in individuals, and these individuals are followed in the field. Much can be learned about a species' social behavior by following the locations of such tagged animals. In addition, they are more readily locatable for direct observation.

Small mammal species that are not readily observable are trapped live, marked, released, and recaptured. Mutually exclusive use of certain areas, areas used in common, and patterns of multiple captures in individual traps are some types of information from trapping that can be interpreted in terms of social behavior. Experiments are sometimes carried out in the natural context. A group or a specific individual is presented with an artificial situation, and any reactions to it are recorded, often on film or videotape.

Laboratory studies are also used to supplement the field observations. Psychological and physiological capabilities of organisms can best be studied in the controlled confines of a laboratory experiment. These data, however, must always be put back in the context of the field observations to make a meaningful contribution to the understanding of the species' social behavior.

Computer simulations and mathematical models have been used to explore the possible reactions of social systems to various environmental pressures. As with laboratory results, it is important to test predictions generated in these ways against the social system in nature before assuming their validity. Comparative studies of all the above types are of great importance. Related species, or different populations of the same species, that occur in different regions are studied and compared; these studies are tantamount to reading the data from a natural experiment.

Social Organization and Food

Mammalian societies are always organized around one or more females and their offspring. Males may also be part of the group, or they may form separate groups. The size and structure of the group are determined by the ecological setting in which it evolves. The particular ecological factors that seem to be of greatest importance in this determination are food supply, the distribution of the food, and predation (including the hiding places and escape routes available in the habitat).

Large groups occur when food is scattered in a patchy distribution. These groups are largest when the patches contain abundant food. Many organisms are more likely to find the scattered patches than is a single individual. As long as the patches have enough food for all members of the group, it is to each member's advantage to search with the group. On the other hand, if food is evenly dispersed in small units throughout the environment, the advantage of a group search is lost. Each individual will be better off searching for itself, and some strategy involving a very small social group or even solitary existence would be advantageous.

A somewhat similar argument follows for predators. If large prey are taken, a group of predators should be able to subdue the prey and protect its remains from scavengers more efficiently. If small prey are taken, solitary predators have the advantage, since the prey is easily dispatched and the predator will have it to itself. Many other factors are involved in determining the final form of a species' social organization, but the family unit and environmental context are fundamental in determination of all mammalian social structures.

Conservation of the mammal species that still exist on the earth requires knowledge of their social organization. Understanding that mammalian social organizations are responses to the environmental context in which they have evolved emphasizes the need to conserve entire ecosystems, not only the individual species that exist within them.

—Carl W. Hoagstrom

See also: Altruism; Communication; Communities; Competition; Ecological niches; Ethology; Groups; Herds; Insect societies; Mammals; Mating; Packs; Population analysis; Primates; Territoriality and aggression.

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MAMMALS

Type of animal science: Classification
Fields of study: Anatomy, systematics (taxonomy), zoology

Mammals are four-legged animals with backbones; they have a number of unique characteristics, including hair, constant warm body temperatures, mammary glands, and specialized teeth that are replaced only once. Mammals originated more than two hundred million years ago from mammal-like reptiles, and they eventually evolved into tree-dwelling, flying, burrowing, and aquatic forms.

Principal Terms

GENUS (pl. GENERA): a group of closely related species; for example, *Felis* is the genus of cats, and it includes the species *Felis catus* (the domestic cat) and *Felis couguar* (the cougar or mountain lion)

MAMMARY GLANDS: the milk glands that female mammals use to nurse their young

MARSUPIAL: a mammal that gives birth to a premature embryo and then lets it finish its development in a pouch

MONOTREME: a primitive mammal, such as the platypus and spiny anteater, which lays eggs and has other archaic features

ORDER: a group of closely related genera; in mammals, orders are the well-recognized major groups, such as the rodents, bats, whales, and carnivores

PLACENTALS: mammals that carry the embryo in the mother until it is born in a well-developed state; it is nourished in the womb by a membrane (the placenta)

VERTEBRATE: an animal with a backbone; this includes fish, amphibians, reptiles, birds, and mammals

Mammals are a group of vertebrates (animals with backbones) that have been the dominant animals on land and in the sea since the dinosaurs died 65 million years ago. Indeed, this period of time, the Cenozoic era, is often called "the age of mammals." About 4,170 species of mammals are alive today, but at least five times that many are now extinct. About 1,010 genera of mammals are living, but according to a 1945 tabulation, there were an additional two thousand extinct genera, and that number has greatly increased since 1945 as taxonomical research has progressed. Mammals have been very successful in occupying a great variety of terrestrial and aquatic ecological niches. These mammals include terrestrial meat-eaters and plant-eaters, tree-dwellers, burrowing forms, and aquatic forms. The largest mammals today are elephants, but the extinct hornless rhinoceros Paraceratherium was much larger, reaching six meters at the shoulder and weighing about twenty thousand kilograms. The largest mammals, however, are whales, which can weigh up to 150,000 kilograms in the case of the blue whale. That is larger than even the largest dinosaurs.

The Features of Mammals

Living mammals are easily distinguished from all other vertebrates by a number of unique evolutionary specializations. Unlike other vertebrates, mammals all have hair, have mammary glands to nurse their young, and bear live young (except for the most primitive egg-laying mammals, the platypus and the spiny anteater). Mammals maintain a constant, relatively high body temperature. They have a four-chambered heart and a very efficient digestive and respiratory system. Mammals grow rapidly as juveniles and then stop growing when they reach adult size, unlike other animals, which grow continuously throughout their lives.

In addition to these features, mammals have a number of features in their skeletons that make them easy to distinguish from birds or reptiles. Their limbs are designed for efficient walking or running and so are aligned straight under the body (rather than sprawling, as in reptiles). Their ribs are locked into a solid rib cage, so they do not use rib muscles to pump their lungs; instead, they have a diaphragm in the chest cavity to aid in breathing. Their skulls are highly modified, with fewer bones than in birds or reptiles. Some of these modifications include a single nasal opening, a bony palate that separates the breathing passages from the mouth, a large opening on the side of the skull for jaw muscles, and a pair of joints around the spinal column to hold up the head. They have only a single bone in their jaw, and the bones that form extra jaw bones in the reptile have been modified to form the three sound-conducting bones of the ear: the hammer, anvil, and stirrup. Finally, unlike the simple, peglike teeth of reptiles, mammal teeth are highly specialized: There are nipping incisors in front, big stabbing canines for grasping prey, and grinding teeth (molars and premolars) in the back of the jaw for processing food. These teeth are replaced only once (baby teeth are replaced by adult teeth), unlike the continuous replacement found in other animals.

Monotreme and Marsupial Mammals

Living mammals can be divided into three major groups, based on their mode of reproduction. These are the monotremes (egg-laying mammals), marsupials (pouched mammals), and placentals (mammals that carry their young to full term). The monotremes include the platypus and the spiny anteater of Australia and New Guinea. They lay a leathery egg much like that of reptiles, although the young is born after ten days and is then carried in a pouch. The females have mammary glands but no nipples, so the young must lap up the milk as it oozes from their skin. Monotremes have a number of other primitive reptilian features, such as a variable body temperature and a venomous claw in male platypuses. The platypus has a flexible, ducklike "bill," webbed feet, and a beaverlike tail, which it uses to swim in streams and catch freshwater insects and crayfish. The spiny anteater is covered with thick spines and lives on ants and termites, which it catches with its long, sticky tongue.

The more advanced mammals bear live young. One group, the pouched mammals, or marsupials, give birth to a premature, partially developed embryo. The embryo then climbs into the mother's pouch and fastens onto a nipple, where it finishes its development. Although this sequence makes the young more vulnerable than a placental embryo, which is always carried in the mother, there are advantages. If conditions are bad, a marsupial mother can abort the baby without losing her own life and survive to breed again. A female marsupial can also carry one baby in the pouch and become pregnant with another, allowing a higher rate of reproduction.

The most familiar marsupials are the kangaroo, koala, Tasmanian devil, and opossum, although there have been many other types of marsupials in the past, and many are still alive today in Australia and South America. Where marsupials lived in isolation with no competition from placental mammals, they evolved into many different body forms, which converge on the body forms of their ecological equivalents in the placentals. In Australia today, there are marsupial equivalents of cats, wolves, mice, flying squirrels, rabbits, moles, tapirs, and monkeys. Among extinct marsupials of South America, there were the equivalents of lions and of saber-toothed cats. As similar as these animals look to their placental equivalents in their external body form, they are not related to true cats, wolves, or the rest, since they are all pouched mammals.

Placental Mammals

Unlike marsupials, placentals must carry the embryo in their womb through their full development. To allow this, the embryo is nourished by an extra membrane surrounding it in the womb. This membrane, the placenta, is shed when the baby is born and is part of the "afterbirth." This mode of

Mammals come in many shapes, colors, and sizes. (PhotoDisc)

reproduction makes the placental embryo less vulnerable than a marsupial, but it means that the mother is more vulnerable, since she must carry a larger embryo for a longer time.

After the extinction of the dinosaurs, about 65 million years ago, the earth was open for a new group of large animals to evolve and take over the vacant ecological niches. Placental mammals underwent a tremendous diversification, until they occupied many ecological niches, and some reached the size of sheep. Most, however, were no larger than a cat. The placentals soon diversified into the edentates (anteaters, sloths, armadillos, and their relatives) and the rest of the mammalian orders (groups of genera). Like marsupials, edentates had their greatest success in isolation in South America, although the armadillo is successfully spreading northward. Edentates have a very primitive womb and a slow, variable metabolism compared to other placentals. Although the name "edentate" means toothless, only the anteaters are actually toothless; sloths and armadillos have simple, peglike teeth. Anteaters and armadillos eat ants and termites, and sloths hang upside down from branches, slowly munching leaves.

The rest of the placental mammals have occupied a variety of niches. One group, the insectivores, includes the shrews, moles, and hedgehogs. All these animals are small in size and have sharp teeth for eating insects and worms. The smallest shrews are only three centimeters long and weigh only two grams. They must eat almost continuously in order to make up for their small body size and rapid heat loss. They are so active and aggressive that they will attack animals many times their size. Moles live exclusively underground; they are nearly blind and have well-developed digging claws. Hedgehogs are covered with thick spines and roll up in a ball when they are threatened.

Carnivores and Archontans

In addition to the insectivores, the primary mammalian predators are the carnivorans. They include the feliforms (cats, hyenas, and mongoose) and the caniforms (dogs, bears, seals, sea lions, walruses, pandas, raccoons, weasels, and their relatives). Carnivora (except the panda) all live by killing prey and eating the meat. For this purpose, they have sharp cutting and slicing teeth and enlarged front canine teeth for stabbing. Most have sharp claws, and cats have claws that are retractable. Some carnivora, such as bears, eat fruit, berries, insects, fish, and almost anything else that is available. The pinnipeds, another group of carnivorans related to the bears, have become secondarily aquatic. These include the seals, sea lions, and walruses. Their aquatic specializations include a streamlined body for swimming, with hands and feet developed into flippers.

Another group of placentals, the archontans, have taken to the trees and the air. These include the primates (lemurs, monkeys, apes, and humans), the bats, the elephant shrews, and the colugos, or “flying lemurs.” Primates developed front-facing eyes with binocular color vision and agile, grasping hands and feet (with nails rather than claws) for life in the trees. Most have long tails, and New World monkeys can grasp with their tails. Apes and humans, however, have lost their tails. Most primates eat fruit, leaves, or seeds, and they have complex social behavior and well-developed brains.

Bats, on the other hand, have developed a membrane between their fingers that allows them to become excellent fliers. Most bats catch insects in flight by means of their sonar, and they fly at night, sleeping in caves during the day. Fruit bats, however, are much bigger, living in trees and eating fruit during the day.

Glires and Ungulates

The most successful group of mammals is certainly the Glires, or rodents and rabbits. There are more than 1,700 species of rodents alone, or about 40 percent of the mammals, and in numbers and rate of reproduction, they also are far more abundant than any other group of mammals. Rodents (including rats, mice, hamsters, gophers, squirrels, chipmunks, beavers, porcupines, guinea pigs, chinchillas, capybaras, and hundreds of less familiar forms) have developed chisellike incisors (front teeth), which are used for gnawing. They have adapted to a tremendous variety of ecological niches, including sheep-sized browsers (capybaras), terrestrial fruit-, seed-, and insect-eaters, tree-dwellers, and a variety of burrowing forms (such as gophers, ground squirrels, prairie dogs, and mole rats). The rabbits, hares, and pikas form another group that is distantly related to the rodents. Like rodents, they have chisel-like gnawing incisors, but there are two pairs instead of the single pair found in rodents.

Most of the large, plant-eating mammals are ungulates, or hoofed mammals. These include the even-toed artiodactyls (pigs, hippos, camels, deer, antelope, goats, sheep, and cattle), the odd-toed perissodactyls (horses, rhinos, tapirs, hyraxes, and their extinct relatives), the tethytheres (elephants, manatees, and sea cows), and the whales, along with a number of extinct archaic groups. Most ungulates have developed hooves, or hard protection on their toes for better running, and many have elongate limbs for fast running. Since they are nearly all herbivorous, most ungulates have developed a complex stomach system to digest large quantities of low-quality, relatively indigestible plant material. Ungulates have also modified their teeth, so that they have larger grinding teeth, which grow almost continuously. That allows them to chew tough, gritty vegetation without becoming toothless. Whales, dolphins, and porpoises are completely aquatic, having lost their hind limbs and developed flippers for front feet. Although they do not look like other hoofed mammals, they had terrestrial ancestors that looked like large bears and were similar to the most primitive ungulates.

Field and Laboratory Studies

Mammalogists use a wide variety of techniques. Traditionally, most studies of the behavior of mammals require going into the wild and observing their ecology. These are the types of studies that are most familiar from nature programs on television. Individual mammals can be studied in detail; in addition, scientists can observe and film their behavior. Often, they are trapped, labeled with a radiocollar or some permanent marking, and freed to be followed or recaptured later. To learn more, however, scientists must collect specimens and study them in the laboratory. There, the anatomy of the specimen can be studied in detail, or the specimen can be kept alive and its behavior and physiology examined much better than in the wild. Mammalogists also have begun to study the details of the biochemistry and molecular biology of mammals. Such studies allow the analysis of the genetic diversity, the evolutionary relationships, and the detailed molecular basis for many of the properties of mammals that were poorly understood before.

—*Donald R. Prothero*

See also: Aardvarks; American pronghorns; Antelope; Armadillos, anteaters, and sloths; Ba-

boons; Bats; Bears; Beavers; Camels; Cats; Cattle, buffalo, and bison; Cheetahs; Chimpanzees; Deer; Dogs, wolves, and coyotes; Dolphins, porpoises, and toothed whales; Donkeys and mules; Elephant seals; Elephants; Elk; Foxes; Fur and hair; Giraffes; Goats; Gophers; Gorillas; Grizzly bears; Hippopotamuses; Hominids; Hormones in mammals; Horns and antlers; Horses and zebras; Hyenas; Hyraxes; Jaguars; Kangaroos; Koalas; Lemurs; Leopards; Lions; Mammalian social systems; Mammoths; Manatees; Marsupials; Meerkats; Mice and rats; Moles; Monkeys; Monotremes; Moose; Mountain lions; Neanderthals; Orangutans; Otters; Pandas; Pigs and hogs; Placental mammals; Platypuses; Polar bears; Porcupines; Primates; Rabbits, hares, and pikas; Raccoons and related mammals; Reindeer; Reproductive system of female mammals; Reproductive system of male mammals; Rhinoceroses; Rodents; Ruminants; Seals and walruses; Sheep; Shrews; Skunks; Squirrels; Tasmanian devils; Tigers; Ungulates; Vertebrates; Warm-blooded animals; Weasels and related mammals; Whales, baleen.

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MAMMOTHS

Type of animal science: Classification
Fields of study: Anatomy, genetics, paleontology, zoology

Mammoths were prehistoric herbivorous mammals that became extinct approximately 10,000 to 3,800 years ago.

Principal Terms

IVORY: a white or honey-colored, bony substance

PATHOGENS: bacterium or viruses which cause diseases

PERMAFROST: soil layer below the earth's surface which never thaws

PLEISTOCENE: epoch occurring from 1.7 million to 10,000 years ago

TUNDRA: vast, mostly treeless area coated by ice and snow

Mammoths lived during the Ice Ages of the Pleistocene epoch. The oldest recovered mammoth fossils, found in Africa, are four million years old. Mammoths migrated from Africa, and several species of varying sizes and appearances evolved on other continents. Some mammoths crossed the Bering land bridge. Most mammoths favored tundra habitats formed when Ice Age glaciers covered parts of the northern hemisphere.

Anatomy

Most mammoths were large mammals, standing 3.5 to 4.3 meters (12 to 14 feet) tall when measured from the ground to the top of their shoulders. They weighed an average of seven metric tons (eight tons). Other mammoths were dwarves that only stood 1.8 meters (6 feet) tall. These small mammoths lived on islands, including Siberia's Wrangel Island and California's Channel Islands.

Woolly mammoths grew long, thick brown fur over a short undercoat, which protected them in cold climates. Fat layers, which were 7.5 centimeters (3 inches) thick, underneath their skin and in their shoulder hump and prominent brow, insulated their bodies. Each mammoth had two ivory tusks, which extended from their upper jaw. Mammoths' tusks were as long as five meters (sixteen feet) and curved toward and crossed over their trunk. During their lifespan, they had a total of twenty-four molars, which they shed. Because of their cold habitat, mammoths' ears were small, to retain heat.

Life Cycle

Mammoths roamed in herds, sometimes covering great distances in their search for vegetation, such as sedge and Arctic sagebrush, to eat. They spent an average of twenty hours a day finding and eating food. Chewing plants smoothed their teeth. When frozen land inhibited plant growth, the mammoths' stored fat provided essential nutrients and vitamins necessary to live.

Mammoths acted protectively toward immature, elderly, and infirm herd members. Males often fought over females during breeding seasons. Gestation lasted twenty-two months. Females usually produced one calf. Mammoths were unique because their mammary glands were near their front legs, unlike other mammals. Young mammoths remained with their mothers for several years, gradually becoming independent. Mammoths reached maturity by the age of twelve years.

Because of their size, adult mammoths had few predators. They moved slowly, which made them more vulnerable. The saber-tooth tiger killed mammoths for their flesh, and prehistoric humans hunted mammoths for their meat, hides, bones, and tusks. Human hunters devised strategies to capture mammoths in traps that confined their legs. Prehistoric people used mammoth tusks and

Image Not Available

bones to build shelters. Many mammoths died when they fell into naturally occurring sinkholes or were mired by quicksand and tarpits. Sometimes, male mammoths' tusks became entangled while fighting, and they starved to death.

Although mammoths were abundant during the Ice Ages, they became extinct in the period between 13,000 and 2000 B.C.E. Paleontologists estimate that the last mammoths died circa 1800 B.C.E. Researchers hypothesize that mammoths' extinction occurred because they were unable to adapt to the altered environment, specifically the warmer climate and different edible plants that existed after the final Ice Age, or that humans hunted them into extinction. Evidence exists for both theories. Mammoths migrated north as glaciers began to recede. When the final Ice Age glaciers disappeared about 9500 B.C.E., many placental mammals became extinct. Fossils suggest that some mammoths survived on an isolated Siberian Arctic island until 1500 B.C.E.

Recovering Specimens

Humans have found mammoth fossils on land and in bodies of water, such as the North Sea, which used to be dry land where mammoths roamed. The Siberian permafrost has preserved carcasses that have not decomposed or become too dry for examination. A baby mammoth that scientists called Dima was located in 1977 and had intact red blood cells. Many mammoth fossils have been located during the digging of the Eastside Reservoir, near Los Angeles, California, including a female found in April, 1999, which is considered to be the best preserved mammoth specimen.

Mammoth Facts

Classification:
Kingdom: Animalia
Subkingdom: Metazoa
Phylum: Vertebrata
Class: Mammalia
Subclass: Eutheria
Order: Proboscidea
Suborder: Elephantoidea (elephant-like)
Family: Elephantidae
Genus and species: Mammathus africanavus (North African), *M. columbi* (Columbian), *M. exilis* (dwarf), *M. imperator* (North American), *M. jeffersonii* (southern North America), *M. meridionalis* (European), *M. primigenius* (wooly), *M. subplanifrons* (southeast Africa), *M. trogontherii* (steppe mammoth)
Geographical location: Africa, Northern Europe, North America, Eurasia, Siberia
Habitat: Tundra, grasslands
Gestational period: Twenty-two months
Life span: Sixty years
Special anatomy: Curved tusks, fatty hump, protruding brow

In 2000, paleontologists recovered what they believed to be the first completely frozen mammoth on Siberia's Taimyr Peninsula. Named the Jarkov mammoth, it was airlifted to a cold cave research facility, encased in a block of permafrost that included plants, insects, and pathogens, which scientists hoped would provide insights to mammoths' environments. They planned to test a hypothesis that mammoths became extinct due to an epidemic. Initially, scientists hoped to secure enough DNA to clone the mammoth, but it turned out that radar readings had incorrectly shown more of the carcass remaining than actually existed.

—Elizabeth D. Schafer

See also: Elephants; Extinction; Prehistoric animals; Teeth, fangs, and tusks.

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MANATEES

Type of animal science: Classification
Fields of study: Conservation biology, ethology, evolutionary science, marine biology, physiology, population biology, wildlife ecology, zoology

Manatees are aquatic, herbivorous animals of the order Sirenia that inhabit warm, shallow waterways. Decreasing habitat and other challenges from humans have caused all four of its species to be threatened or endangered.

Principal Terms

METAZOA: organisms which are multicellular
MOLARS: flat, stout teeth used for grinding food
NOTOCHORD: longitudinal, flexible rod located between the gut and nerve cord
PLACENTA: structure that connects a fetus to the mother's womb; indicative of internal gestation of young
SIRENIAN: refers to animals in the family Sirenia, the only completely aquatic herbivorous mammals; the two families, those of the dugongs and manatees, contain four species
VIBRISSAE: whiskers or bristles, used to provide positional information to an animal

The Florida manatee (*Trichechus manatus latirostris*) is found primarily in the Florida peninsula, but can occasionally be sighted as far north as Virginia and west to Mississippi. The Antillean manatee (*Trichechus manatus manatus*) shows a patchy distribution, including northeastern South America, southern Texas, Mexico, and the Caribbean. *Trichechus senegalensis*, the West African manatee, can be found on the west coast of Africa from Senegal to Angola. The Amazonian manatee, *Trichechus inunguis*, is found throughout the Amazon river drainage basin.

The species are distinguished by their geographical distributions, and while they are physically very much alike, some differences exist. Manatees all exhibit a streamlined body, full around the middle with no visible neck, tapering to a paddle-shaped tail used for propulsion. They have two small pectoral flippers on their upper bodies that are used for steering and bringing food to the mouth. The lips are long and flexible, and help in funneling plants into their mouths. Manatees are grayish-brown in color and have sparse, bristly hair scattered thinly over their torsos. They have molars at the back of their mouths, and unlike most other mammals, as the front molars wear down they are continually replaced by new teeth from the back of the mouths. Adult West Indian and West African manatees average about ten feet in length and weigh approximately 800 to 1200 pounds. Amazonian manatees are smaller, shorter, and more slender, averaging about eight feet in length and less than eight hundred pounds.

Adapted for the Aquatic Life

Streamlined bodies and flippers are ideal for the aquatic life of a manatee. They are agile and typically cruise in search of food at speeds of two to six miles per hour, but can swim as fast as fifteen miles per hour. While they have been sighted diving to depths of about thirty-three feet, they primarily forage for food no deeper than ten feet. Manatees can stay underwater for up to twenty minutes, but typically surface every two to three minutes for air.

Manatees spend most of their day foraging for aquatic plants and will consume between 4 and 9 percent of their body weight in wet vegetation daily. The animals are nonaggressive and non-

Manatees have streamlined bodies with no visible neck, which increases their efficiency in swimming. (Digital Stock)

territorial and spend the rest of their time traveling, investigating objects, and socializing. Manatees are considered semisocial, and the typical social unit is a female and her calf; however, congregations of up to two hundred individuals can be found near warm water sources such as power plant outfalls and hot springs, especially during winter months.

Male manatees are sexually mature at about nine to ten years of age, and females at about seven to eight years. Mating takes place in the water, and the female is accompanied by, and mates with, several males. Gestation takes about twelve months; the newborn calf measures about four feet and weighs sixty to seventy pounds. Calves remain close to their mothers for up to two years. The calf is dependent on its mother for nutrition, and for learning about feeding and resting areas, migratory routes, and warm water refuges. It is believed that manatees can live to sixty years in the wild; however, habitat destruction and injury by boats and fishing lines are seriously endangering manatees worldwide.

—*Karen E. Kalumuck*

See also: Fins and flippers; Lakes and rivers; Marine animals; Marine biology; Seals and walruses.

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Manatee Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebra
Class: Mammalia
Subclass: Eutheria
Order: Sirenia
Family: Trichechidae (manatees)
Genus and species: Trichechus manatus (West Indian manatee, with subspecies *latirostris*, the Florida manatee, and *manatus*, the Antillean manatee); *T. senegalensis* (West African manatee); *T. inunguis* (Amazonian manatee)
Geographical location: Florida, Caribbean, and northern South America; West Africa; Amazon River basin
Habitat: Warm tropical and subtropical water, including shallow coastal waters, estuaries, and rivers
Gestational period: Approximately twelve months
Life span: Twenty-eight years in the wild; fifty to sixty years in captivity
Special anatomy: Flat, paddle-shaped tail; two pectoral flippers; nasal openings at the top of the snout; large, flexible upper lip equipped with vibrissae attached separately to nerve endings and each with its own blood supply

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MARINE ANIMALS

Type of animal science: Ecology
Fields of study: Behavior, marine biology, oceanography, physiology

The world's oceans contain the largest and most varied array of life forms on earth. The marine environment is divided into coastal, open water, deep-sea, and bottom zones, and the lives of animals living in each of these regions are dictated by the physical conditions present in these zones. Due to the inaccessibility and hostility to human life of most of the ocean environment, much remains to be learned about the biology and ecology of most of the animals living in the marine world.

Principal Terms

BENTHOS: organisms living upon, or below, the surface of the substrate that forms the ocean floor

ESTUARY: the region where freshwater rivers empty into and mix with the marine environment of oceans or seas

INTERTIDAL ZONE: the portion of the marine environment located between low and high tide marks

NEKTON: larger marine animals that have sufficient powers of locomotion to move independently of water currents

NERITIC ZONE: the shallow water areas that extend over the continental shelves up to the low tide mark

PELAGIC ZONE: portions of the marine environment that are located away from the shorelines; the open ocean environment

PLANKTON: small animals and plants that drift with the water currents in the marine environment

Approximately 71 percent of earth's surface is covered by salt water, and the marine environments contained therein constitute the largest and most diverse array of life on the planet. Life originated in the oceans, and the salt water that comprises the largest constituent of the tissues of all living organisms is a vestigial reminder of the aquatic origins of life.

Marine Zones

The marine environment can be divided broadly into different zones, each of which supports numerous habitats. The coastal area between the high and low tide boundaries is known as the intertidal zone; beyond this is the neritic zone, relatively shallow water that extends over the continental shelves. The much deeper water that extends past the boundaries of the continental shelves is known as the oceanic zone. Open water of any depth away from the coastline is also known as the pelagic zone. The benthic zone is composed of the sediments occurring at the sea floor. Areas in which freshwater rivers empty into the saltwater oceans produce a continually mixed brackish water region known as an estuary. Estuarine zones often also include extensive wetland areas such as mud flats or salt marshes.

Zones in the marine environment are distributed vertically as well as horizontally. Life in the ocean, as on land, is ultimately supported by sunlight in most cases, used by photosynthetic plants as an energy source. Sunlight can only penetrate water to a limited depth, generally between one hundred and two hundred meters; this region is known as the photic or epipelagic zone. Below two hundred meters, there may be sufficient sunlight penetrating to permit vision, but not enough to support photosynthesis; this transitional region may extend to depths of one thousand meters and is known as the disphotic or mesopelagic zone. Below this depth, in the aphotic zone, sunlight cannot penetrate and the environment is perpetually dark, with the exception of small amounts of light produced by photoluminescent invertebrate and vertebrate animals. This aphotic zone is typically divided into the bathypelagic zone, between seven hundred and one thousand meters as the upper range and two thousand to four thousand meters as the lower range, where the water temperature is between 4 and 10 degrees Celsius. Beneath the bathypelagic zone, overlying the great plains of the ocean basins, is the abyssalpelagic zone, with a lower boundary of approximately six thousand meters. Finally, the deepest waters of the oceanic trenches, which extend to depths of ten thousand meters, constitute the hadalpelagic zone. In each of these zones, the nature and variety of marine life present is dictated by the physical characteristics of the zone. However, these zones are not absolute, but rather merge gradually into each other, and organisms may move back and forth between zones.

Plankton

Marine life can be divided broadly into three major categories. Those small organisms that are either free-floating or weakly swimming and which thus drift with oceanic currents are referred to as plankton. Plankton can be further divided into phytoplankton, which are plantlike and capable of photosynthesis; zooplankton, which are animal-like; and bacterioplankton, which are bacteria and blue-green algae suspended in the water column. Larger organisms that can swim more powerfully and which can thus move independently of water movements are known collectively as the nekton. Finally, organisms that are restricted to living on or in the sediments of the seafloor bottom are referred to as the benthos.

The phytoplankton, which are necessarily restricted to the photic zone, are by far the largest contributors to photosynthesis in the oceans. The phytoplankton are therefore responsible for trapping most of the solar energy obtained by the ocean (the primary productivity), which can then be transferred to other organisms when the phytoplankton are themselves ingested. The phytoplankton are composed of numerous different types of photosynthetic organisms, including diatoms, which are each encased in a unique "pillbox" shell of transparent silica, and dinoflagellates. The very rapid growth of some species of dinoflagellates in some areas results in massive concentrations or blooms that are sometimes referred to as red tides. Chemicals that are produced by red tide dinoflagellates often prove toxic to other marine organisms and can result in massive die-offs of marine life. Smaller photosynthetic plankton forms comprise the nanoplankton and also play an important role in the photosynthetic harnessing of energy in the oceans.

The zooplankton are an extremely diverse group of small animal organisms. Unlike the phytoplankton, which can make their own complex organic compounds via photosynthesis, the phytoplankton must ingest or absorb organic compounds produced by other organisms. This is accomplished by either preying upon other planktonic organisms or by feeding on the decaying remains of dead organisms. A number of zooplankton species also exist as parasites during some portion of their life cycles, living in or upon the bodies of nekton species. The largest group of zooplankton are members of the subphylum Crustacea, especially the copepods. These organisms typically possess a jointed exoskeleton, or shell, made of chitin, large antennae, and a number of jointed appendages. Space precludes a definitive listing of all of the zooplanktonic organisms; however, virtually all of the other groups of aquatic invertebrates are represented in the bewildering variety of the zooplankton, either in larval or adult forms. Even fishes, normally a part of the nekton, contribute to the zooplankton, both as eggs and as larval forms.

The bacterioplankton are found in all of the world's oceans. Some of these, the blue-green algae (cyanobacteria), play an important role in the photosynthetic productivity of the ocean. Bacterioplankton are usually found in greatest concentrations in surface waters, often in association with organic fragments known as particulate organic carbon, or marine snow. Bacterioplankton play an important role in renewing nutrients in the photic zones of the ocean; such renewal is important in maintaining the photosynthetic activity of the phytoplankton, upon which the rest of marine life is in turn dependent.

One of the principal problems facing plankton is maintaining their position in the water column. Since these organisms are slightly denser than the surrounding seawater, they tend to sink. Clearly this is a disadvantage, particularly since plankton typically have very limited mobility. This is especially true for the photosynthetic phytoplankton, which must remain within the photic zone in order to carry on photosynthesis. A number of strategies have evolved among planktonic species to oppose this tendency to sink. Long, spindly extensions of the body provide resistance to the flow of water. Inclusions of oils or fats (which are less dense than water) within the body provide positive buoyancy by decreasing the overall density of the plankton. Finally, some species, such as the Portuguese man-o'-war, generate balloonlike gas bladders, which provide enough buoyancy to keep them at the very surface of the epipelagic zone.

Nekton

The nekton is composed of those larger animals that have developed locomotion to a sufficient degree that they can move independently of the ocean's water movements. Whereas the plankton are principally invertebrates, most of the nekton are vertebrates. The majority of the nekton are fishes, although reptile, bird, and mammalian species are also constituent parts. The oceanic nekton are those species which are found in the epipelagic zone of the open ocean. These include a wide variety of sharks, rays, bony fishes, sea birds, marine mammals, and a few species of reptiles. Some members of the oceanic nekton, such as blue sharks, oceanic whitetip sharks, tuna, flying fish, and swordfish, spend their entire lives in the pelagic environment; these are said to be holoepipelagic. Others, the meroepipelagic nek-

The nekton is made up of animals with independent locomotion, such as fish. (Digital Stock)

Hydrothermal Vents

One of the most exciting discoveries made by deep-sea biologists occurred as recently as 1977. Scientists aboard the deep submersible *Alvin* happened upon a previously unknown hydrothermal vent community while studying the Galápagos Rift Zone, 2,700 meters below the sea surface. These communities were composed of high densities of organisms never before seen by humans, in an otherwise barren landscape of sparse benthic life. Since their discovery, over four hundred species have been recovered from hydrothermal vents, including one new class, three new orders, and twenty-two new families of animals. Among the more notable animals are giant clams, mussels, and vestimentiferan tubeworms. Vestimentiferan tube worms are about two meters long and lack a digestive tract.

These dark ecosystems obviously cannot be supported by photosynthetic organisms, but instead, chemoautotrophic bacteria that derive energy from sulfide are the primary producers that feed this unique food web. Vestimentiferan tube worms have these chemoautotrophic bacteria living symbiotically within their tissues. These bacteria directly provide the tube worms with the fixed carbon they need to survive, which is why the worms do not have digestive tracts. They do not need to eat. Since the discovery of hydrothermal vent communities in the Galápagos rift, similar communities have been discovered along rifts in the Atlantic, Indian, and western Pacific Oceans.

ton, only spend a portion of their lives in the epipelagic zone, returning to coastal areas to mate, as with herring and dolphins, or returning to freshwater, as with salmon and sturgeon. Sea birds are a special case: Although they spend much of their time flying over the epipelagic zone and nest on land, they feed in the epipelagic zone and some species may dive as deep as one hundred meters in search of prey. Some members of the nekton enter the epipelagic only at certain times in their life cycle. Eels of the family Anguillidae spend most of their lives in freshwater but return to the epipelagic zone to spawn. Additionally, at night many species of deep-water fishes migrate up into the epipelagic to feed before returning to deeper waters during the daylight hours.

The pelagic environment, unlike the terrestrial one, is profoundly three-dimensional. Nektonic animals can move both horizontally and vertically within the water column. Furthermore, since most of the pelagic environment is essentially bottomless, since there is no apparent or visible ground or substrate, the environment is basically uniform and featureless. These characteristics play an important role in the evolution of the behavior of nektonic animals. Fishes suspended in an essentially transparent and featureless medium have no shelter in which to hide from predators, nor are there any apparent landmarks to serve as directional cues for animals moving horizontally from place to place. Life in the open ocean has therefore favored adaptations for great mobility and speed with which to move across large distances and escape from predators, as well as camouflage and cryptic coloration designed to deceive potential predators or prey.

As is the case for plankton, most nektonic animals are denser than the surrounding seawater, and maintaining position in the water column is of the first importance. Most fishes possess a swim bladder, a gas-filled membranous sac within their body that opposes the tendency to sink and provides the fish with neutral buoyancy. Sharks and rays lack a swim bladder, but accumulate large concentrations of fats and oils in their liver, which also help counter the tendency to sink. Large, fast-swimming species of shark, tuna, and many billfish also rely on the generation of hydrodynamic lift to maintain vertical position in the water column. The tail and body of these fishes generate forward thrust, moving the animal through the water, and the fins, notably the pectoral fins, generate lift from the water flowing over them in a manner similar to that of an airplane's wing. Thus these animals fly through the water, but are in turn required to move continuously in order to generate lift.

All members of the nekton are carnivores, feeding on other nektonic species or upon plankton, particularly the larger zooplankton. In general, the size of the prey consumed by nekton is directly related to the size of the predator, with larger species consuming larger prey. However, the organisms that feed upon plankton, the planktivores, include a wide variety of fish species such as herring, salmon, and the whale shark, the largest extant fish species. They also include the largest marine animals of all, the baleen whales. The case of large animals feeding upon very small plankton directly addresses the need of all animals to meet their energy requirements. For all animals, the amount of energy obtained from food consumed must necessarily exceed the energy expended in acquiring the prey. Very large animals, such as whales and whale sharks, require a great deal of energy to move their bodies through the aquatic environment, but because of their great size they are necessarily less agile than smaller forms. The amount of energy required to chase and catch these smaller animals would generally exceed the energy derived from ingesting them. Plankton, however, are relatively easy to obtain due to their very limited mobility. However, because of their small size, vast quantities of plankton must be ingested in order to meet the metabolic requirements of large marine animals. Some very large species that are not planktivores solve the energy problem by evolving behaviors for acquiring specialized diets that yield higher energy. White sharks, for example, feed on fish when young, but as they age and increase in size, marine mammals, notably seals and sea lions (pinnipeds), become a major part of their diet. Marine mammals all possess blubber, an energy-rich substance that yields much more energy than fish. Similarly, sperm whales, the largest hunting carnivores on the planet, have a diet that consists in large part of giant squid, which are hunted in the ocean depths largely using the whale's acoustic echolocation sense. Orcas (killer whales) effectively use pack hunting techniques to hunt larger whales and other marine mammals.

The deeper regions of the ocean are dominated by different types of nekton. However, we know even less about their ecology due to their relative inaccessibility. The disphotic or mesopelagic zone contains many animal species that migrate vertically into surface waters at night to feed upon the plankton there. Many of these organisms possess large, well-developed eyes and also possess light organs containing symbiotic luminescent bacteria. The majority of the fish species in this group are colored black and the invertebrates are largely red (red light penetrates water less effectively than do longer wavelengths, and these animals appear dark-colored at depth). Beneath this zone, in the bathypelagic and abyssalpelagic zones, there are many fewer organisms and much less diversity than in the shallower levels. Animals in this region are typically colorless and possess small eyes and luminescent organs. Because organisms in these deep regions are few and far between, many species have become specialized in order to maximize their advantages. Thus, deep-sea fish are characterized by large teeth and remarkably hinged jaws that allow them to consume prey much larger than might be expected from their size. Similarly, since encounters with potential mates are presumably scarce, a number of unique reproductive strategies have evolved. In the anglerfish (Ceratius), all of the large individuals are female and the comparatively tiny males are parasitic, permanently attaching themselves to the female. Much, however, still remains to be learned of the ecology of these deep-sea organisms.

Benthos

The benthos of the world's oceans consists of animals that live on the solid substrate of the water column, the ocean floor. Scientists typically divide benthic organisms into two categories, the epifauna, which live on the surface of the bottom at the sediment-water interface, and the infauna, those organisms living within the sediments. In shallow water benthic communities, members of virtually every major animal group are represented. Ecologists generally differentiate between soft bottom benthic communities (sand, silt, and mud, which comprise the majority of the benthic zone) and rocky bottom communities, which are less common proportionately. Soft bottom communities have an extensive diversity of burrowing infauna, such as polychaete worms, and mollusks, such as clams. Rocky bottom communities possess a larger proportion of epifauna, such as crustaceans and echinoderms (starfish, sea urchins, and brittle stars), living on the surface of what is essentially a two-dimensional environment. Vertical faces of the hard bottom environment, such as canyon walls or coral reefs, are often home to a wide variety of animals occupying various crannies and caves. In some parts of the world, kelp plants that are anchored to the substrate and which extend to the water surface dominate the rocky bottom substrate. In these kelp forests, large kelp plants (actually a species of brown algae) form a forestlike canopy that plays host to a wide and complex array of animals extending throughout the water column. On the deep ocean floor, the benthos is composed of representatives of virtually every major animal group: crustaceans such as amphipods, segmented polychaete worms, sea cucumbers, and brittle stars. Less common are starfish, sea lilies, anemones, and sea fans. The fishes of the deep benthos include rat tails and a number of eel species.

Estuaries, where freshwater rivers empty into marine environments, are typified by large, cyclic changes in temperature and salinity. Although estuaries have played an important role in human history as the sites of major ports, the variety and number of estuarine species tend to show less diversity of animal species due to the difficulty in adapting to the large swings in environmental conditions.

Animal life in the sea, like that on land, shows an astonishing variety of forms and behaviors, the result of natural selection. The inaccessibility and hostility of much of the world's oceans to human exploration and observation leaves much yet to be learned about the biology of marine life. Much remains to be achieved in order to obtain a useful body of knowledge concerning life in the sea.

—*John G. New*

See also: Bioluminescence; Clams and oysters; Coral; Crabs and lobsters; Crustaceans; Deep-sea animals; Dolphins, porpoises, and toothed whales; Echinoderms; Eels; Elephant seals; Fins and flippers; Fish; Horseshoe crabs; Ichthyosaurs; Jellyfish; Lakes and rivers; Lampreys and hagfish; Lungfish; Manatees; Marine biology; Mollusks; Octopuses and squid; Otters; Penguins; Protozoa; Reefs; Reptiles; Seals and walruses; Salmon and trout; Seahorses; Seals and walruses; Sharks and rays; Snakes; Sponges; Starfish; Swamps and marshes; Tentacles; Tidepools and beaches; Turtles and tortoises; Whale sharks; Whales, baleen; White sharks; Zooplankton.

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MARINE BIOLOGY

Type of animal science: Fields of study
Fields of study: Conservation biology, ecology, environmental science, invertebrate biology, marine biology, oceanography, zoology

Marine biology is the study of the plants, animals, fungi, protists, and microbes that live in the oceans. Because humans are not well adapted to marine environments, it is difficult to observe and study marine organisms in their natural surroundings. However, with modern technology such as scuba, submarines, and remote cameras, marine biologists are gaining considerable information about marine organisms.

Principal Terms

AUTOTROPHS: primary producers; organisms that are self-feeding; includes photosynthetic and chemoautotrophic organisms

BENTHIC: the area of the ocean floor; organisms associated with the sea bottom

EPIFAUNA: animals that live on the sea floor

HETEROTROPH: consumers; organisms that must acquire energy by consuming organic material

INFAUNA: animals that live in the sea floor

INVERTEBRATES: animals that lack backbones

LITTORAL: the area in the intertidal zone; organisms that live in the intertidal

NEKTON: organisms that are strong swimmers and can move against ocean currents

PELAGIC: the area of open water in the oceans; organisms that occur in the water column

PLANKTON: organisms that drift in the ocean currents because they have limited power of locomotion

The earliest known life forms were marine. The oceans cover 71 percent of earth's surface and have an average depth of 3,800 meters, which means that they represent 99 percent of the living space on the planet. Marine biology is the study of all the organisms that occupy this space. Despite having 99 percent of the planet's living space at their disposal, only 250,000 of approximately 1.8 million described living species (14 percent) are marine. While the oceans may lack diversity at the level of species, they are home to members of thirty-one of thirty-four animal phyla, about twice the number of phyla that are found on land or in freshwater.

Because of its vastness and humans' inability to easily visit deep waters, the oceans remain the least studied habitats on earth. For example, scientists know that giant squid eighteen meters in length, larger than any other invertebrate, exist because they have been found in the stomachs of sperm whales and washed up on beaches. However, no human has ever seen one of these creatures living in their natural habitats. If this sheet of paper represented the area of the ocean, the area directly observed by people would be smaller than the period at the end of this sentence. Despite the small amount of study in marine biology, research in these systems has contributed greatly to the understanding of living systems.

Oceanographers divide the ocean into zones that have distinct physical characteristics. These physical conditions, in turn, select for different organisms that are adapted to the set of conditions. The benthic realm refers to the sea floor and extends from the high intertidal zone, where ocean meets terrestrial land, to depths of eleven kilometers at oceanic trenches, the deepest parts of the ocean where the ocean floor slowly sinks back in to the interior of the earth. Organisms that live in, on, or near the ocean floor are appropriately called benthic organisms, and represent 98 percent of all marine creatures. The pelagic realm of the ocean refers to the open ocean, basically the space between the benthos and the sea surface. Pelagic organisms, representing the remaining 2 percent of marine species, live in the water column. The pelagic zone can be divided into the photic and aphotic zones, a distinction that is especially important for photosynthetic organisms. The photic zone is the shallow part of the ocean that receives enough sunlight to support photosynthesis, which is about two hundred meters deep in the clearest waters, and as shallow as three meters in turbid coastal waters. The aphotic zone is where there is not enough light to support photosynthesis, and extends from the bottom of the photic zone to the ocean floor.

Organisms of the Open Ocean

Pelagic creatures can be further categorized into plankton, which drift around in the ocean currents, and nekton, which are capable of swimming against currents. Photosynthetic plankton live in the photic zone and are called phytoplankton. These algae form the base of the food web in the open ocean and are eaten by zooplankton (heterotrophic plankton including protists and small crustaceans such as copepods). Zooplankton are eaten by small fishes, which are eaten by larger fishes, which are eaten by sharks, birds of prey, and people. The open ocean food web is one of the longest food webs known, partly because it starts with the smallest photosynthetic organisms.

The largest animal migrations on earth occur every day in the open oceans, in a process called diel vertical migration. Zooplankton, midwater fish, squid, and krill migrate to shallow waters at night and then return to the dark depths during the day. The main reason for this daily migration is probably to feed, and to avoid being eaten. Food densities are highest in the shallow productive waters, so these predators move to the shallows to feed at night. Because they would be susceptible to their own visually oriented predators in the well-lit shallows, they return to the dark depths during the day to avoid being eaten.

In the aphotic zone, there are only heterotrophic organisms that are supported mostly by organic material that rains down from the lit environments above. These animals live in darkness, with the exception of light produced by the animals themselves, called bioluminescence. It is common for sea creatures (especially ones at intermediate depths) to house luminescent bacteria within their tissues, which are able to produce light for communication, as a lure to attract prey, or to light their bottom surface to conceal their silhouette against the dimly lit background from above. Anglerfish are deep-sea predators that attract prey near their mouths by dangling a bioluminescent lure in front of their head.

The density of organisms in the deep sea is low. Because of this low density, a long period of time can pass between meals, or between encounters with the opposite sex. To deal with the problem of infrequent meals, deep-sea creatures are often gigantic compared to shallow-water relatives. Large size allows for storage of food reserves that sustain the animals between meals. Predatory fish also have large mouths and stomachs that allow them to take full advantage of any meal, regardless of size. To overcome the problem of rare mates, the miniature males of some anglerfish have the unusual adaptation of attaching themselves to the female, where they live the rest of their lives as parasitic sperm producers.

Organisms of the Bottom

Most marine species are found at the ocean floor. They occur in such familiar marine habitats as mud flats, sand flats, beaches, coral reefs, kelp forests, and the rocky intertidal. The main primary producers in benthic habitats are macroscopic seaweeds that grow attached to the bottom or microscopic algae that grow within the tissues of animals such as corals, sponges, and bryozoans. Benthic animals include mobile creatures such as fish, crabs, shrimp, snails, urchins, sea stars, and slugs. Additionally, there are numerous animals that, unlike familiar terrestrial animals, never move around as adults. These sessile animals include

Oases on the Deep Ocean Floor

Although animal life exists on the ocean floor, much of that zone is barren, with relatively few animals distributed at large intervals. One of the most exciting discoveries in marine biology during the last quarter of the twentieth century occurred in 1977 with the discovery of abundant animal life in the regions immediately surrounding four hot water geysers on the ocean floor. These hydrothermal vents, located in the eastern Pacific Ocean at a depth of approximately 2,700 meters, boasted a spectacular variety of species all located within a few meters of the vent. The geyser is caused when water is heated by Earth's mantle and rises rapidly through the cooler waters above. Water in the geyser reaches temperatures of 8 to 16 degrees Celsius, as opposed to the surrounding water, which is about 2 degrees Celsius. This warm water is also rich in dissolved hydrogen sulfide gas, which serves as a source of energy for bacteria at the vent. The bacteria, in turn, act as food for the various animal species in the area of the vent. Similar hydrothermal vents, each with a population of animals surrounding it, have since been discovered at other sites in the Atlantic and Pacific Oceans.

The largest animals located at these vents include large clams and mussels and several species of tube (vestimentiferan) worms. Other species include crabs, snails, segmented worms and spaghetti worms, so called because of their appearance. Many of these species had not been previously observed or described. All vent communities appear to have similar types of organisms in association, but not always the same species. Current estimates indicate that the life span of the vents is quite short (probably in the tens of years) and that when the vent dies, so do the animal communities surrounding it. How these vents are located and colonized by organisms living on the deep ocean floor is just one of many interesting questions concerning these deep-sea oases that remain to be answered.

barnacles, sponges, oysters, mussels, corals, gorgonians, chrinoids, hydroids, and bryozoans.

The commonness of sessile animals in the marine benthos suggests that it is a successful way of life. These animals' lifestyle combines facets of plant and animal lifestyles. Sessile invertebrates are plantlike in that they obtain some of their energy from sunlight (the animals themselves do not photosynthesize, but they house photosynthetic symbionts), they are anchored in place, and they grow in a modular fashion just as the branches of a tree do. They are animal-like in that they capture and digest prey and they undergo embryonic development, often involving metamorphosis. In fact, nearly all benthic animals start life in the pelagic realm, drifting around as planktonic larva, dispersing to new habitats as they develop and feed. After a few hours to weeks of pelagic living, they sink to the ocean floor to complete life as adults.

Being stuck in one place presents special challenges for sessile animals, including food acquisition, predator avoidance, and mating. Sessile animals feed by having symbiotic algae and by filtering organic particles from passing water currents. Like plants, sessile animals use structural and chemical defenses against predators, and have tremendous regenerative abilities to recover from partial predation events. Most benthic animals mate via external fertilization: Sperm and eggs are spawned into the water column and fertilization occurs outside the body of the female. Amazingly, sessile barnacles must copulate to achieve internal fertilization. These animals increase their reproductive success by being hermaphroditic, thus assuring that any neighbor is a potential mate; being gregarious to assure a high density of mates; and by having a penis long enough to deliver sperm to an individual seven shell lengths away.

Trophic Cascades and Keystone Predators

Marine organisms live in environments that are foreign to humans, and they have lifestyles that are unique to them and different from terrestrial creatures. However, the study of marine organisms has led to advances in ecological theory that have proven to be useful in understanding terrestrial communities as well. The concept of keystone species, where a relatively rare species has a disproportionately large effect on the community structure, was discovered from research conducted on rocky intertidal habitats. Professor Robert Paine removed starfish from rocks off the coast of Washington state and observed that mussels soon crowded out seaweeds and barnacles, resulting in about a 50 percent reduction in species richness. He concluded that starfish are keystone predators because their predation prevented mussels from excluding less-competitive species from the habitat.

Not far offshore from the rocky intertidal in kelp forests, another keystone species was shown to influence the community by a trophic cascade (where the effects from a top predator "cascade" down to lower trophic levels). Sea otters, by preying on sea urchins, protect the kelps that make kelp forests, an important habitat that many marine species rely on. In the 1800's, hunters greatly reduced the number of otters by harvesting their thick furs. As a result, sea urchin populations exploded because they were relieved from predation, resulting in a decimation of kelps by the herbivorous urchins. Once otters received government protection, their numbers increased, urchins decreased, and kelp forests returned, at least in some areas. Interestingly, Aleutian killer whales began preying on otters in the 1980's, causing kelp forests to begin disappearing again. The reason orcas began eating otters is probably due to concurrent declines in seal and sea lion numbers, the normal prey of these killer whales. The ultimate causes of these altered food webs is uncertain, but it almost certainly is the result of human activity. Even though humans are poorly adapted for a marine existence, the evidence is mounting that humans are altering marine ecosystems in complex, novel, and unpredictable ways. The science of marine ecology is best equipped to study these effects and offer information to protect and manage ocean life.

—*Greg Cronin*

See also: Bioluminescence; Clams and oysters; Coral; Crabs and lobsters; Dolphins, porpoises, and toothed whales; Echinoderms; Eels; Fins and flippers; Fish; Horseshoe crabs; Jellyfish; Lakes and rivers; Lampreys and hagfish; Lungfish; Manatees; Marine animals; Mollusks; Protozoa; Reefs; Reptiles; Salmon and trout; Seals and walruses; Sharks and rays; Snakes; Sponges; Starfish; Swamps and marshes; Tentacles; Tidepools and beaches; Turtles and tortoises; Whale sharks; Whales, baleen; White sharks; Zooplankton.

The interrelationship between orcas (pictured), seals, sea otters, and kelp forests can cause a trophic cascade when one element of the food chain is disturbed. (Corbis)

The Problem of Ocean Navigation

The epipelagic environment is essentially a featureless one, without many of the landmarks or other indicators that might serve as directional indicators for migratory ocean species. Yet many animal species are known to make long and highly accurate migrations through the apparently trackless regions of the world's oceans.

The best-known example of oceanic migration is probably in salmon, which as young animals move from the freshwater streams in which they hatched out to the open ocean in which they mature. Upon reaching sexual maturity, the salmon return to their natal freshwater streams, where they spawn and die. The later portions of this return migration, when the animals are moving up the river system and locating the precise stream in which they were born, has been the most intensely studied, and the sense of smell appears to play an important role. However, the salmon are also faced with the difficult navigational task of locating the mouth of their home river from the vast expanse of the open ocean. How they accomplish this task is completely unknown.

Other astonishing examples of animals making precise migratory movements are known. Green sea turtles (*Chelonia mydas*) from the Caribbean and North and South America are known to accurately navigate to Ascension Island in the middle of the Atlantic Ocean to lay their eggs. American and European eels leave their freshwater homes in streams and ponds upon reaching sexual maturity and migrate out to sea. Upon reaching the marine environment, these animals transform from freshwater eels to marine deep-sea eels of strikingly different appearance, and navigate to a region in the North Atlantic known as the Sargasso Sea, where they spawn and die.

The cues that are used by these animals in their migrations are unknown. Although it is tempting to call this instinctive behavior, instinct is merely a label for mechanisms that are unlearned and innate. These animals are clearly making choices of which direction to proceed in order to reach their goal, but the manner in which those choices are made remain mysterious and fascinating.

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MARK, RELEASE, AND RECAPTURE METHODS

Type of animal science: Ecology
Fields of study: Conservation biology, genetics, population biology, wildlife ecology

The number of animals present within an area can be determined by the ratio of marked to unmarked animals. Knowledge of these numbers provides the biologist with information on the impact of environmental events. It is often necessary to know animal abundance to prevent exploitation, allow effective management of the population, and project future animal numbers.

Principal Terms

DENSITY: the number of animals present per unit of area being sampled

EMIGRATION: the movement of animals out of an area; one-way movement from a habitat type

HABITAT: the physical environment, usually that of soil and vegetation as well as space, in which an animal lives

HOME RANGE: the space or area that an animal uses in its life activities

IMMIGRATION: the movement of animals into an area; a one-way movement into a habitat type

MARKED: an individual animal that is identifiable by marks that may be either human-made, such as metal bands or tags, or natural, such as the pattern of a giraffe

N: a standard abbreviation for the size of an actual population; if capped with a ^ ($\hat{n}$) it is an estimated value

POPULATION: a group of animals of the same species occupying the same physical space at the same time

RECAPTURED: a previously marked animal that is either seen, trapped, or collected again after its initial marking

SAMPLING: the process of collecting data, usually in such a manner that a statistically valid set of data can be acquired

There are four different ways to determine the number of animals within a habitat or population: counting the total number of animals present, sampling part of the area (a quadrat) and extrapolating to find a total, sampling along a line-transect and measuring the distance and angle to where the animal being counted was first seen, and using the mark-recapture approach. Different types of animals require different techniques for population estimation. The mark-recapture approach is often used for groups of animals whose populations are too large or too secretive for other methods. These are usually vertebrates, although mark-recapture procedures have also been used for invertebrates, such as grasshoppers.

All mark-recapture calculations are based on how many individual animals are marked (denoted M) in the population being studied, how many animals are captured during sampling (n), and how many of the captured animals have been previously marked (m). The estimated population is commonly indicated $\hat{n}$. The basic mathematical relationship of these data is $\hat{n}/M = n/m$, when $\hat{n} = Mn/m$. An estimate of population density can be obtained by dividing the area being sampled by the estimate of N.

Marking

Animals may be either temporarily or permanently marked. Temporary marking may be daubing paint on an animal's body, clipping some hair off a mouse's back, or pulling off a few scales from a snake's belly. If each animal is given a unique mark, such as a number or symbol, then it is possible to determine how long the particular animal lives, its home range, and patterns of movement, such as immigration and emigration rates. Some mark-recapture calculations require that the number of times an individual animal is captured be known; "recaptured" must be separated individually for these calculations.

There are pitfalls in this census method that should not be overlooked. Several conditions must hold if mark-recapture population estimates are to be valid. The marked animals must neither lose nor gain marks. Care must be taken if natural marks, such as missing toes on a mouse, are used; additional mice losing toes would lead to an error in population estimation. Marked animals must be as subject to sampling as unmarked ones. Because of the excitement of being captured, many animals will not return to a live-trap a second time, leading to an overestimation of animal abundance. If an animal becomes easily caught and returns frequently to the trap, such as kangaroo rats often do in the desert, then this trap-happy animal produces an underestimate of population size. The marked animals must also suffer the same natural mortality as unmarked ones, and the stress of being captured and marked may cause a higher mortality rate in the animals that are marked. If this occurs, the population estimate will be too high.

The marked animals must become randomly

Image Not Available

mixed with the unmarked ones in the population, or the distribution of sampling effort must be proportional to the number of animals in different parts of the habitat being studied. If the animals are "clumped," population estimates will be either too high or too low, depending on whether the clumps of marked animals are included in the sample. Marked animals must be recognized and reported on recovery. Technicians working with the animals must be able to recognize marked animals and/or read the individual numbers per animal correctly. If marked animals are not recognized, population estimates are too high. There can only be a negligible amount of recruitment or loss to the population being sampled during the sampling period; emigration, if occurring, should be balanced by immigration. A short time between marking the animals and collecting the additional samples for the population estimate is necessary, or the ratio of N to M changes from that existing when n:m was established.

Even under the ideal conditions above, it is apparent, according to the laws of chance, that the ratio of marked to unmarked animals in the sample will not always be the same as that of marked to unmarked animals in the population; in fact, the two ratios may seldom be the same. Possibilities for sampling error can be decreased by enlarging the size of the sample. As the sample size approaches the population in size, chances for error become smaller. When the point is reached where the sample includes the entire population, there can be no error in estimation. In general, at least 50 percent of the population should be marked, and the number of marked animals in the sample should be 1.5 times the number of unmarked animals in the sample. In actual practice, it is difficult (if not impossible) to meet all these requirements. Consequently, it is often best that mark-recapture population estimates be used as measures of trends in major population fluctuations from year to year.

Applications of the Method

There are many different formulas for utilizing the mark-recapture data to produce estimates of population size for any animals that can be marked and recaptured or observed later. The first use of the ratio of marked to unmarked animals for population estimation was for fish and ducks; the technique is usually called the Lincoln-Petersen method or index. Its formula is $N = Mn/m$, where N is the total estimated population, n is the number of animals sampled or captured, M represents the number of animals marked in the population before sample size n is drawn, and m equals the number of previously marked animals recovered in sample size n.

An example of how the calculations for the Lincoln-Petersen index would be made is shown by the following information. If 375 quail were banded and later, in a sample of 545, there were 85 previously banded birds recovered, therefore $N = Mn/m$, or 375 × 545/85 = 2,404 quail estimated to be present in the population being sampled.

When, as is the case with ring-necked pheasants, there is a variation in the capture of the sexes, caused perhaps by capturing technique, the formula can be applied to both sexes, or even to age classes, to arrive at a better estimate of the total population. For example, if 500 males and 750 females were banded before hunting season and then 360 males and 150 females were recovered after the harvest, with 150 banded males found in the 360 males checked and 50 banded females recovered in the 150 females checked, a population estimate can be made. The estimate would be 500 × 360/150, equaling 1,200 males in the population. The female population estimate would be 750 × 150/50, equaling 2,250 females in the population. The total population of pheasants would be estimated to be 1,200 males and 2,250 females, equaling a total of 3,450 pheasants.

The Lincoln-Petersen index differs from other mark-recapture calculations in that only two periods, the initial period when animals are marked and the second period when the sample (n) is collected, are used. If several capture periods are used, sequential formulas, such as the Schnabel method, must be utilized. In each sample taken, all unmarked animals are marked and returned to the population; marking and recapture are done concurrently. The sequential approach makes allowances for the increasing number of marked animals in the population (M). M usually increases with time, but it may decrease with known mortality or removal of marked animals from the population. All the assumptions for the Lincoln-Petersen index should also be met for the Schnabel method to produce accurate population estimates.

The Schnabel method formula for multiple sampling periods is $N = \Sigma(C_T M_T)/R_T$. Each line of the Schnabel method calculation corresponds to a line in the Lincoln-Petersen index calculation. C represents the number captured during sampling time one, M is the total marked, and R is the number of recaptures. The subscript T is the sample time.

An example of the Schnabel calculation can be demonstrated with the following data. For four days of trapping, the following data were obtained: day one, five animals captured, no recaptures; day two, ten animals captured, five previously marked animals in the population at the start of the second day of trapping, three previously marked animals in the day two sample; day three, fifteen animals captured, fifteen previously marked animals in the population at the start of day three of trapping, three previously marked animals in day three of trapping; day four, ten animals captured, twenty previously marked animals in the population at the start of day four, and four previously marked animals among the animals captured on day four. For the four days of trapping, then, ten animals were recaptured. From these data, the Schnabel method estimate of population density would be $N = (5 \times 0) + (10 \times 5) + (15 \times 15) + (10 \times 20)/(0 + 3 + 3 + 4)$ with $N = 50.5$.

Another approach to the estimation of animal numbers has been developed that differs from the usual approach to mark-recapture population estimation calculations. The Eberhardt method is based not on the ratio of marked to unmarked animals but on the number of times an individual is recaptured during the recovery operations; the assumption is that this recapture frequency is related to the total population size. The relationship is believed to be a hypergeometric one. Eberhardt's formula is $N = n/1 - (n/t)$, where n = number of individuals handled in recovery operations and t = the total number of captures of individuals. In this tally, t will always be greater than n unless all animals are captured only once. To use these modified mark-recapture data, individual animals must be recognizable. This calculation has been used for a number of mice studies. For example, if twenty different kangaroo rats in the Mojave Desert were captured thirty-five times, the estimated population would be $N = 20/1 - (20/35)$; $N = 46.67$ animals.

These represent only a few of the mark-recapture formulas available for the estimation of population size and animal density. Many other, more complicated, formulas for calculation of population estimates based on mark-recapture ratios (such as the Schumacher-Eschymeyer, DeLury, and Jolly procedures) exist, but the simplest formulas often provide the best, most usable estimates of animal numbers.

Uses of the Method

The use of mark-recapture procedures allows the biologist to determine numbers of animals present in a given area. Without these numbers, the future of these animals cannot be predicted. This knowledge allows appropriate management strategies to be developed, either protecting them or providing needed control activities, such as spraying insecticides on agricultural crops before severe economic damage to the crops results. Information about animal populations is essential for determining the effects of environmental changes or human activities, such as construction, on animal communities.

The populations of different areas may be compared; population numbers between seasons or years may also be studied. The fact that certain areas have high numbers of individuals implies that these areas have good conditions for them. Wildlife managers need to know why these areas have higher numbers so that they can improve the relevant conditions in other areas. Learning this would not be possible without knowing population sizes on these respective sites. The success of management work can be judged by changes in population size.

Mark and recapture techniques are applicable to more population situations than are the other options for population estimation. The wide variety of methods available for marking animals often allows previously marked animals to be identified without actually being handled. This minimizes the stress on the marked animal by reducing human contact.

If information on how long an animal lives in the wild is needed, individual marking from population work can also serve this purpose. From their recapture points, the area used by individuals on a daily, seasonal, and yearly basis, known as the home range, can be determined. The degree of movement of individuals within the population can also be estimated. These data are economical to obtain, because the marking and capture of the animals for the population estimate also funds the cost of obtaining home range, movement, and longevity data. The rate of exploitation of the population and the rate of recruitment of new members into it can also be calculated from the ratio of marked to unmarked animals collected during the population studies. The biology of organisms in the wild cannot be adequately studied without accurate estimates of their population levels and fluctuations being known. Mark and recapture procedures are among the important scientific tools for the collection of this information.

—David L. Chesemore

See also: Demographics; Ecology; Extinction; Population analysis; Population fluctuations; Population growth; Wildlife management.

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MARSUPIALS

Types of animal science: Anatomy, classification, ecology, evolution, geography, reproduction
Fields of study: Anatomy, ecology, physiology, zoology

Marsupials are a primitive group of mammals that separated early from the dominant group of mammals today, the placentals. Their present strongholds are in Australia, New Guinea, Tasmania, Mexico, Central America, and most of South America.

Principal Terms

ADAPTIVE RADIATION: the rapid evolution of new animal forms to fill unoccupied ecological niches

CONVERGENT EVOLUTION: the process by which unrelated animals tend to resemble one another as a result of adaptations to similar environments

MARSUPIUM: the abdominal pouch possessed by most marsupials, in which immature young attach to nipples to complete their development

MONOTREME: the egg-laying mammals, including the platypus and spiny anteaters

OMNIVOROUS: description of a diet utilizing a great variety of food material

Marsupials are pouched animals that form a distinctive group within the class Mammalia. They possess the diagnostic features of typical mammals, including high and stable body temperature, furry pelt, simple lower jaw, and mammary glands. However, there are other features that distinguish them from what are considered to be typical mammalian features.

The kangaroo is the most commonly known marsupial, but a vast array of marsupials exist. Most marsupials are crepuscular or nocturnal, so most zoo visitors are unable to observe them. Most marsupials are found in Australia and New Zealand. Outside of Australia, it is rare to see marsupials in zoos. Australian authorities impose strict export sanctions to protect their numerous endangered species. The only naturally occurring marsupial found in the United States is the opossum, *Didelphis marsupialis*. The opossums of North and South America are the most diverse of three families of extant marsupials outside of Australia.

There are three families of marsupials, Didelphidae, Microbiotheriidae, and Caenolestidae, that inhabit South and Central America. One species of didelphid, the Virginia opossum, extends across North America and beyond the Canadian border. The American marsupials alive today are mostly small, ranging from mouse to rabbit size. These are generally either carnivorous or omnivorous, living in forests and feeding on insects.

Marsupial Development

Marsupials are an example of adaptive radiation. This adaptation to their varied habitats has led to their enormous diversity of forms and niches. They are also an example of convergent evolution, as indicated by the similarities between marsupials and placentals in the rest of the world. The marsupial gliders resemble the flying squirrels and lemurs, the Tasmanian tiger or thylacine was doglike, and marsupial moles resemble eutherian moles. There are many physiological similarities as well. Wombats process grasses and sedges as horses do and numbats feed on termites as anteaters do.

With few exceptions, marsupials are not conspicuous in coloration or any external physical attributes. The greatest majority of them are small, ranging in size between that of a mouse and of a small rabbit. They developed from small carnivores into herbivores the size of hippopotamuses. The larger marsupials died out only several thousand years ago.

For the most part, marsupials have remained curiosities for the general public. Humans have not traditionally exploited marsupials. They have never been kept as pets, the meat of larger kangaroos is mostly used for dog and cat food, and the furs of only a few marsupials have commercial value.

Marsupials include 18 families, 76 genera, and over 266 species, but these divisions and categorizations are currently being debated. Marsupials are the only order in the subclass Metatheria. There is no other group within the higher mammals that contains such a diversity of higher species, genera, and families as the marsupials.

There are marsupials that spring about on their hind legs, as well as climb, glide, burrow and even swim, and they range in adult size from 147 pounds to only 0.1 ounce. They are found in habitats as diverse as freshwater, alpine areas, hot deserts, and tropical rain forests. Their diet ranges from purely insects to vertebrates, fungi, underground plant roots, bulbs, rhizomes and tubers, plant exudates such as saps and gums, seeds, pollen, terrestrial grasses, herbs and shrubs, and tree foliage. Because of this vast diversity it is impossible to categorize marsupials with a simple description. Instead, the physiology of marsupials must be used to categorize them.

Physiology

There are three types of reproductive patterns in mammals. There are monotremes, which are egg-laying mammals, such as the duck-billed platypus. There are placentals, whose embryo develops inside the uterus, and the placenta formed in the uterus provides nutrients to the developing embryo. In placentals, the offspring are born completely developed, as in humans. Finally, there are marsupials, which functionally fall in between monotremes and placentals.

Marsupial Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Subclass: Theria
Infraclass: Metatheria
Order: Marsupialia
Suborders: Polyprotodonta and Diprotodonta
Families: Didelphidae (American opossums, eleven genera, seventy-five species); Microbiotheriidae (Monito del montes); Caenolestidae (shrew or rat opossums, three genera, seven species); Dasyuridae (quolls, dunnarts, and marsupial mice, eighteen genera, fifty-two species); Myrmecodoiidae (numbats); Thylacinidae (thylacines); Notoryctidae (marsupial mole); Peramelidae (bandicoots, seven genera, seventeen species); Phalangeridae (cuscuses and brishtails, three genera, fourteen species); Burramyidae (pygmy opossums, four genera, seven species); Pseudocheiridae (ringtail opossums, two genera, sixteen species); Petauridae (gliders, three genera, seven species); Macropodidae (kangaroos and wallabies, eleven genera, fifty species); Potoridae (rat kangaroos, five genera, ten species); Phascolarctidae (koalas); Vombatidae (wombats, two genera, three species); Tarsipedidae (honeypossums)

Geographical location: Australian region; North, Central, and South America

Habitat: Varied depending on species, but includes major terrestrial habitats and some arboreal habitats

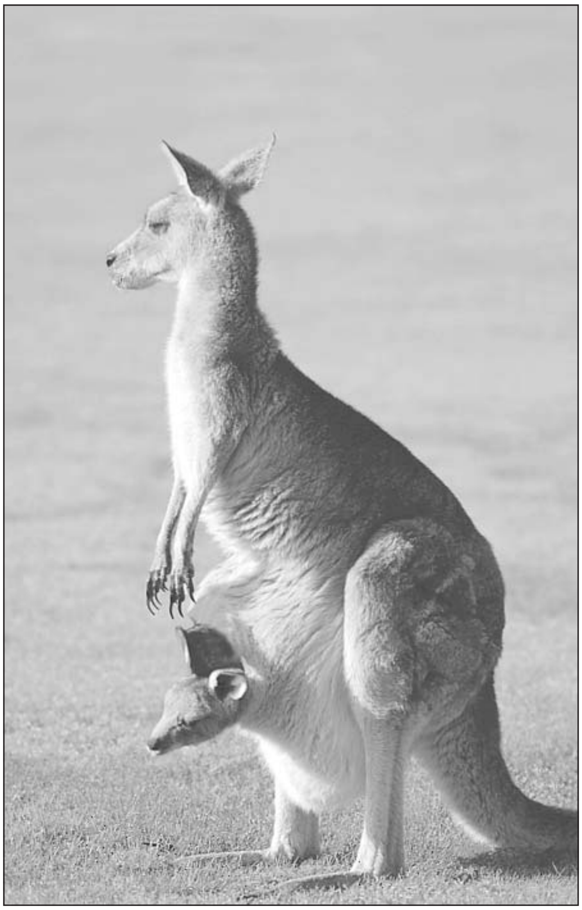
Gestational period: Characteristically short, as the newborn completes its development attached to a nipple inside the marsupium

Life span: Varies by species

Special anatomy: The marsupium, or abdominal pouch, is characteristic, although some forms, such as the murine opossum of Central and South America, lack one

Marsupials are often thought of as pouched mammals. Their embryo develops inside the uterus but, unlike placental mammals, the marsupial is born very early in its development. It completes its embryonic development outside the mother's body, attached to teats of abdominal mammary glands, which are often but not always enclosed in a pouch called the marsupium. The helpless embryonic form has forelimbs that are strong enough to climb from the birth canal to the mother's nipples, where it grabs on and nurses for weeks or months depending on the species.

When the young are born, their eyes and ears are closed, hind limbs and tails are stumps, and they are completely hairless. Their olfactory senses are greatly developed, as are their tactile senses, allowing them to navigate their way to the marsupium.


Kangaroos are the archetypal marsupials, carrying their young in an abdominal pouch, or marsupium, for up to eleven months. (Digital Stock)

The marsupium is formed in diverse ways, ranging from the "primal pouch" (the annular skin creasing around each teat), to common marsupial walls surrounding all teats, and finally to a closed marsupium, which can be opened to the front or to the rear. Marsupials are usually woolly, with shortened forelimbs and elongated hind limbs. In kangaroos, these physical features allow locomotion in a hopping movement only. However, at an equivalent speed, allowing for the differences in weight, a hopping kangaroo uses less energy than a running horse or dog.

In several families, second and third toes of the hind foot function as grooming claws and the first toe is always clawless, except in the shrew opossum. Vision is usually poorly developed and olfactory, tactile, and auditory senses are well developed.

The gestation period is eight to forty-two days, after which the young is carried in the marsupium for between thirty days and seven months. Litter sizes range from one to twelve per birth. The young are weaned anywhere between six weeks and one year. The relationship between mother and offspring is long lasting in many species. Sexual maturity is reached between ten months and four years, depending on the species. The longer range is associated with the male koala.

Behavior

Marsupials range from pure carnivores to pure herbivores, with all the intermediate stages in between. They are usually nocturnal and crepuscular. Some species are solitary, while others live in family groups.

In all mammals, because of the milk produced by the mother, male assistance in feeding the young is less important than in birds, for example. In many marsupials, the role of the male is further reduced because the pouch takes over the functions of carrying and protecting the young and keeping it warm. A female's need for assistance in rearing young does not appear to be an important

The Tasmanian Tiger

One unique marsupial is the Tasmanian tiger, or thylacine, a carnivorous marsupial now believed to be extinct. This mammal has attracted special attention because of its striking similarity to the dog. Also unique to this animal is its tigerlike dorsal stripes, thirteen to nineteen dark, transverse stripes that were distinct over the light gray to yellow brown coat. Reports of size vary, but it was similar in size to the American wolf. Reliable biological and behavioral information on this animal is very rare.

With the arrival of sheep ranchers, the Tasmanian tiger's numbers declined rapidly. Due to a government bounty program, between 1888 and 1905 more than two thousand Tasmanian tigers were officially killed, with the actual numbers likely much higher. What was believed to be the last wild Tasmanian tiger was shot in 1930. Tasmanian tigers never reproduced in captivity. Ironically, the Tasmanian tiger embellishes the Tasmanian coat of arms, designated by King George of England in 1917.

factor promoting the formation of long-lasting male-female pairs or larger social groups. The majority of marsupial species mate promiscuously. There are few examples of long-lasting bonds and they do not live in groups. Some species form monogamous pairs and harems. It is hypothesized that the lack of frequent examples of this sort is due to the lack of external pressures.

Evolution

Marsupial evolutionary development is not yet clearly understood. Fossil records suggest that they may have evolved simultaneously with the placental animals about 100 million years ago, in the Cretaceous period. The oldest geological finds come from the recent Upper Cretaceous of North America, about seventy-five million years ago. Although there was some development of marsupials in North America, they later declined as placentals increased in diversity. In contrast, South America has a considerable diversity of marsupial fossil forms, indicating their persistence for more than sixty million years. Seven families of living and fossil marsupials are known from South America. About two to five million years ago, a land connection between the two Americas was established again, and more placental animals reached South America, including carnivores such as the jaguar. In the face of such competition, the large carnivorous marsupials disappeared, but the small omnivores have persisted successfully to the present day. Some of them moved north to colonize in North America.

The earliest marsupials found in Australia are dated from twenty-three million years ago. Most modern families and forms were clearly established by that time. There is no clear evidence to establish whether marsupials originated in North America, South America, or Australia. The lack of fossil records of marsupials in Asia or Africa makes the most likely route of migration from South America to Australia via Antarctica. At that time, all three southern continents were united in the land mass known as Gondwanaland. This mass of land began breaking up 135 million years ago, with South America and Antarctica still being connected until about 30 million years ago. One land mammal fossil has been found in Antarctica which is a marsupial dated to be forty million years old. The Australian plate then gradually drifted northward for another thirty million years before reaching its current latitude. This long isolation allowed the extensive development of the marsupials in Australia in the absence of competition from other placentals.

As marsupials evolved in Australia, so did the placentals in the rest of the world, filling the same ecological niches. In many cases, they adopted similar morphological solutions to ecological problems. One example is the convergent evolution of the carnivorous Tasmanian devil, a marsupial, and placental wolves of other continents. The marsupial mole is very similar in form to the placental mole. The marsupial sugar glider and the two flying squirrels of North America are also very similar.

Habitat

The arrival of European settlers and the influx of new species—sheep, cattle, rabbits, foxes, cats, dogs, donkeys, and camels—have caused a large-scale modification of the marsupial's habitat in Australia. The first major change was in the late Pleistocene, with the extinction of whole families of large terrestrial marsupials. Included in this extinction was Diprotodon, the largest browsing kangaroo. It is likely that the climatic fluctuations increased aridity and reduced the available favorable habitat. Many of the species were already under stress when man arrived.

Approximately nine species have become extinct in Australia and fifteen to twenty have suffered gross reduction in range. The most affected have been small kangaroos, bandicoots, and large carnivores such as the thylacine and native cats.

Not all the environmental changes have been unfavorable for marsupials. Many of the larger herbivores have fared well with the advent of ranching and available grazing land and watering holes already set up for stock animals. As these marsupials become competition for sheep and cattle, Australian authorities have developed programs to keep their population controlled by allowing a certain number to be shot. Most species of marsupials have little or no importance as pests and their continued existence depends largely on the maintenance of sufficient habitat to support secure populations. The control of feral foxes and cats is very important to keep predation limited.

Marsupials outside Australia appear to have suffered no ill effects due to the destruction of habitat in North and South America.

—*Donald J. Nash*

See also: Embryology; Fauna: Australia; Fertilization; Kangaroos; Koalas; Opossums; Pregnancy and prenatal development; Reproduction; Reproductive strategies; Reproductive system of female mammals; Tasmanian devils.

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MATING

Type of animal science: Behavior
Fields of study: Ethology, invertebrate biology, zoology

Mating is the process by which individuals of a species accomplish the fertilization of ova, or eggs. Mating systems vary widely in the animal kingdom, but every system must bring together two animals, usually of different sexes of the same species.

Principal Terms

ASEXUAL REPRODUCTION: reproduction without the union of male and female sex cells

DIOECIOUS: having two separate sexes, namely male and female

ESTRUS: the period of the sexual cycle during which a female is sexually receptive

GAMETE: a sex cell, either male or female

HERMAPHRODITE: an animal with both male and female sex organs

MONOGAMY: a mating system in which one male and one female comprise the main breeding unit

POLYGAMY: a mating system in which a single adult of one sex mates with several members of the opposite sex.

As one observes the diverse and elaborate movements and behaviors seen in courtship displayed by all types of animals, it is easy to lose sight of what courtship is meant to accomplish. Whether it is relatively simple or highly complex, the ultimate goal of courtship is to bring together two animals of different sexes of the same species to bring about successful mating and reproduction. Although they may not always be as obvious, mating patterns among animals also are quite diverse.

Reproduction, one of nature's most fundamental and essential functions, is the process by which all living organisms produce offspring. The need to propagate is a cardinal necessity for the preservation of the species. Each living organism has its own unique way of accomplishing this requirement. The higher the animal, the more intricate the process. In one-celled organisms reproduction is usually asexual, where only one living entity is required for procreation. The one-celled animal simply splits in two, losing its original identity and thereby creating two new organisms that are characteristically exact duplicates of the parent. The process is known as fission. Some single-celled entities reproduce sexually, where two similar organisms fuse, exchange nuclear materials, and then break apart, after which each organism reproduces by fission. This form of unicellular reproduction is known as conjugation. Sometimes after conjugation, the participating organisms do not reproduce. It appears that the process is merely to revitalize the organisms. This is the most primitive method of sexual reproduction. The new organisms that are produced are from two distinct parents, having definite genetic characteristics of their own.

The procreation process in most multicellular animals involves a more complex form of sexual reproduction. Here, unique and differentiated male and female reproductive cells called gametes unite to form a single cell known as the zygote. The zygote undergoes successive divisions to form a new multicellular organism, where half the genes in the zygote come from one parent and half from the other, creating a singularly different living creature.

Since most species of animals have sexual reproduction, it must offer some advantages. Sexual reproduction results in maintaining high levels of genetic variability within a population. Genetic variability produces variability in behavior, structure, and physiology and provides a species with greater flexibility in meeting changing environmental conditions. There must also be some long-term evolutionary advantages.

A dictionary definition of mating encompasses the idea of individuals coming together to form a pair, with the implication of doing so to produce offspring. If an emphasis is placed on the latter part of the definition, then it is seen that mating may involve all degrees and types of relationships and interactions among animals. In animals that have sexual reproduction, the union of male and female sperm and eggs, also known as gametes or sex cells, may be accomplished by either external or internal fertilization. Simple or elaborate courtship rituals ready animals for mating and fertilization. Several factors may influence reproduction. Most animals have a distinct time of the year, the breeding season, when reproduction is possible. Depending on the species, the breeding season may be the spring, summer, fall, or winter. In other species, including the human and some primates, breeding may occur throughout the year. The breeding season starts with the onset of courtship and is finished when the last offspring are weaned. The same species may have different breeding seasons depending on where they live. In temperate regions of the world, there may be much variation in the breeding in different years. Any factor that affects the health of animals may modify their breeding season, including food availability, temperature, light, and population density. In general, the breeding season usually is coordinated to maximize the likelihood of survival of the young.

Mating Systems

The means by which males and females are brought together in courtship and, ultimately, copulation is achieved is by some type of mating

Sexual reproduction, the form of mating that involves the mixture of genetic material from a male and a female organism, increases a species' genetic flexibility in coping with environmental changes. (Corbis)

Sexual Reproduction—With and Without Copulation

When one thinks of mating and sexual reproduction, one usually thinks of the act of copulation and the physical coupling of the male and female. However, sexual reproduction does not always involve actual copulation and there is much variation among animals. Sexual reproduction which involves the union of male and female sex cells may be achieved by means of internal or external fertilization. In most animals, the male and female sex cells are of unequal size, and typically, a small gamete fertilizes a large gamete. In certain flagellates, however, the two gametes are identical but still function to produce a new individual.

External fertilization is accomplished in a number of invertebrates as well as in some vertebrates. Among many aquatic animals, large numbers of sperm and eggs may be simply expelled into the water, and although the system is inefficient, the large number of sex cells assures that some fertilization will be effected. Among the vertebrates, fertilization is internal in some fishes and external in others. Most frogs and toads have external fertilization: As eggs are released by the female, they are fertilized by the males.

Even in those vertebrates that have internal fertilization, the copulatory organ may not necessarily be a penis. Among fishes, there are modified fins and claspers which serve to transfer sperm for internal fertilization. In most species of birds there is no penis, and during copulation sperm from the male is transferred from his cloaca (a common cavity into which the reproduction, urinary, and intestinal canals open) to the female's cloaca by direct contact, in what biologists refer to as a "cloacal kiss." All mammalian males have a copulatory organ, although there is much variation in the size and structure of the penis. In the egg-laying mammals, the penis is attached to the wall of the cloaca and its canals are used only for the transfer of sperm to the cloaca of the female.

In many mammals, but not all, the penis contains a bone, the os penis or baculum. A baculum is found in most carnivores and aquatic mammals, as well as in some rodents and a variety of other mammals. Other interesting structural variations in the penis include the corkscrew-shaped penis of the pig and the forked tip of the penis of the opossum.

Regardless of the way in which sexual reproduction is accomplished, it succeeds in producing new genetic combinations, and this increased genetic variability appears to be a major advantage to species.

system or pattern. Systems vary widely throughout the animal kingdom, but there are several general groupings. (A reading of the literature in cultural anthropology shows that virtually all of these mating systems can be found in different human cultures, as well.) Mating systems typically are classified under three headings: promiscuity, monogamy and polygamy. It also is useful to delineate subcategories within some of these.

Promiscuity, as it defines a mating system, means that no pair bond is formed between individuals. A technical term for this system is polybranchygamy. which literally means "many brief matings." In this system, any male may mate with any female and no one individual has exclusive rights over any individuals of the opposite sex. Males and females may copulate with from one to many of the opposite sex. Promiscuity is found more often in males than in females, and this observation is probably related to the fact that in such species males have a far lesser investment in offspring than do females. The system is found in a small percentage of bird species and many species of mammals. Promiscuity is demonstrated well in those species that form leks. A lek is an area or territory used for communal courtship displays and mating by certain species. Leks have been observed among grouse, some African antelope, a species of bat, and some insects. Leks are used solely for mating. Females are attracted to the leks by elaborate courtship displays by the males, and mate with one or a small number of the males. Usually, only a select few of the males perform most of the matings. In one study of grouse, less than 10 percent of the males carried out more than 75 percent of all copulations. The African antelope, the Uganda kob, is an example of a mammal that utilizes a lek. Here, also, a small percentage of males breed most of the adult females. The system is very effective, as nearly all of the females produce offspring.

A second major type of mating system is monogamy. It is a system in which a pair-bond is formed between one female and one male. The pair-bond may exist for only one breeding season (annual monogamy) or it may persist for one or more breeding seasons (perennial monogamy). Monogamy is very common in birds, with a large majority of species showing it. Swans and eagles are examples of species showing perennial monogamy, and sparrows and warblers are examples of species showing annual monogamy. Although it has been thought that many birds practice true monogamy, evidence has accumulated that in monogamous birds there are frequent matings of the males with females outside of the primary pair-bond relationship. These matings are known as extra-pair-bond copulations, and offer advantages to the males if they result in successful fertilization of additional eggs. Monogamy seems to occur when both the male and female have nearly identical roles in the rearing of the young.

Monogamy is far less common in mammals than it is in birds, but there are some good examples. If monogamy is likely to occur where there is equal parental investment by both males and females, it might be predicted there is less need for male mammals to practice monogamy, since only the females nourish the young with milk. Among mammals, monogamy can be observed in gibbons, foxes, wolves, beaver, red fox, and even among some small rodents. Why should there be monogamy among any mammals? It would be advantageous for males to be monogamous if by doing so they increased the likelihood of survival of their offspring. Males could do so if they helped to feed the young and helped to defend the territory against predators. Monogamy can also be looked at from the perspective of the female, a so-called female-enforced monogamy, which may take place if females can gain sole benefit from the male's efforts without having to share them with other females.

The third major type of mating system is polygamy. In polygamy, an individual of one sex forms a pair-bond with several members of the opposite sex. The two major subtypes of polygamy are polyandry, where one female mates with more than one male, and polygyny, where one male mates with more than one female. Within both polygyny and polyandry there may be either a serial type or a simultaneous type. In the former case, one male or one female bonds with several members of the opposite sex but only one at a time. In the latter case, one male or one female bonds with several individuals of the opposite sex at the some time. Simultaneous polygyny is often referred to as harem polygyny. Although it appears to resemble promiscuity, it differs from promiscuity in that a pair-bond is formed even though it may be temporary. In altricial birds, in which the young are born in a helpless state, it is often observed that polygyny is present in habitats where food is unevenly distributed and one male is able to provide food for more than one female. Polygyny also may result in cases where there is a lack of availability of suitable territories for breeding and where there may be a pressure of heavy predation.

Hermaphroditism

Although most species of animals are dioecious, meaning that they have two separate sexes, male and female, some individuals and even whole species are monoecious and have both sexes in one individual. Monoecious individuals are also called hermaphrodites. Although hermaphroditism is unusual in humans and most mammals, in some species it is the rule. There are many invertebrates in which the same individual produces both eggs and sperm. Some examples of hermaphroditic species include garden snails, free-living flatworms, the common earthworm, and some fish. It might seem that the hermaphroditic condition is a beneficial and efficient one, since any single individual is capable of producing and delivering both eggs and sperm. However, there is at least one major drawback to the system, the possibility of self-fertilization. Self-fertilization does not lead to as much genetic variability in the offspring compared to what might be expected if there was cross-fertilization. In species in which hermaphroditism is the rule, there are a number of processes at work which make self-fertilization unlikely, if not impossible. Some animals produce eggs at one time and sperm at a different time, making it impossible to self-fertilize. In animals in which the sex organs mature at different times, a condition known as protandry, an individual alternates between being different sexes, functioning as a female or male first and then becoming the other sex at a later time. In some species, including the earthworm, two individuals come together to engage in a mutual copulation. The two worms are held together by a secretion produced by both of them. The togetherness allows sufficient time for sperm from one worm to travel to the other worm and fertilize that worm's eggs and vice versa. Although in most animals the act of copulation is quite short, in the earthworm it may last three hours.

It would be remiss not to mention briefly an example of parthenogenesis in invertebrates. There are a few species of fish and lizards in which only females are known and in which the offspring are produced from eggs without fertilization by sperm. The Amazon moly, a fish, goes through the acts of courtship and mating with a male, but it is with males of other species, and sperm do not fertilize any of her eggs. The eggs develop parthenogenetically and produce another generation, apparently only of females.

Even a brief discussion of mating in animals reveals the complex and diverse methods that are used to produce another generation of the rich diversity of animal life on earth.

—Donald J. Nash

See also: Asexual reproduction; Breeding programs; Cleavage, gastrulation, and neurulation; Cloning of extinct or endangered species; Copulation; Courtship; Determination and differentiation; Development: Evolutionary perspective; Estrus; Fertilization; Gametogenesis; Hermaphrodites; Hydrostatic skeletons; Parthenogenesis; Pregnancy and prenatal development; Reproduction; Reproductive strategies; Reproductive system of female mammals; Reproductive system of male mammals; Sexual development.

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MEERKATS

Type of animal science: Classification
Fields of study: Ethology, population biology, wildlife ecology, zoology

Meerkats are close relatives of mongooses and are particularly noted for their close, cooperative societies.

Principal Terms

CARNASSIAL TEETH: teeth designed to sheer flesh; the characteristic that unites all members of the order Carnivora
DENTITION: referring to the teeth
DIURNAL: active during the day
METAZOA: organisms which are multicellular
NOTOCHORD: longitudinal, flexible rod located between the gut and nerve cord
PLACENTA: structure that connects a fetus to the mother's womb; indicative of internal gestation of young

Meerkats, also called suricates, have the long body and short legs characteristic of most mongooses. The body length is from ten to thirteen inches, and the tail adds an additional seven to nine inches in length. The short fur of the meerkat is grayish-brown to light gray in color, featuring dark stripes across the back. The eyes and nose are dark and form a contrast with the light-colored head and throat. The belly fur of the meerkat is rather thin, which helps to regulate the animal's body temperature. To warm up, the animal will bask in the sun while sitting up or lie belly-down on warm earth, and to relieve itself from the hot desert sun, a meerkat will lie belly-down in a cool, shaded area or inside its burrow.

Meerkats are desert creatures, primarily inhabiting the Kalahari and Namib deserts and other dry, open areas of southern Africa. One of the most notable characteristics of meerkats is their extreme gregariousness. They typically live in family units of up to thirty individuals. The colony of animals occupies a home territory, and digs several systems of burrows with multiple entrances connected by tunnels and a number of distinct chambers. The colony moves several times during a year as food becomes depleted, and establishes a new system of burrows or occupies those left from a previous occupation by the group.

Group Life

Because life in the open desert is harsh and predators, such as jackals, hyenas, and birds of prey, are plentiful, the meerkat group social structure ensures that there are many individuals to act as sentries while the group is foraging for food. The sentry takes its place on a raised area such as a sandbank, bush, or tree, and constantly scans the sky and the horizon for potential predators. The keen eyes and ears of meerkats aid in their constant vigil against danger. Should a predator be spotted, the sentry barks a warning and all members rush to the protection of the burrows. When larger animals, such as hyenas, have threatened the safety of the meerkats inside the burrow, the entire meerkat colony has been seen to band together, stand on their hind legs, and confront the intruder with barking threats, successfully repelling the threatening advances of the much larger animal.

The diet of meerkats consists largely of whatever is available in the harsh desert habitat. Insects, spiders, centipedes, scorpions, lizards, snakes, small mammals, birds and their eggs, roots, tubers, and other plant matter are all staples of the meerkat diet. Each individual takes its turn

The meerkat's distinctive upright pose allows it to search the environment for possible predators. (Digital Stock)

Meerkat Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebra
Class: Mammalia
Subclass: Eutheria
Order: Carnivora
Family: Viverridae
Genus and species: Suricata suricatta (gray meerkat)
Geographical location: Southwestern Angola to southern Africa
Habitat: Desert, open country, savanna, and bush
Gestational period: Approximately eleven weeks
Life span: About ten years in the wild, up to seventeen in captivity
Special anatomy: Long, stiff tails that are used to stand upright; keen eyes located at the front of their heads provide good depth of vision

at sentry duty while the others forage, and the sentry is changed about every thirty minutes. Meerkats are diurnal creatures, spending much of their time foraging for food during daylight hours, except for the hottest portion of the day when they rest in the shade.

Mating generally occurs between October and April, and females give birth to two to five young after a gestational period of about seventy-seven days. Mothers give birth in a specific chamber in the burrow and young are born blind, but their eyes open in twelve to fourteen days. Meerkat young begin eating solid food at about three or four weeks of age but typically nurse for eight to twelve weeks. In meerkat society, there are many individuals who "babysit" young while the mothers forage for food. Meerkat young are sexually mature about one year after birth.

—*Karen E. Kalumuck*

See also: Altruism; Communities; Deserts; Fauna: Africa; Groups; Mammalian social systems.

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METABOLIC RATES

Type of animal science: Physiology
Field of study: Biochemistry

Metabolic rate is a measure of the amount of energy used by an organism in a period of time (calories per hour). By studying factors that affect metabolic rates, scientists can calculate food requirements for animals in particular conditions and explain energy adaptations to different habitats.

Principal Terms

ADENOSINE TRIPHOSPHATE (ATP): the primary energy storage molecule in cells; links energy-producing reactions with energy-requiring reactions

ANABOLISM: a series of chemical reactions that builds complex molecules from simpler molecules using energy from ATP

BASAL METABOLIC RATE (BMR): the rate of metabolism measured when the animal is resting and has had no meals for twelve hours; used to compare different species

CATABOLISM: a series of chemical reactions that break down complex molecules into simple components, usually yielding energy

ELECTRON TRANSPORT CHAIN: a series of electron carrier molecules found in the membrane of mitochondria; oxygen is used and ATP is made at this site

HORMONE: a chemical messenger molecule within organisms; acts as a regulator of cell activities

MITOCHONDRION (pl. MITOCHONDRIA): a cell organelle found in plants, fungi, animals, and protists; the site of most aerobic metabolism

SPECIFIC METABOLIC RATE: the rate of metabolism per unit body mass (calories per gram per hour)

All living things require energy to sustain life as well as to carry out normal activities, develop, and grow. All the chemical reactions that allow energy acquisition and use are collectively called metabolism. Animals usually obtain energy by breaking down food in the presence of oxygen, so the amount of oxygen they use can be considered a measure of their rate of metabolism. Oxygen consumption is not always a good indicator of rate of energy conversion and use. Some organisms, such as fish, that live in oxygen-poor environments gain energy without using oxygen through anaerobic metabolism. Since all energy used by living things is eventually converted to heat, metabolic rate can be defined as the total amount of heat produced by an organism in a certain time period.

Rates of metabolism measured on whole organisms can be used to study the effects of factors such as temperature, size, age, and sex on rates of energy use. Studies of metabolic rates of different species of organisms are used to determine food requirements and energy adaptations in different environments. Metabolic rate can also be measured on isolated tissues, cells, or cell organelles in order to study the different biochemical reactions that occur in tissues and cells.

Factors Affecting Metabolic Rate

One of the most important factors that affects metabolic rate is the temperature of the organism, since within limits all chemical reactions of metabolism proceed faster at higher temperatures. The internal temperature of most invertebrate animals, fish, and amphibians is the same as the temperature of the environment in which they live. Such organisms are called poikilotherms. In poikilothermic organisms, metabolic rate increases as the environmental temperature increases. Such organisms move slowly and grow slowly when the temperature is cold, since their metabolic rate is very low at cold temperatures. To compare the metabolic rates of different poikilotherms, one must measure their rate of metabolism under standard conditions. Standard metabolism is usually defined as the rate of energy use when the animal is resting quietly, twelve hours after the last meal, and is at a temperature of 30 degrees Celsius; however, for small invertebrates, protists, and bacteria, only temperature is usually controlled. Most reptiles, birds, and mammals can maintain their body temperature at a constant level even when the environmental temperature changes greatly. Such organisms are called homeotherms. Birds and mammals can maintain their body temperature through internal heat production (endothermic homeothermy), while reptiles must acquire the necessary heat from their environment by changing their behavior, body posture, or coloration (ectothermic homeothermy). Most endotherms can maintain a constant body temperature over a range of temperatures (thermal neutral zone) without affecting their rate of metabolism. At temperatures outside the thermal neutral zone, metabolic rate increases to maintain constant body temperature. At colder temperatures, increased muscular activity and shivering require increased metabolic rate. Sweating and panting can increase the rate of metabolism at high temperatures. To compare the metabolic rates of endothermic homeotherms, scientists measure the basal metabolic rate (BMR), which is also referred to as the energy cost of living.

Body size (mass in grams or kilograms) is another major factor that affects basal or standard metabolic rate. A 3,800-kilogram elephant has a metabolic rate of about 1,340 kilocalories per hour, while a 2.5-kilogram cat has a rate of 8.5 kilocalories per hour, which means an elephant needs about 150 times as much food as a cat each day. A different picture emerges if one looks at energy use per kilogram of mass. For each kilogram of mass, the cat actually uses ten times the energy of a kilogram of elephant. Metabolism per unit of mass (specific metabolism) decreases as body size increases for all organisms. Since small organisms or cells have a larger surface area relative to their total volume than large ones, they can lose more heat from the surface. For two organisms of the same mass, the taller or thinner organism will have a larger surface area and higher BMR than a shorter, fatter one. More oxygen, food, and waste products can diffuse across the larger surface area; thus cell size in single-celled organisms and in different types of cells in multicellular organisms is limited by rate of energy metabolism. Small animals move faster, breathe faster, and their hearts pump faster. A mouse has a heart rate of six hundred beats per minute, while an elephant's heart rate is thirty beats per minute. Even the length of life appears to be related to the faster metabolic rate of these small creatures. Mice live only two to three years, while an elephant can live sixty years or longer.

Age and sex also influence basal metabolism. Young animals that are growing rapidly have a higher BMR than adults. As adults age, the proportion of skeletal muscle decreases and the BMR declines. Muscle tissue is metabolically very active even at rest, contributing to the higher BMR in males as opposed to females, since males have a higher proportion of body mass that is muscle. Physical or emotional stress can increase metabolic rates by increasing the catabolism of fats through the action of the hormones epinephrine and norepinephrine.

Skeletal muscle activity causes rapid short-term increases in metabolic rate. In humans, for example, a few minutes of vigorous exercise causes a twentyfold increase in the rate of metabolism, and the metabolic rate remains high for several hours. Walking, swimming, running, and flying require more energy than sitting still; however, each of these activities influences metabolic rate differently. Water is denser and has higher viscosity and resistance to movement compared to air, so more energy must be expended to swim than to walk at a given speed. Running also increases energy use, and the faster one runs, the more energy is required. Large animals, however, increase their rate of metabolism less per kilogram of mass than do small animals, so there is a metabolic advantage to large body size. Intriguingly, for the same size animal, flying is less energy-expensive than running.

Measuring Metabolism

Rate of metabolism can be measured as the amount of heat produced by an organism in a time period. The traditional unit of heat is the calorie; a kilocalorie is one thousand calories. The two terms are frequently confused in popular literature. In the international system of units, heat is measured in joules, and 1 calorie is equal to 4.184 joules.

Metabolic rate can be determined from the energy budget of an animal. If the total energy excreted in urine and feces is subtracted from the total energy in food eaten during a period of time, the result would be a measure of metabolic rate. The energy content of food and waste products can be determined by burning these materials in a calorimeter. The amount of heat produced is used to raise the temperature of a known amount of water. This method assumes that the organism is not growing or changing the amount of fat stored during the measurement period. It is also difficult to control metabolic activity of gut microorganisms. Although this technique is cumbersome, it may be the best way to assess energy metabolism in a normally active state for animals in their natural habitat.

More controlled measures of basal and standard metabolism can be made by isolating the animal in a calorimeter and directly measuring heat produced. This method is more accurate than the energy budget approach but still assumes that no new molecules are being produced and no activity or work is being performed. This technique is most useful for birds and small mammals that have relatively high rates of metabolism. Normal behavior and function may be altered by the confined conditions.

Indirect calorimetry is the most often used method in assessing metabolic rate in whole organisms, isolated cells, and cell components. Some factor related to energy use, such as oxygen consumed or carbon dioxide produced, is measured as an index of energy use. For aerobic metabolism, the amount of heat produced is related to oxygen use by the organism. Respirometry is the method used to monitor the oxygen used and carbon dioxide produced by an organism in a closed chamber. Oxygen consumption can be measured by absorbing carbon dioxide with soda lime and measuring the change in gas pressure in the closed system by a manometer. Oxygen electrodes can also be used to measure the decrease in oxygen concentration in water within the chamber if the animal is a water-dweller. For air-breathing animals, oxygen in the gas phase can be measured by a mass spectrometer. Carbon dioxide can also be measured by an infrared unit. In such closed systems, the gases can be monitored in the air as it enters and leaves the chamber. Respirometry can also be accomplished in open systems if the animals are fitted with breathing masks and the respired air is collected and analyzed. Oxygen consumption is a good index of metabolic rate for most animals at rest, since most of their metabolism is aerobic. Animals that live in oxygen-poor environments, such as internal parasites and mud-dwelling invertebrates, and all animals under extreme exercise often metabolize anaerobically.

To translate the amount of oxygen used into heat produced, one must know the proportion of fat, carbohydrate, and protein in the diet, since the amount of heat produced for each liter of oxygen consumed differs. In practice, it is usually assumed that only carbohydrates are being used.

Assimilating and digesting food cause large increases in metabolic rate. This increase reaches a maximum about three hours after a meal and remains above basal level for several hours in birds and mammals and up to several days in poikilotherms. Foods differ in the amount of increase in metabolic rate. Proteins, for example, cause about three times the increase in rate compared to carbohydrates or fats. The increase partially results from increased activity in cells of the digestive tract and partly from higher activity of liver and muscle cells preparing these foods for storage. Basal metabolism must then be measured after a twelve-hour fast to minimize this effect.

Since body temperature, body size, and activity affect metabolic rate of organisms, one can see that available food supplies, oxygen levels, and environmental temperatures limit the physiology of energy metabolism in different habitats. Scientists study metabolic rates in whole organisms to explain their food habits and their distributions in different habitats and to calculate energy requirements for raising animals under different conditions.

—Patricia A. Marsteller

See also: Carnivores; Cold-blooded animals; Digestion; Hibernation; Ingestion; Omnivores; Thermoregulation; Warm-blooded animals.

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METAMORPHOSIS

Types of animal science: Development, physiology
Fields of study: Biochemistry, entomology, invertebrate biology, zoology

Metamorphosis is the major change in body form that occurs after embryonic development is complete in many types of animals, including insects.

Principal Terms

- CORPORA ALLATA: a gland in insects that synthesizes and secretes juvenile hormone (JH)
- ECDYSONE: a hormone that triggers both molting and metamorphosis in insects as well as in many other species of animals
- IMAGINAL DISK: flat sheets of cells within an insect larva; these cells will change shape during metamorphosis and form the external structures of the adult
- JUVENILE HORMONE (JH): a species-specific hormone which controls whether a molt will produce a larger larva or initiate metamorphosis
- LARVA: the reproductively immature feeding stage in the development of many species of animals, including those insects which undergo complete metamorphosis
- NYMPH: the sexually immature feeding stage in the development of those insects which undergo incomplete metamorphosis
- PROTHORACIC GLAND: the gland where ecdysone is made in insects
- PROTHORACICOTROPIC HORMONE (PTTH): a hormone made in the brain of insects which stimulates the prothoracic gland to make ecdysone
- PUPA: the stage of insect development during which metamorphosis occurs

Unlike mammals, most animals become adults by first going through a distinctly different immature, or larval, stage of development. Larvae look nothing like the adults they will form. They are specialized primarily for growth and feeding and are unable to reproduce. At a certain time in their growth, often in response to signals from hormones or the environment, the larva undergoes a second spurt of development called metamorphosis.

The word “metamorphosis” comes from the Greek word for transformation and is today defined as a major change in body form that occurs after embryonic development is completed. Metamorphosis is very widespread in the animal kingdom but it has been studied most thoroughly in three different groups of organisms: the arthropods (crabs, lobsters, and insects), the amphibians (frogs and salamanders), and the echinoderms (sea urchins and starfish).

Metamorphosis affects the ways animals eat, breathe, and move; it can also change the nature of the environment in which they live. In echinoderms, the larval stage is microscopic and free swimming, while the adults are large and move very little if at all. The changes in body form thus coincide with significantly different ways of feeding and moving.

Amphibian Metamorphosis

In amphibians, metamorphosis prepares the organism for its transition from living in water to living on land. Internally, the digestive system changes to accommodate the new diet as the animal switches from consuming plants to animals. Sense organs like the eyes and ears also change to adapt to functioning predominantly in air. Finally, many of the chemical reactions which occur in the individual cells of the frog also change at this time.

Metamorphosis in amphibians is controlled by a pair of hormones. Prolactin, a protein secreted by the anterior pituitary gland, controls the rate of growth of the tadpole and suppresses metamorphosis. Thyroxine is a modified amino acid made in the thyroid gland of the tadpole and causes metamorphosis to begin. After the tadpole has grown to a certain minimal size, the thyroid gland is stimulated by environmental conditions to produce large quantities of thyroxine, which reverses the suppression exerted by prolactin and begins metamorphosis. The hormones pass through the tadpole's circulation and instruct different tissues to activate and deactivate different sets of genes that cause some tissues to degenerate, others to change, and others to grow.

These same hormones, prolactin and thyroxine, are produced by other vertebrates; nature often uses the same molecules to produce very different results in different animals. In humans, thyroxine regulates the rate of metabolism, while prolactin is crucial for milk production in nursing women. In fish, however, prolactin is crucial for keeping the cell's content of salt in balance.

Insect Metamorphosis

The hormonal control of metamorphosis in one group of animals, the insects, has yielded basic information about how genes and hormones interact to guide development in all animals. This process is understood in greater detail in insects than in any other group of animals.

Insects, like all arthropods, have a rigid exoskeleton, called a cuticle, that supports their body mass and allows the attachment of muscles for movement. Because it is external and fixed in size, however, the cuticle must be shed periodically for growth to occur. The process of insects shedding their cuticle and producing a new, larger one is called molting, and the number of molts normally occurring is regulated by the insect's genes. Many insects have developed complex behaviors to ensure that they molt in a secluded location and avoid predation. Without their hard, external covering, they are relatively defenseless.

About 10 percent of all insect species, such as the grasshoppers and true bugs, go through a process of incomplete metamorphosis. Here, the egg hatches into a juvenile form called a nymph that resembles the adult but is much smaller and is not capable of reproduction. At each molt, the nymph sheds its cuticle and grows before the newly produced cuticle hardens. When the signal for metamorphosis arrives, the molt produces an adult, often with wings, but, more important, fully capable of reproduction. Male and female adults can then mate and lay a new generation of eggs.

Complete metamorphosis, on the other hand, is a very different process that is undergone by 90 percent of all species of insects, including the ants, bees, flies, butterflies, and moths. Here, the larval form looks nothing like the adult. For example, the larval form of a butterfly is a caterpillar and the larval form of a fly is a wormlike maggot. Each

When an insect nymph undergoes metamorphosis within a chrysalis, its tissues completely break down into a kind of sludge, which is reformed under the directions of cellular imaginal discs. (Digital Stock) larva undergoes a series of molts so as to be able to grow. The larva of the cecropia moth increases in mass by five thousand times during its larval development. When the trigger for metamorphosis occurs, the insect undergoes a radical change. The larva stops feeding and moving, anchors itself to a twig, leaf, or rock, and either spins a cocoon or encloses itself in its own hardened cuticle.

Silkworm Metamorphosis

The silkworm, *Bombyx mori*, undergoes complete metamorphosis, and its development begins when the egg hatches and includes five distinct larval stages. Each stage is larger than the one preceding as the larva eats, voraciously consuming several times its own body weight in food each day. At the end of the fifth larval stage, the molting event that follows is very different from the previous larval molts as the caterpillar spins a cocoon made out of silk (which is the commercially valuable product of this organism) and becomes a pupa. The next molt occurs within the pupal case when metamorphosis begins. When the adult has formed, the cocoon breaks open and the adult emerges to begin reproduction.

Metamorphosis involves the complete replacement of one body form with another. Inside the pupal case, the larval tissues break down and their molecules are reutilized in the construction of the cells and tissues of a very different looking animal, the adult. Certain groups of cells, called imaginal disks, along with the larval brain are generally the only tissues that are not broken down in this process. Opening a cocoon at this time shows that it is filled with a white, milky sap and little else as the caterpillar has been completely broken down.

The imaginal disks, round, flat sheets of cells, begin to evert or "telescope" and form the external structures characteristic of the adult cuticle. There is an imaginal disk for each eye, for each antenna, for the two or four wings, and for each of the six legs. These structures attach and the adult insect is constructed. In the well-studied fruit fly, *Drosophila*, this process takes about a week, while it can take months for other insects.

Hormonal Regulation of Metamorphosis

In insects, three very different hormones combine to regulate the timing of both molting and metamorphosis. Each of these three hormones is produced in a different tissue, and each has a different chemical structure and mode of function. The signal to molt originates in a small group of cells within the caterpillar's brain in response to neural or environmental signals. The hormone produced there, prothoracicotropic hormone (PTTH), is a small protein that passes through the insect's hemolymph (blood) to all parts of the body. As is true of all hormones, only certain target tissues are genetically programmed to respond to the production of this hormone. In this case, the prothoracic gland responds by producing a second hormone called ecdysone, the molting hormone. Ecdysone is a steroid, a chemical derivative of the cholesterol that the insect requires in its diet. Ecdysone is not actually the molting hormone itself, but must first undergo some minor chemical changes before it becomes active. More important, ecdysone and its derivatives are the molting hormone not only for all insects, but for all arthropods and many other animals. This chemical signal thus evolved before divergence of these organisms from a common ancestor.

Different tissues respond differently to ecdysone, but the hormone's major effect is to trigger molting by causing the hardening of the cuticle and the separation of the living cells beneath the cuticle from it. The cuticle then dries and cracks and the larva can then emerge from its old skin and grow. If PTTH production stops, the amount of ecdysone released from the prothoracic gland also falls. This happens normally in the period between molts, but can also occur during a molt. In cecropia moths, the level of PTTH drops during the pupal stage and the subsequent drop in ecdysone production causes diapause, a programmed pause in development. The pupa will remain in diapause until an environmental signal, consisting of a minimum of two weeks in the cold followed by a normal spring warming, triggers the resumption of PTTH secretion and the completion of metamorphosis.

Ecdysone acts specifically on certain groups of insect genes and not others. Many genes required for larval functions are turned off in response to ecdysone, while those genes required for molting and metamorphosis are turned on. This effect can be seen when imaginal disks are placed in a culture dish along with physiological levels of ecdysone. The disks stop growing and begin metamorphosis. Such development can even produce normal-looking legs floating free in a culture dish. The changes in shape of the disk cells can be directly attributed to the function of genes turned on by ecdysone.

The hormone ecdysone therefore not only causes metamorphosis, but also triggers certain simple molts. The third hormone involved in the control of metamorphosis is responsible for this choice, the choice to molt and grow or to undergo metamorphosis to the adult form. This compound is called juvenile hormone (JH). JH is produced in a gland called the corpora allata, and the hormone has yet a third chemical structure, a derivative of a class of molecules called terpenes. Unlike ecdysone, however, the JH of each species has a different chemical structure.

When a molt is triggered by the production of ecdysone, the type of molt that occurs will be determined by the level of JH present. During larval development, the amount of JH in the hemolymph is high and the tissues respond to ecdysone by undergoing a molt to become a larger larva. Later in development, the corpora allata stops producing JH and any new molt triggered by ecdysone causes the organism to proceed to the pupal stage and begin metamorphosis. The interaction of ecdysone and JH thus governs which type of molt will occur.

Although these hormones are crucial for controlling molting and metamorphosis, they play other roles as well. For example, adult female insects produce large quantities of ecdysone and adult males do not because ecdysone is important to egg production.

Laboratory Studies of Metamorphosis

Various parts of the elaborate interplay of the three hormones that regulate metamorphosis in insects were discovered in a number of laboratories. The role of ecdysone was discovered first by Carroll Williams and Vincent Wigglesworth, who found that the prothoracic gland of the larva was responsible for producing a substance that triggered metamorphosis. They tied a fine string around the middle of a cecropia larva and observed that only the front half underwent metamorphosis. The signal was thus produced somewhere in the front half and could not reach the rear of the insect. The prothoracic glands were later discovered to be the source of the molting signal when glands transplanted to the rear half of a ligated larva caused metamorphosis to occur there as well.

Ecdysone was painstakingly purified and chemically identified by Peter Karlson's group in Germany. In a monumental effort, they extracted twenty-five milligrams of pure ecdysone from a ton of silkworms. Much of the difficulty encountered in this isolation stemmed from the lack of an easy method for identifying the presence of ecdysone in the extract they were producing.

A tedious and relatively insensitive bioassay was used. In this assay, the extract to be tested during the isolation was dissolved in an organic solvent and painted on the cuticle of an insect. If the extract contained ecdysone, the larva would begin to molt. Although time-consuming and not very reproducible, the bioassay allowed the purification of ecdysone from insects.

The role of the corpora allata and JH was found by a similar set of experiments. Wigglesworth found that if he decapitated a fourth-stage Rhodnius nymph and sealed the body with wax to that of a decapitated fifth-stage nymph, the insects could survive for a long period of time. This technique is called parabiosis. The mature nymph never underwent metamorphosis but rather molted in response to its own ecdysone or to ecdysone painted on its cuticle to form a larger nymph. Once again, tissue transplantation experiments showed that the hormone coming from the immature nymph that prevented metamorphosis was produced by the corpora allata. Removing the corpora allata from a larva or nymph caused either death or premature metamorphosis to the adult stage.

The role played by PTTH was also elucidated by a similar set of surgical experiments. Removing the brain of a larva prevented the production of ecdysone from the prothoracic gland so long as the removal occurred before the brain released the PTTH. After the PTTH signal was released, removing the brain had no effect on the subsequent production of ecdysone for that molt.

Today, the presence and amount of the three hormones are measured by easy, sensitive, and highly reproducible immunological techniques. In these procedures, antibodies, proteins having the chemical ability to bind tightly to a specific insect hormone, are produced. If an extract contains one of these hormones, adding its specific antibody will cause the hormone to bind to the antibody, and the amount of bound antibody can be accurately measured in a number of different ways.

These immunological procedures have allowed researchers to monitor the changing levels of the three hormones during the development of any insect and to correlate these changes with the progress of metamorphosis. Coupled with new information about the ability of hormones to turn genes on and off directly, these procedures have advanced the understanding of the mechanisms of control of metamorphosis at the molecular level.

—Joseph G. Pelliccia

See also: Amphibians; Determination and differentiation; Endocrine systems of invertebrates; Insects; Morphogenesis; Physiology.

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MICE AND RATS

Types of animal science: Behavior, classification, ecology
Fields of study: Ecology, physiology

House mice and Norway rats are found worldwide and almost always are found related to humans and human activities. No other mammals are greater pests than are mice and rats.

Principal Terms

ALTRICIAL: born in a helpless state and completely dependent on the parent(s)
COMMENSAL: living in close association with humans; the word means "sharing the table"
OMNIVOROUS: eating all kinds of food, both plant and animal
RODENTS: the gnawing mammals characterized by specialization of the incisor teeth into gnawing teeth

Although there are many types of mouse and rat, the words most often are used to refer to the house mouse, *Mus musculus*, and the Norway rat, *Rattus norvegicus*. These two species belong to a family of rodents known as the Muridae, the Old World mice and rats, and there are over 450 species within this group. Both species underwent their early evolution in the wilds of Asia. As humans appeared and began to settle in farms and villages, mice and rats became associated with them. As humans migrated to other parts of the world and as commercial exchanges took place around the world, mice and rats went along for the ride and became established in the Old World and the New World, and today may be found almost any place on earth where humans are found.

At birth, mice and rats are unimposing animals, as the pups are born in an altricial state and are naked, sightless, and helpless. They develop rapidly, however, and by three weeks of age are weaned from their mother. By 1.5 to 2 months of age for the mouse, and 2 to 3 months of age for the rat, they are sexually mature. Their powers of reproduction are phenomenal and many litters, some containing more than a dozen young, can be produced in a single year. A single female mouse may produce over one hundred young in one year.

As adults, mice and rats still are not imposing. They have a long, scaly, scantily haired tail, and are a grayish brown color, which is somewhat paler in the belly. Although they have poor sight, their senses of smell, hearing, and taste are all excellent.

The Good and Bad of Mice and Rats

All of the other mammalian species combined, as well as all other animals, do not cause as much damage and destruction to humans as do mice and rats. The two species have been able to adjust to living with and near humans and their habitations. Their diets are omnivorous and include all types of foods, grains, and grain products. They can climb, burrow, and swim, and can invade nearly all buildings, houses, barns, warehouses, and other structures. As a result, they cause billions of damage each year around the world. Human food is eaten or destroyed by contamination with urine and feces. The urine may contain bacteria, causing diseases such as leptospeosis. Food poisoning may be caused by salmonellosis in their feces. Many children and some adults are bitten each year by rats, especially in rundown urban areas. Even those mice and rats that live under semi-wild conditions may affect humans in their effect on other wildlife. Ground-nesting birds and the young of other animals are susceptible to predation by mice and rats. The costs of these pests to humans is tremendous.

Some consolation for having to deal with the extensive bad side of mice and rats may be found in their beneficial use as laboratory animals. Both species are used widely in medical and genetic research. The mouse has been used to elucidate many basic principles of genetics, and today, its many genetic variants serve as models for many human disorders, including genetic diseases and cancer. As studies define the human genome, similar studies are defining the mouse and rat genomes. The laboratory rat, although not as

Mouse and Rat Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Subclass: Theria
Infraclass: Eutheria
Order: Rodentia
Suborder: Myomorpha
Family: Muridae, with fifteen subfamilies, 241 genera, and 1,082 species

Geographical location: Worldwide, through introduction by humans

Habitat: Occurs in highly varied habitats, usually in association with humans

Gestational period: Nineteen to twenty-two days, although this may be lengthened in nursing females due to delayed implantation

Life span: Around one year in the wild; laboratory rats and mice may live three to four years or longer

Special anatomy: The scantily haired tail helps to distinguish house mice and Norway rats from most other types of mice and rats

Image Not Available

genetically well known as the mouse, has been used extensively in physiological and psychological research.

It is unlikely that humans will ever be able to eliminate completely mice and rats and control their destruction, but it also is unlikely that their importance to both basic and applied science will ever be diminished, at least in the foreseeable future.

—Donald J. Nash

See also: Beavers; Gophers; Porcupines; Rodents; Squirrels.

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MIGRATION

Type of animal science: Behavior
Fields of study: Biophysics, ethology, neurobiology, marine biology, ornithology

Migration is an important ecological process that results in the redistribution of animal populations from one habitat to another. Adaptive habitat changes are fundamentally important aspects of the life histories of many species.

Principal Terms

BIOLOGICAL CLOCK: an inherent sense of timing regulating certain types of behavioral activity such as migration

CLOCK SENSE: an inherent awareness of time or time intervals used, for example, to compensate for celestial movements in navigation

DISPERSAL: the spreading apart of individuals away from one another and away from a place; includes a directional component when passive animals are moved by winds or currents

HABITAT: a specific, recognizable geographical region in which a particular kind of organism lives

MIGRANT: a group or species of animal that moves from one habitat or geographical region to another

NAVIGATION: to follow or control the course of movement from the place of origin to a specific destination

NOMADS: migrants without a specific habitat; wanderers

ORIENTATION: an inherent sense of geographical location or place in time

POPULATION: a group of individuals of the same species geographically located in a given habitat at the same time

Migration is a general term employed by ecologists and ethologists to describe the nearly simultaneous movement of many individuals or entire populations of animals to or between different habitats. As defined, migrations do not include local excursions made by individuals or small groups of animals in search of food, to mark territorial boundaries, or to explore surrounding environments.

Nomads are migrants whose populations follow those of their primary food sources. Such animals (the American bison, for example) do not have fixed home ranges and wander in search of suitable forage. Some scientists view nomadic movements as a form of extended foraging behavior rather than as a special case of migration. In either context, the important point is that populations change habitats in response to changing conditions.

In contrast to migrations made by populations and excursions made by individuals, the spreading or movement of animals away from others is known as dispersal. Examples of dispersal include the drift of plankton in currents and the departure of subadult animals from the home range of their parents. In numerous species (sea turtles, rattlesnakes, and salmon, for example), dispersed members of a population may return to the place of origin after a variable interval of time.

Means and Reasons

Some migratory species can orient themselves—that is, they know where they are in time and space. Many birds and mammals, for example, have an inherent sense of the direction, distance, and location of distant habitats. Orientation and travel along unfamiliar routes from one place or habitat to another is called navigation. Navigators use environmental and sensory information to reach distant geographical locations, and many of them do so with a remarkably accurate sense of timing. Homing pigeons are perhaps the best-studied animal navigators. These birds are able not only to discover where they are when released but also to return to their home loft from distant geographical locations.

Much has been learned about how animals successfully navigate over long distances from the pioneering studies of Archie Carr. Carr proposed that green sea turtles successfully find their widely separated nesting and feeding beaches by means of an inherent clock sense, map sense, and compass sense. His investigations and those of many others continue to stimulate great interest in the physiology and ecology of navigating species and in the environmental cues to which they respond. Sensory biologists, biophysicists, and engineers have incorporated knowledge of how animals detect and use environmental information to develop new and more accurate navigational systems for human use.

Animals use a variety of cues to locate their positions and appropriate travel paths. Most species have been found to use more than one type of information (sequentially, alternatively, or simultaneously) to navigate. Among the animals known to navigate are birds (the best-studied group), lobsters, bees, tortoises, bats, marine and terrestrial mammals, fish, brittle starfishes, newts, toads, and insects. Included among the orientation guideposts that one or more of these groups may use are the positions of the sun and stars, magnetic fields, ultraviolet light, tidal fluctuations caused by the changing positions of the moon and sun, atmospheric pressure variations, infrasounds (very low frequency sounds), polarized light (on overcast days), environmental odors, shoreline configurations, water currents, and visual landmarks. Celestial cues also require a time sense, or an internal clock, to compensate for movements of the animal relative to changing positions of celestial objects in the sky. In addition to an absolute dependence on environmental cues, young or inexperienced members of some species may learn navigational routes from experienced individuals, such as their parents, or other experienced individuals in the population. Visual mapping remembered from exploratory excursions may also play a role in enhancing the navigational abilities of some birds, fish, mammals, and other animals.

The different categories of animal movements, however, are perhaps not so important as the reasons animals migrate and the important biological consequences of the phenomenon. As a general principle, migrations are adaptive behavioral responses to changes in ecological conditions. Populations benefit in some way by regularly or episodically moving from one habitat to another.

An example of the adaptive value of migratory behavior is illustrated by movement of a population from a habitat where food, water, space, nesting materials, or other resources have become scarce (often a seasonal phenomenon) to an area where resources are more abundant. Relocation to a new habitat (or to the same type of habitat in a different geographical area) may reduce intraspecific or interspecific competition, may reduce death rates, and may increase overall fitness in the population. These benefits may result in an increase in reproduction in the population. Reproductive success, then, is the significant benefit and the only biological criterion used to evaluate population fitness.

Programmed and Episodic Movements

While many factors are believed to initiate migratory events, most fall into one of two general categories. The first and largest category may be called programmed movements. Such migrations usually occur at predictable intervals and are important characteristics of a species' lifestyle or life cycle. Programmed migrations are not, in general, density-dependent. Movements are not caused by overcrowding or other stresses resulting from an excessive number of individuals in the population.

The lifestyle of a majority of drifting animals whose entire lives are spent in the water column, for example, includes a vertical migration from deep water during the day to surface waters at

Bird migrations are among the most noticeable animal migrations, with huge flocks passing through the skies on their way to a seasonal home. (Corbis)

night. Thus, plankton exhibit a circadian rhythm (activity occurring during twenty-four-hour intervals) in their movements. An abundance of food at or near the surface, and escape from deep-water predators, are among the possible reasons for these migrations. Daily vertical movements of plankton are probably initiated by changes in light intensity at depth, and the animals follow light levels as they move toward the surface with the sinking sun. It is interesting to note that zooplankters living in polar waters during the winter-long night do not migrate.

Monarch butterflies and many large, vertebrate animals, such as herring, albatross, wildebeests, and temperate-latitude bats, migrate from one foraging area to another, or from breeding to foraging habitats, on a seasonal or annual basis. Annual migrations usually coincide with seasonal variation. Changes in day length, temperature, or the abundance of preferred food items associated with seasonal change may stimulate mass movements directly, or indirectly, through hormonal or other physiological changes that are correlated with seasonal environmental change. The onset of migration in many vertebrates is evidenced by an increase in restlessness that seems, in human terms, to be anticipatory.

In addition to their daily vertical migrations (lifestyle movements), the life cycles of marine zooplankton involve migrations, and it is convenient to use them as examples. As discussed, most adult animal plankters are found at depth during the day and near the surface at night. In contrast, zooplankton eggs and larvae remain in surface waters both day and night. As the young stages grow, molt, and change their shapes and food sources, they begin to migrate vertically. The extent of vertical migrations gradually increases throughout the developmental period, and as adults, these animals assume the migratory patterns of their parents. Patterns of movement that change during growth and development are examples of ontogenetic, or life-cycle, migrations.

The second large category of migratory behavior includes episodic, density-dependent population movement. Such migrations are often associated with, or caused by, adverse environmental changes (effect) that may be caused by overlarge populations (cause). Local resources are adequate to support a limited number of individuals (called the “carrying capacity” of the environment), but once that number has been exceeded, the population must either move or perish. Unfortunately, migration to escape unfavorable conditions may be unsuccessful, as another suitable habitat may not be encountered. Migrations caused by overpopulation or environmental degradation are common. Pollution and habitat destruction by humankind’s activities are increasingly the cause of degraded environments, and in such cases, it is reasonable to conclude that humans have reduced the carrying capacity of many animal habitats. Familiar examples of density-dependent migrations are those of lemmings, locusts, and humans.

Studying Migration

Methods used by scientists to study the mass movements of animals are quite varied and depend on the investigator's research interests and on the kinds of organisms being investigated. Environmental or physiological factors that initiate migrations may be of interest to sensory biologists and physiological ecologists; knowledge of variation in population distributions is important to biogeographers and wildlife biologists; and migrations in predator-prey relationships, competition, pollution, and life-history strategies are important aspects of classical ecological studies.

In addition to the specific aspect of migration being studied, the particular group of animals under investigation (moths, eels, elephants, snails) requires that different methods be used. Some of the approaches used in migration-related research illustrate how information and answers are obtained by scientists.

Arctic terns migrate from their breeding grounds in the Arctic to the Antarctic pack ice each year. The knowledge that these birds make a twenty-thousand-mile annual round-trip comes from the simplest and most practical method: direct observation of the birds (or their absence) at either end of the trip. Direct observation by ornithologists of the birds in flight can establish what route they take and whether they pause to rest or feed en route. Many birds have also been tracked using radar or by observations of their silhouettes passing in front of the moon at night. Birds are often banded (a loose ring containing coded information is placed on one leg) to determine the frequency of migration and how many round-trips an average individual makes during its lifetime. From this information, estimates of longevity, survivorship rates, and nesting or feeding site preferences can be made.

Factors that initiate migratory behavior in terns and in other birds can often be determined by ecologists able to relate environmental conditions (changes in temperature, day length, and the like) to the timing of migrations. Physiological ecologists study hormonal or other physiological changes that co-occur with environmental changes. Elevated testosterone levels, for example, may signal the onset of migratory behavior.

How Arctic terns orient and navigate along their migratory routes is usually studied by means of laboratory-conducted behavioral experiments. Birds are exposed to various combinations of stimuli (magnetic fields, planetarium-like celestial fields, light levels), and their orientation, activity levels, and physiological states are measured. Experiments involving surgical or chemical manipulation of known sensory systems are sometimes conducted to compare behavioral reactions to experimental stimuli. In such experiments, the birds (or other test animals) are rarely harmed.

Tags of several types are used to study migrations in a wide variety of animals, including birds, bees, starfishes, reptiles, mammals, fish, snails, and many others. Tags may be transmitting collars (located by direction-finding radio receivers); plastic or metal devices attached to ears, fins, or flippers; or even numbers, painted on the hard exoskeleton of bees and other insects. Additional types of tagging (or identifying) include radioactive implants and microchips that can be read by computerized digitizers; the use of brands and tattoos; and, of great interest, the use of biological tags. Parasites known to occur in only one population of migrants (nematode parasites of herring, for example) provide an interesting illustration of how the distribution of one species can be used to provide information about another.

The Importance of Migration

The causes, frequency, and extent of animal migration are so diverse that several definitions for the phenomenon have been proposed. None of these has been accepted by all scientists who study animal movements, however, and it is sometimes difficult to interpret what is meant when the term "migration" is used. Most researchers have adopted a broad compromise to include all but trivial population movements that involve some degree of habitat change.

It is important to recognize that few populations of animals are static; even sessile animals (such as oysters and barnacles) undergo developmental habitat changes, which are referred to as ontogenetic migrations. Aside from certain tropical and evergreen forest areas where migrations are relatively uncommon, a significant number of both aquatic and terrestrial species move from one habitat to another at some time during their lives. In the face of environmental change, including natural events such as seasonal variation and changes caused by resource limitations and environmental degradation, animals must either move, perish, or escape by means of drastic population reduction or by becoming inactive until conditions become more favorable (hibernation, arrested development and dormancy, and diapause in insects are examples of behavioral-ecological inactivity). Migration is the most common behavioral reaction to unfavorable environmental change exhibited by animals.

One cannot understand the biology of migrators until their distribution and habitats throughout life are known. The patterns of animal movements are fascinating, and it is useful to summarize some of the major differences between them. First, many species travel repeatedly during their lives between two habitats, on a daily basis (as plankton and chimney swifts do) or on an annual basis (as frogs and elks do). Second, some species migrate from one habitat (usually suitable for young stages) to another (usually the adult habitat) only once during their lives (for example, salmon, eels, damselflies, and most zooplankton, which live on the bottom as adults). Third, some species (many butterflies, for example) are born and mature in one geographical area (England, for example), migrate as adults to a distant geographical area (Spain, for example), and produce offspring that mature in the second area. These migrations take place between generations. In a fourth pattern, one may include the seasonal swarming of social arthropods such as termites, fire ants, and bees. A fifth but ill-defined pattern is discernible, exemplified by locust "plagues," irruptive emigration in lemmings and certain other rodents, and some mass migrations by humankind, as caused by war, famine, fear, politics, or disease. These are episodic and often, if not primarily, caused by severe population stress or catastrophic environmental change.

—Sneed B. Collard

See also: Birds; Competition; Demographics; Eels; Gene flow; Geese; Hormones and behavior; Instincts; Learning; Population fluctuations; Population growth; Reproduction; Reproductive strategies; Salmon and trout; Whales, baleen.

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MIMICRY

Types of animal science: Development, ecology, evolution
Fields of study: Ecology, evolution science, genetics, population biology

Mimicry is the process whereby one organism resembles another and, because of this resemblance, obtains an evolutionary advantage.

Principal Terms

ADAPTATION: a phenotype that allows those organisms that have it a competitive advantage over those that do not have it

CAMOUFLAGE: patterns, colors, and/or shapes that make it difficult to differentiate an organism from its surroundings

WARNING COLORATION: the bright colors seen on many dangerous and unpalatable organisms that warn predators to stay away

The broadest description of mimicry is when one organism, called the operator or dupe, cannot distinguish a second organism, called the mimic, from a third organism or a part of the environment, called the model. There are many different types of mimicry. Some mimics look like another organism; some smell like another organism; some may even feel like another organism. There are many ways that mimicking another organism could be helpful. Mimicry may help to hide an organism in plain sight or protect a harmless organism from predation when it mimics a harmful organism. It can even help predators sneak up on prey species when the predator mimics a harmless organism.

In the case of hiding in plain sight, the line between camouflage and mimicry is not sharply defined. Spots or stripes that help an organism blend with the surroundings are classified as camouflage, since those patterns allow the organism to remain hidden in many areas that have mixtures of sunlight and shadow, and the organism does not look like any particular model. As an organism's appearance begins to mimic another organism more and more closely, rather than being just a general pattern, it moves toward mimicry. As in all other areas of biology, there are arguments about where camouflage ends and mimicry begins. The stripes of a tiger and the spots on a fawn are certainly camouflage. The appearance of a stick insect is more ambiguous. Its body is very thin and elongated and is colored in shades of brown and gray. Is this mimicry of a twig or just very good camouflage? Many biologists disagree. The shapes and colors of many tropical insects, especially mantids, also fall into this gray area of either extremely good camouflage or simple mimicry.

Batesian and Müllerian Mimicry

In contrast to camouflage, which hides its bearers, many species of dangerous or unpalatable animals are brightly colored. This type of color pattern, which stands out against the background, is called warning coloration. Some examples are the black and white stripes of the skunk, the yellow and black stripes of bees and wasps, red, black, and yellow stripes of the coral snake, and the bright orange of the monarch butterfly. Several species of harmless insects have the same yellow and black pattern that is seen on wasps. In addition to mimicking the coloration of the more dangerous insects, some harmless flies even mimic the wasps' flying patterns or their buzzing sound. In each case, animals that have been stung by wasps or bees avoid both the stinging insects and their mimics. This mimicry of warning coloration

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is called Batesian mimicry. Batesian mimicry is also seen in the mimicry of the bright red color of the unpalatable red eft stage of newts by palatable salamanders. Sometimes two or more dangerous or unpalatable organisms look very much alike. In this case, both are acting as models and as mimics. This mimicry is called Müllerian mimicry. Müllerian mimicry is seen in monarch and viceroy butterflies. Both butterflies have in their bodies many of the chemicals found in the plants they ate as larvae. These include many unpalatable chemicals and even toxic chemicals that cause birds to vomit. If a bird eats either a monarch or a viceroy that has these chemicals, the bird usually remembers and avoids preying on either species again—a classic Müllerian mimicry. Interestingly, not all monarchs or viceroys are unpalatable. It depends on the types and concentrations of chemicals in the particular plants on which they fed as larvae. Birds that have eaten the palatable monarchs or viceroys do not reject either monarchs or viceroys when offered them as food, but birds that have eaten an unpalatable monarch or an unpalatable viceroy avoid both palatable and unpalatable members of both species. This represents both Batesian and Müllerian mimicry at work.

Aggressive Mimicry

Mimicry by predators is called aggressive mimicry. The reef fish, called the sea swallow, is a cleaner fish, and larger fish enter the sea swallow's territory to be cleaned of parasites. The saber-toothed blenny mimics the cleaner in both appearance and precleaning behavior, but when fish come to be cleaned, the blenny instead bites off a piece of their flesh to eat. Anglerfish have small extensions on their heads that resemble worms. They use the mimic worms to lure their prey close enough to be eaten. The alligator snapping turtle's tongue and the tips of the tails of moccasins, copperheads, and other pit vipers are also wormlike and are used as lures. Certain predatory female fireflies respond to the light flashes of males of a different species with the appropriate response of the female of that species. This lures the male closer, and when the unsuspecting male is close enough to mate, the female devours him. This mimicry is quite complex, because the predatory females are able to mimic the response signals of several different species.

There are many other instances of mimicry, but the world champion mimics may be octopuses. As predators, these animals show unbelievable aggressive mimicry of other reef organisms. Octopuses can take on the color, shape, and even texture of corals, algae, and other colonial reef dwellers. As a prey species, the octopus can use the same type of mimicry for camouflage, but can also be a Batesian mimic, taking on the color and shape of many of the reef's venomous denizens.

Since in each case, being a mimic helped the organism in some way, it is not hard to understand how mimicry may have evolved. In a population where some organisms were protected by being mimics, the protected mimics were the ones most likely to mate and leave their genes for the next generation while the unprotected organisms were less likely to breed.

—Richard W. Cheney, Jr.

See also: Adaptations and their mechanisms; Butterflies and moths; Camouflage; Coevolution; Defense mechanisms; Octopuses; Predation.

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MOLES

Types of animal science: Anatomy, classification, reproduction
Fields of study: Anatomy, reproduction, zoology

Moles spend most of their time in underground burrows, digging for food with specialized front paws. They perform a service to farmers by destroying grubs, caterpillars, and insects.

Principal Terms

BOLTRUN: mole burrow tunnel used as an emergency exit
GESTATION: time in which mammalian offspring develop in the uterus
MARSUPIAL: nonplacental mammal having a marsupium
MARSUPIUM: abdominal pouch containing mammary glands and sheltering offspring until they are fully developed

Moles inhabit Africa, Europe, Asia, North America, and Australia. They are voracious, continually burrowing in the ground for food, for a mole must eat its weight in food daily. This is accomplished by digging approximately twenty-five feet of burrow per hour. Mole burrows are close to ground surfaces and can cause surface ridges. A mole's home is also recognized by its large, central mound of earth. This mole hill is created from the earth dug up in the mole's search for food. There are twelve mole genera worldwide, five of which inhabit the United States.

Types of Moles

Moles have pointy snouts, rudimentary eyes, velvety fur, short legs, and powerful digging nails on their front legs. Moles are nearly or totally blind; however, their hearing is acute and they detect sounds from great distances. Common garden moles are six inches long with furless tails, and have huge forelegs whose broad, thick nails gouge out earth. The largest species in the United States, *Scapanus townsendii*, is nine inches long. Shrew moles, the smallest, are 3.5 inches long.

European moles inhabit grasslands and pastures in the British Isles, continental Europe, and Asia. They dig elaborate burrows that hold central chambers with round connected galleries. Passageways radiate in all directions from galleries (for example, there will be a boltrun exit in case of danger). Each burrow has a warmly lined nest

Mole Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Insectivora
Family: Talpidae, with twelve genera and twenty-nine species, including *Scalopus aquaticus* (common garden mole), *Scapanus townsendii* (largest U.S. mole), *Neurotrichus gobbsi* (shrew mole), *Talpa europaea* (European mole), *Condylura cristata* (star-nosed mole), *Notoryctes typhlops* (marsupial mole)
Geographical location: Europe, Asia, North America, and Australia
Habitat: Most inhabit grasslands and pastures, though some live in freshwater
Gestational period: Two to six weeks
Life span: Three to six years
Special anatomy: Huge forelegs with broad nails; leathery pads or tentacle rings covering nasal passages

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for the mole. Tunnels run from just below ground level to 2.5 feet deep and may be 170 feet long. European moles eat worms, beetle and fly larvae, and slugs. They are active day and night, alternating every four hours between digging or eating and resting, and they live alone except when mating.

Golden moles inhabit grassy forests, riverbanks, mountains, and semidesert areas of Africa. The smallest species is Grant's golden mole, 2.5 inches long, and the largest species is the giant golden mole, 9 inches long. Their golden fur repels water, keeping them dry while digging. When burrowing, leathery pads cover their noses, keeping dirt out. Burrowing allows foraging for insects, larvae, earthworms, crickets, slugs, snails, and spiders. Golden moles cannot see well and find food by touch. Sometimes they come to the surface (for mating, as an example). They live alone and defend their homes when other moles—even others of their own species—intrude.

Star-nosed moles, of eastern Canada and the northeastern United States, are black-furred, five inches long (excluding the tail) and weigh three ounces. They live near water, swim well, and dig in soil along shorelines. They burrow day and night, foraging for earthworms, aquatic insects, fish, and mollusks. Their nose tips hold a twenty-two-tentacle, touch-sensitive star which is their main sense organ. Star-nosed moles are solitary.

The Australian central desert holds the only species of marsupial mole. Their bodies range from 2.5 to 8.5 inches long, and they weigh from 0.3 to 6 ounces. Like other moles, they have short legs and front paws holding digging claws. A bare patch of skin atop each mole's nose pushes aside dirt as it digs. They have yellow fur, small nose slits, and no functioning eyes.

Marsupial moles burrow in soil near rivers and grasslands in Australian desert. While burrowing, they eat moths and beetle larvae. They do not dig permanent burrows but travel widely, sleeping in temporary burrows. They are solitary and their females have marsupiums, to carry young.

Life Cycles of Moles

Life cycles are best known for the star-nosed, European, and golden moles. Male and female star-nosed moles mate between February and April. The female builds a nest of leaves and moss in her burrow and has two to seven furless, blind, helpless young after a six-week gestation. They develop quickly, leave the nest in three weeks, and can mate after ten months.

Male European moles enter the tunnels of females to mate. After a five-week gestation, three to seven blind, hairless young are born. The young grow fur, open their eyes, and leave the nest in five weeks. European moles live for three years.

Male golden moles wishing to mate can attract mates at any time of the year. Litters contain two to three hairless young. They are two inches long, blind, and weigh less than one ounce. After nursing, when they weigh about 1.5 ounces, the young leave the nest for good.

Moles are considered to be pests by farmers and home gardeners, who think they eat plant roots and kill crops. However, moles never eat plants and perform a real service by killing grubs, caterpillars, and insects. Nonetheless, farmers, gardeners, and people with lawns consider them nuisances and poison them or set traps in their tunnels because they "spoil gardens and fields."

—Sanford S. Singer

See also: Home building; Mammals; Marsupials; Shrews; Vision.

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MOLLUSKS

Type of animal science: Classification
Fields of study: Anatomy, invertebrate biology, physiology

Mollusks, the phylum Mollusca, have soft, boneless bodies. Most also have shells. There are fifty thousand species of mollusks, including snails, oysters, and clams.

Principal Terms

FOOT: bottom portion of gastropods, on which they walk; it subdivides into tentacles in cephalopods

HERMAPHRODITE: an organism having both male and female reproductive systems

MANTLE: the outermost living tissue of mollusks; it makes shells, mother-of-pearl, and pearls

RADULA: a tonguelike, toothed organ used to grind food or drill holes in shells of prey

SESSILE: an organism incapable of moving from its point of origin

Mollusks first appeared in early Cambrian times, 650 million years ago. They are the second largest animal phylum, Mollusca (from Latin *mollis*, "soft"). The only larger animal phylum is Arthropoda. According to current estimates, there are approximately 49,000 mollusk species. All mollusks have soft, boneless bodies. Most have shells, though some shells are poorly developed and are even absent in some cases. Mollusk shells are like coats of armor.

Mollusks form seven classes. Best known are gastropods, including approximately 38,000 species of snails and slugs; bivalves or pelecypods, approximately 8,000 species of clams and scallops; cephalopods, approximately 600 species of squid and octopuses; and polyplacophora, approximately 600 species of chitons. The other classes contain under 1 percent of mollusk species and are not discussed.

Mollusks are present in all of earth's habitats. However, most of them, comprising the greatest species diversity, are in the oceans. There, the largest number are various species of gastropods (snails). All gastropods are univalves, possessing one shell. Many other mollusks are the familiar pelecypod—bivalve—mollusks (clams), which have two shells. Mollusk bodies look undeveloped and many lack apparent heads. However, all have well-developed nervous, circulatory, respiratory, and sensory systems. Except for cephalopods, mollusks are slow-moving, sluggish, or immobile (sessile). In many cases they spend their adult lives attached to rocks or dug into sand or mud, awaiting the approach of prey.

Some mollusks, mostly gastropods, occur in freshwater and on land. For example, snails and slugs are seen at the bottoms of ponds, rivers, and lakes, or under fallen trees and decaying logs. Some land snails even live in tree branches. Characteristic features of gastropods are a true head, a creeping surface (or foot), eyes, and tactile feelers. The foot gives gastropods their name, which means "foot on belly" in Latin. Most gastropods have a univalve shell, but some species have no shell. Others, such as garden slugs, have tiny, internal shells.

Physical Characteristics of Mollusks

The largest mollusk is the giant squid, which is also the largest invertebrate. It can be fifty-five feet long and weigh several tons. Most mollusks, however, range from 0.5 to 10 inches in length and only weigh up to a few pounds. One exception to the size rule is the tropical giant clam, maximum diameter 4.5 feet, maximum weight five hundred pounds.

Mollusk Facts

Classification:
Kingdom: Animalia
Phylum: Mollusca (soft-bodied)
Classes: Bivalva (two-shelled, no distinct head); Cephalopoda (no shell or internal shell, very mobile, tentacled, has head and eyes); Gastropoda (univalve shell, moves slowly, tentacled, has head); Polyplacophora (simple crawling mollusks or chitons); Scaphopoda (elongated, open-ended tusk shells, tentacled, but no head)
Orders: Protobranchia, Septibranchia, Filibranchia (mussels and oysters), Eulamellibranchia (clams), Tetrabranchia (Nautilids), Dibranchia (octopuses, squid, cuttlefish)
Geographical location: Every ocean and many bodies of freshwater on every continent except Antarctica
Habitat: Mostly salt water, although many live in freshwater and on the land
Life span: Some live for under a year, others for one to five years; giant squid and giant clams may live for twenty-five years or longer
Special anatomy: Foot (for locomotion), siphons (for jet propulsion), a shell of calcium carbonate and protein, gills or lungs, a tonguelike radula for drilling or grinding food

Mollusk shells thus function protectively, like the rib cages and pelvic bones of vertebrates. The shells of bivalves are divided into two valves, which are opened or tightly closed by strong muscles. These muscles must be cut in order to open the shell for examination. The gastropods possess one asymmetrical shell, often of spiral shape, into which they retreat from the world. In cephalopods the shell is internalized, but still yields organ protection.

The organs and their positions in mollusks, especially gastropods, are as follows. At the anus end of the body are two or more gills (lungs in land forms) for breathing. At the front end of the body are jaws and a tonguelike, toothed radula. It grinds food or procures it by drilling into shells of prey or ship timbers (in shipworm snails).

There are many mollusk variations. However, some features can be generalized in mollusk bodies, based on gastropods and bivalves. In motile forms, locomotion is due to crawling on flat, muscular, snail-like feet, though jet propulsion occurs in cephalopods. Also, the mollusk body has a head at one end and an anus at the other. Furthermore, much of the body is covered by a shell (internalized in cephalopods) of calcium carbonate and protein. Shells are made by mantle tissue. Inside a shell is a large part of the body, fragile parts of cardiovascular, digestive and excretory, nervous, reproductive, and respiratory systems.

Most mollusks, such as this swimming scallop, are distinguished by their calcified, bivalve shells, which provide armorlike protection for their soft, boneless bodies. (Digital Stock)

Around the jaws are tentacles, used for sensation in gastropods. Cephalopod tentacles are used to capture prey. Between the radula and the anus are the stomach and the gut. A heart, near the hind end of the body, receives blood and sends it into the body cavity. The mollusk nervous system—comparable to that in fish—is composed of nerves that surround the gut, a brain, and sense organs. Mollusks also have kidneys and gonads.

Many mollusks are herbivores, grazing on underwater plants. Some terrestrial gastropods, such as slugs, eat cultivated plants and are serious garden and agricultural pests. Scaphopoda feed on organic matter deposited on ocean and lake bottoms. Bivalves filter protozoa, eggs of sea animals, and diatoms out of the water in which they live. Many gastropods are hunter carnivores, eating slower-moving or sessile animals, such as other mollusks. Cephalopods are very active predators and prey on animals such as crabs.

The Life Cycles and Senses of Mollusks

Most mollusks have separate sexes and a few exhibit courtship behavior. With or without courtship, mollusks usually spawn sperm and many thousands of eggs into waters around them. There, fertilization and development of offspring occur. When eggs hatch, offspring undergo a larval stage. Larvae of most mollusk species are, at first, free-swimming, using for locomotion a ring of cilia. Most settle to lake, ocean, or stream bottoms as crawlers who mature into adults.

Many mature mollusks, such as oysters and mussels, are sessile, permanently affixed to rocks. Gastropods are capable of slow crawling on a muscular foot. Cephalopods, such as squid and octopuses, are an exception to the mobility rule for mollusks. They are very mobile at all stages of their lives. Adult cephalopods move very quickly by expelling jets of water from mantle cavities, using an organ called a siphon. Jets are expelled in the direction opposite to movement. Jet propulsion makes cephalopods the fastest-moving mollusks. It also suits them to a life of vigorous predation. In cephalopods, the foot differentiates to ten arms (squid) or eight arms (octopuses) that seize prey.

In some cases, fertilization in mollusks is internal, with protective coverings secreted around eggs. In others, fertilization and development are internal in females and offspring are delivered alive, as with live-bearing snails. Slow-moving snails and related mollusks are often hermaphro-

Oysters, Beds, and Pearls

Edible oysters, such as *Ostrea virginica*, are plentiful on European and North American coasts. Oysters were a major food of coastal Native American peoples. Colonists ate them too, and natural oyster supplies were severely depleted by the late 1800's. Cultivated oyster beds were then developed to enhance nature's yield. In the twenty-first century, many food oysters come from cultivated beds.

The beds begin with the millions of eggs spawned yearly by every female oyster. They are started by finding places holding many newly hatched oyster larvae. Bricks, flowerpots, old shells, and other objects are placed on shallow sea bottoms beneath them. Then, a week after hatching, larvae produce tiny shells and, weighed down, drop to the sea bed. They attach to the objects and remain attached for the rest of their lives. After attachment, oyster-laden objects are dredged up and moved to the new beds.

Some oysters are invaded by foreign bodies that lodge between mantle and shell. These irritants cause the mollusks to produce mother-of-pearl to seal them off. In time, an irritant encased inside many layers of mother-of-pearl becomes a pearl. Most pearls are irregularly shaped and much less valuable than a few perfectly spherical pearls used in pearl necklaces. Pearl color depends on oyster diet and bed temperature. The pearls sought most are white, rose, steel blue, or black. They arise naturally in small numbers, or are cultured by the insertion of mother-of-pearl beads into oysters.

dites (both male and female). This doubles the number of mates available to each such organism, and often self-fertilization occurs. Both options have great survival value. A few species reproduce by parthenogenesis, without fertilization. Also, mother mollusks may protect developing eggs, and some oysters raise their offspring within the mantle cavity.

The mollusks live for periods ranging from under a year to two years for many small to medium-sized varieties and four to five years for some snails and shellfish. Giant squid and giant clams reportedly can live for over twenty-five years. Such life spans occur only when organisms reach old age, an uncommon situation for wild animals.

Sensory ability varies in mollusks. Most mollusks see poorly or not at all. However, the cephalopods have eyes like vertebrates, complete with lenses and retinas. Squid eyes reportedly lack eyelids but otherwise look very much like those of humans. Although it is not ubiquitous in mollusks, some gastropods have well-developed abilities to smell and find food at considerable distances. Predators are often detected in this way, too. Conclusive studies of intelligence have not been carried out in mollusks. However, ability to learn from experience has been claimed for cephalopods.

Beneficial and Destructive Mollusks

Mollusks are very abundant. On the benefit side, they are important foods for bottom-feeding fish and whales. Numerous mollusks are also valuable foods for humans. Especially widely eaten are clams, mussels, oysters, octopuses, and scallops. More exotic food mollusks include land snails. Mollusks (especially oysters) also produce pearls, the only gems made by living organisms.

On the debit side, gastropod and cephalopod carnivores do serious damage. Gastropods prey on slow-moving or sessile organisms, wreaking havoc on clam and oyster beds that provide shellfish for human consumption. Also, cephalopods are active predators, diminishing the sea's yield of meats sought by humans.

Another mollusk problem is foreign invasion, exemplified by zebra mussels (*Dreissna polymorpha*). These pistachio-nut-sized European saltwater mussel invaders were released into the Great Lakes from the hulls of ocean-going vessels in the late 1980's. They flourish in the Arkansas, Hudson, Mississippi, Ohio, and Saint Lawrence rivers. Superabundant reproduction (a female lays a million eggs per year) yields myriad larvae that, as adults, clog power plant and factory water intakes, requiring costly cleanup. More problematically, they eat microbes in the water, damaging the lifestyles of indigenous wildlife that also use this food. It is estimated that the mussels cost industry and consumers over $500 million per year.

—*Sanford S. Singer*

See also: Clams and oysters; Locomotion; Marine animals; Octopuses and squid; Reproduction; Shells; Snails; Tentacles.

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MOLTING AND SHEDDING

Type of animal science: Development
Fields of study: Developmental biology, invertebrate biology, physiology

Molting or shedding is a hormonally regulated process during which animals lose and then replace either their entire body surface covering or structures associated with the body surface such as hair or feathers.

Principal Terms

ARTHROPODS: animals with jointed exoskeletons, including insects, crayfish, and spiders

EXOSKELETON: a skeleton made up of proteins and minerals, found on the outer surface of an animal

HORMONES: chemical messengers produced by specialized organs and cells either in the endocrine system or the nervous system; they have specific effects on different cells of the body

INVERTEBRATE: animal without an internal skeleton made up of individual bones or vertebrae

METAMORPHOSIS: a change in the physical state of an animal, such as the transformation of a tadpole into a frog or the development of a moth from a caterpillar

STEROID HORMONE: a hormone that is made from cholesterol

As a normal part of growth and development, some species of invertebrate and vertebrate animals undergo a process commonly called molting or shedding. Scientists term this process ecdysis, which is derived from a Greek word meaning "to escape or slip out." It is common for animals to molt more frequently as larvae or juveniles and less often as they mature and become adults. Molting is also an integral part of metamorphosis. Immediately after a molt, animals may not be fully protected from the environment, and they may be more vulnerable to predators. For example, the new exoskeleton of arthropods may not be fully hardened, or some birds may lose flight feathers. During a molt, animals may shed and replace their entire body covering or structures associated with the body surface. Molting may involve the replacement of the skin, an exoskeleton, or a cuticle in its entirety. In temperate regions, it is not unusual in the summertime to see the old exoskeleton of a cicada still clinging to a tree. Feathers, fur, or hair, which are derived from skin cells, are often shed in a cyclic fashion rather than all at once. Animals may also lose body structures during a molt. Adult male deer shed their antlers at the end of the mating season and lemmings replace their claws. In most animals the interval between molts is called the intermolt, except insects, where it is referred to as an instar.

The Molting Process

Environmental factors such as stress, temperature, and light cycle can serve as stimuli to molting in different species of animals, but the actual sequence of events leading up to shedding and replacement is strongly influenced by hormones and by specific interactions between the nervous system and the endocrine system. Hormone production is the primary function of the endocrine system. However, regions of the brain also produce hormones, which in this case are called neurohormones. One class of hormones in particular, steroid hormones, is actively involved in the regulation of molting.

Before an animal molts, a new skin or exoskeleton will have formed beneath the old one. Often

Life Cycles and Molting

Animals in the phylum Arthropoda and class Insecta undergo many molts and possibly several metamorphoses as a normal part of their life cycle. By responding to appropriate environmental stimuli, the arthropod brain controls the processes of molting and metamorphosis. It does so by regulating the release of specific hormones. The amount of one hormone, commonly referred to as ecdysone, controls molting and growth. This hormone also stimulates the digestion and reabsorption of the old exoskeleton. Another, called juvenile hormone, controls metamorphosis. Some insects such as grasshoppers have a nymph stage where the juvenile undergoes considerable growth in body size as the nymph makes the transition to an adult. When an exoskeleton is shed, the new one will not immediately harden. This allows time for the skeleton to expand to the new body size. Greater than 80 percent of insects including moths and butterflies have a caterpillar or larval stage during which active growth occurs. The overlying cuticle, the exoskeleton, acts like a jacket to confine the caterpillar to a maximum size and therefore limit growth at each stage of development. Thus, the exoskeleton needs to be periodically shed. Animals often swallow air as one way to rupture the old skeleton and to resize the new one. After several molts in the caterpillar stage, the amount of juvenile hormone is decreased and the caterpillar transforms to a pupa. Finally, in the absence of juvenile hormone, a final molt will occur and the pupa undergoes metamorphosis into an adult. Once they become adults, insects no longer molt. However, the adults of other arthropods, such as crayfish and lobsters, continue to have periodic molts their entire life.

the old exoskeleton splits along the midline of the posterior surface and the animal then crawls out. Different animals have specific ways to stretch the new exoskeleton before it hardens. The best way to stretch the skeleton is by increasing body size. This might be accomplished by a growth stage or by artificially increasing size. A lobster, for example, might absorb enough water to increase body size by 20 percent, while other animals take up air.

Molting in Amphibians and Reptiles

Molting of an entire body surface such as the skin or exoskeleton requires the separation of the layer being shed from the underlying tissue that will become the new outer surface. The chemical and physical processes leading up to the separation will vary slightly between animal groups. Amphibians such as frogs, toads, and salamanders periodically shed the outermost surface layer of their skin. Prior to molting, mucus is secreted beneath this layer of cells. Since the mucus is secreted between the old and new surface layer, it may assist in the separation by creating a space between them. The mucus may also act as a lubricant and aid the animal in removal of the old skin. Frogs are also known to bloat themselves and increase movement to break out of the old skin. Animals will often eat the skin they have shed as a way to recycle nutrients.

Reptiles show a good deal of variability in the replacement of their scales. In fact, snakes may shed their skin several times a year. In the time immediately preceding ecdysis in snakes, a fragile zone develops. Old skin will now separate from the underlying, newly developed scales. During the molt the snake's eyes will appear cloudy, because the outer part of the eye, which is a part of the skin, is also detaching. The rattlesnake's rattle is formed from the part of the skin that remains attached to the tail at the end of each shedding cycle. Snakes shed their skin in one piece, but lizards do not. Turtles are different from both snakes and lizards. First, their scales do not overlap to form sheets and second, most turtles add new growth to existing scales and do not molt. The molting pattern in crocodiles and alligators, which shed and replace individual scales, more closely reflects events in birds than other reptiles.

Molting in Birds

Birds shed their feathers each year and it is not unusual for some species to molt several times during the year. During the molting season, a bird's behavior may be affected in several ways, including events associated with reproduction. Molting will be influenced by the time of year and the mating season. Many female chickens often stop laying eggs when they are molting. New feathers will develop in the same area of the skin as the old ones. As the new feathers grow from the follicle they may push the old feathers out of the skin or they may be pulled out. The primary purpose of molting is to replace worn feathers with new ones, and often a pattern of feather loss will be noted. Wing feathers closest to the body are lost first and the molt progresses outward along the wings.

It is common for male birds to molt so that they can replace their duller plumage with more colorful feathers associated with attracting a mate. This is called a prenuptial molt and generally occurs in late winter or early spring. A postnuptial molt is common in both males and females. The chicks will lose their original feathers (down) when they undergo a postnatal molt to juvenile feathers. If it is a species of bird where the males have a coloration pattern different from the females, the early juvenile coloration more closely resembles the female. As the juveniles mature they will undergo successive molts to adult plumage. The time frame for maturation can vary considerably. Eagles can take up to five years before a final molt into full adult feathers. Mature birds that depend upon flight as a method of escaping predation will not molt all of their feathers at one time. A complete molt would result in the loss of flight feathers on the wings as well as tail feathers which assist in stability and guidance during flight. Flight is less adversely affected if there is a symmetrical loss of feathers on the wings and if tail feathers are

Image Not Available

shed in groups. Birds such as ducks and geese, which are able to spend extended periods of time in the water, are able to avoid most predators by swimming or hiding in tall grass. These birds do molt all of their flight feathers at one time. Male ducks are also somewhat unusual because, during the summer months, they molt from mating colors to plumage similar in color to females. This change is called an eclipse and makes it more difficult to tell males from females.

Molting in Mammals

When they lose hair, mammals, including humans, are molting. Like feathers, a hair grows outward from a follicle in the skin and, as new hairs grow, old hairs will be lost. Under normal conditions in humans, hair loss will be a gradual process over an individual's lifetime and it does not occur all at once. Molting in many mammals is directly influenced by length of day and interactions between the endocrine system and the nervous system. The number of molts per year varies, and many mammals molt twice a year, once in the spring and once in the fall. Foxes, however, molt once a year in the summer, and the snowshoe hare molts three times: summer, autumn, and winter. In general, it is common for the summer coat of mammals to be thinner than the winter one, and it is not unusual for the two coats to be different colors. Changing hair color provides one method of camouflage. White fur lacks pigment and blends well with snow and light surroundings. In contrast, darker shades blend better in the summer and fall. In mammals, like other animals, the transition from juvenile into adult can be associated with a molt. Deer fawns, for example, have very pronounced white spots, but when they become further developed they molt into the solid coloration of adults.

—Robert W. Yost

See also: Amphibians; Arthropods; Birds; Crustaceans; Feathers; Flight; Fur and hair; Hormones and behavior; Hormones in mammals; Insects; Reptiles; Shells; Skin; Snakes.

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MONKEYS

Type of animal science: Classification
Fields of study: Anatomy, wildlife ecology, zoology

Monkeys are a favorite in zoos around the world. Representing more than 140 species spread throughout the tropics, the term "monkey" is often misused as a synonym for any primate.

Principal Terms

ARBOREAL: living completely or primarily in the trees
OPPOSABLE: a thumb which can be turned so that its pad makes contact with the pad of each of the fingers (as in the human)
PREHENSILE: capable of grasping
QUADRUPEDAL: walking on all four feet
SEXUAL DIMORPHISM: the occurrence of anatomic or physiologic differences that distinguish males from females of a particular species

The term "monkey" is used to denote any higher primate (suborder Anthropoidea) that is not an ape. Thus, it includes both members of the New World monkeys (infraorder Platyrrhini) as well as the Old World monkeys (infraorder Catarrhini, superfamily Cercopithecoidea). Monkeys have little in common with each other except for the fact that most are quadrupedal, but this does not eliminate all other primates. It is unclear where the name "monkey" originated, although a common interpretation is that it relates to the medieval term "moneke," meaning manikin.

Old World (Catarrhine) Monkeys

The Old World monkeys are the largest and most diverse family of primates, covering about ninety-five species and ranging over most of Africa, Asia, and Indonesia. The name Catarrhine means "downward-nosed," referring to the fact that the nostrils are close together and point forward and down. Catarrhine monkeys include macaques, mangabeys, baboons, mandrills, velvet monkeys, guenons, colobuses, proboscis monkeys, and langurs. There are two subfamilies: the leaf-eating, arboreal Colobinae (examples include the colobus and the langur), and the omnivorous, often ground-dwelling Cercopithecinae (including the baboons, mandrills, macaques, and guenons). The Colobinae have a rather complex stomach and digestive system, whereas the Cercopithecinae have a simple stomach combined with cheek pouches in which food can be stored.

The macaques are the greatest in number among the Old World species, as well as the most widespread. The most northerly is the Japanese macaque, which can live in cold, snowy climates. Other macaques live in dry, almost desertlike conditions in the tropics.

Old World species are generally larger than New World species, and there is considerable sexual dimorphism. Most have bare buttock pads, which may be brightly colored. Their tails are seldom fully prehensile, and may be significantly reduced in size. Almost all are active during the day, with excellent vision, hearing, and sense of smell. They communicate almost entirely by sight and sound, displaying a wide range of calls. Many display a range of facial expressions, used for communication with their own species as well as with other species nearby. Most are fully arboreal, but baboons are ground feeders, and macaques live both on the ground and in the trees.

When more than one species of monkey dwells in the same locality, the various species generally occupy different vegetation levels in order to avoid competition. This behavior is known as arboreal stratification. Most authors recognize four layers of vegetation in the tropics: the ground layer, lower canopy, middle canopy, and upper canopy. For instance, in the African guenons (*Cercopithecus* spp.), DeBrazza's monkey lives at the ground level, the red-tailed monkey sleeps in the middle canopy but spends the day on the ground, the blue guenon lives in the upper canopy but forages in the middle, and the Diana monkey lives solely in the upper canopy.

New World (Platyrrhine) Monkeys

The New World monkeys are a highly successful and diversified group colonizing Central and South America. The term usually refers to the infraorder Platyrrhini, meaning "flat-nosed." As compared with the Catarrhine monkeys, the nostrils of the Platyrrhines are broadly separated and usually point to the sides. Members of the Platyrrhines include capuchins, howler monkeys, sakis, woolly monkeys, squirrel monkeys, and uakaris, a total of about forty-five species.

New World monkeys have long, thin fingers on each hand, with flattened or curved nails. Although their thumbs are not opposable, as they are in the human, the big toe can be opposed against the other toes for gripping branches tightly. New World monkeys are excellent runners and jumpers, swinging and leaping through their densely wooded habitats. Their tails are fully prehensile; they can grasp objects at the tip and curl around a branch and support the full body weight of the animal. In almost all cases, the tail is at least as long as the head and body, and it acts as a balancing organ, often being held in a curled pattern.

None of the New World monkeys are ground dwellers, unlike the baboons and other Old World monkeys. None of them have cheek pouches, and sexual dimorphism is rarely seen. New World monkeys are gregarious and live in family-based

Most monkeys live in social groups that range over a defined territory in search of food. (PhotoDisc)

Monkey Facts

Classification:
Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Primate
Suborder: Anthropoidea
Families: Cercopithecidae (Old World monkeys, eight genera, forty-five species); Cebidae (New World, capuchin-like monkeys, eleven genera, and thirty species)
Geographical location: Africa and Asia (Catarrhines), Central and South America (Platyrrhines)
Habitat: Mostly forests, some grasslands
Gestational period: Old World monkeys, 5 to 6 months; New World monkeys, 4 to 7.5 months
Life span: Old World monkeys, twenty to thirty-one years; New World monkeys, twelve to twenty-five years
Special anatomy: Opposable thumbs, forward-facing eyes for binocular vision, large brain case

groups with much vocal and visual communication. They have highly developed olfactory organs that may also be used for communication. Males of many species contain a glandular patch on the sternum (breastbone) which they rub against tree branches to act as scent markers. Marking by means of urine and feces is also common. For instance, night monkeys coat their hands and feet with urine so that they leave a telltale scent wherever they go.

Families are well developed in most species of monkeys, although females do most of the caring for their offspring. Mothers usually carry their young on their backs until they are ready to move through the canopy on their own. Group size seems to depend primarily on the productivity and abundance of the foods typically eaten by the species. Species that live in small groups tend to feed on small, scattered, or scarce resources such as insects, small vine fruit, or newly emerged leaves of bamboo. Species that form large groups use abundant or clumped resources, such as fruits on large fig trees. Small family groups are typically one to three animals, while large groups may involve seven to twenty members.

—Kerry L. Cheesman

See also: Apes to hominids; Baboons; Cannibalism; Chimpanzees; Communication; Communities; Evolution: Animal life; Evolution: Historical perspective; Fauna: Africa; Gorillas; Groups; Hominids; *Homo sapiens* and human diversification; Human evolution analysis; Infanticide; Learning; Lemurs; Mammalian social systems; Orangutans; Primates.

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MONOTREMES

Types of animal science: Reproduction, development
Fields of study: Biochemistry, cell biology, developmental biology, embryology, physiology, reproductive science

Monotremes represent an ancient developmental line of mammals. They retain many reptilian characteristics, including the laying of eggs. Monotremes are found primarily in Australia.

Principal Terms

BROOD POUCH: a temporary external pouch created by folding the skin of the abdomen together; used to carry young as they continue to develop

CLOACA: a bodily opening at the end of the gut into which both the waste disposal and reproductive systems open

ECHIDNA: a long-snouted, insect eating, egg-laying mammal; also known as the spiny anteater

MONOTREME: reptilelike mammals, distinguished from other mammals by the fact that they lay eggs and have a cloaca

PLATYPUS: web-footed, duck-billed, semi-aquatic, egg-laying mammal

The monotreme order of mammals is comprised of two families, Ornithorhinchidae and Tachyglossidae. The first family contains just one genus and species, that of the duck-billed platypus, while the second contains two genuses and two living species of echidnas (short-nosed and long-nosed). These animals have much of the conventional appearance of mammals, but they are also quite different in some respects from the rest of the mammals. Both the platypus and the echidnas lay eggs which are incubated and hatched outside the body of the mother.

Monotreme Anatomy

The monotremes are more closely related in evolution to the reptiles than are any other recent mammals. They are not the ancestors of the marsupials or the placental mammals, but rather they represent a distinct line of mammalian evolution. They possess certain mammalian features, such as hair and mammary glands, and they are warm-blooded. On the abdomens of the females, milk oozes from paired areas of tubular glands (they possess no teats for suckling) and is lapped up by the young. They have a four-chambered heart and skeletal features associated with mammals. Other features, such as the presence of a cloaca, along with features of the vertebrae and ribs, are very reptilian.

In male monotremes, the penis is attached to the ventral wall of the cloaca, and is divided at the tip into paired canals used only for the passage of sperm. In female monotremes, the oviducts, which carry the eggs from the ovary, open separately into the cloaca. In the oviducts, the eggs are fertilized and then covered with albumen (a protein like that found in chicken egg whites) and a flexible, sticky, leatherlike shell. This reptilian feature of a shell-covered egg is found in no other order of mammals.

Both living animals and fossil records indicate a range for the monotremes that includes only Australia, Tasmania, and New Guinea.

Duck-Billed Platypus

W. H. Caldwell, in 1884, first demonstrated that platypuses lay eggs, unlike other mammals. There are still many unknowns regarding platypus reproduction and development, especially in terms of biochemistry and endocrinology. Copulation generally takes place during the spring months of

August and September, and usually occurs in water. The female then withdraws to a rather complicated nesting burrow dug into the side of a streambed. Inside the burrow is a nesting chamber consisting of a bed of grass, reeds, and leaves. Generally, two sticky eggs are laid here. There is no pouch for the eggs to incubate in, and the exact mechanism of incubation remains unclear. It is likely that the female curls around the eggs and protects them with her body heat. Incubation is seven to ten days, after which the hatchlings use an egg tooth (much like reptiles) to emerge from the egg. At birth the hatchlings are about 17 millimeters (0.65 inches) long. They feed on ill-defined milk patches hidden under dense fur on the ventral side of the mother. Hatchlings have very large, strong forelimbs that are used for holding on to the fur over the milk patches. Because they are so well protected in the dense fur, hatchlings are nearly impossible to detect by looking at the mother.

As the young grow, the mother's mammary glands also grow. These mammary glands are very similar to those seen in other mammals, and the chemical composition of the milk is also similar. Until they emerge from the burrow, hatchlings feed on only the milk from their mother. Young platypuses emerge from the burrow for the first time in December or January, generally being thirty to thirty-five centimeters (twelve to fourteen inches) long. They will eventually grow to forty to forty-five centimeters as adult females, or fifty to fifty-five centimeters as adult males.

Echidnas

Previously known as spiny anteaters, echidnas have compact, rounded bodies covered with short, thick spines. They have elongated, slender snouts and strong limbs, and are powerful diggers. They have no teeth and, like other ant- and termite-eating mammals, have a long sticky tongue that reaches well beyond the snout. Termites, ants, and other small arthropods are swept into the mouth by its action.

Adult echidnas are solitary animals, except when it is time to mate. During the breeding season (late June to September), males will follow females for several weeks at a time before being allowed to mate. Often several males will be seen in single file following a female, this being referred to as an echidna train. It is not known exactly how males find breeding females, although it is likely that females secrete a scent that can be detected several miles away.

Females develop a brood pouch during breeding season. Following mating, a single fertilized egg is transferred from the cloaca to the pouch, although the actual mechanism for this transfer is not clear. The leathery-shelled eggs average 14-17 millimeters (0.55-0.65 inches) in length. The egg is incubated for ten days in the pouch before the hatchling appears. The young echidna (who is about 1.2-1.3 centimeters, or 0.5 inches, in length when it is born) remains in the brood pouch for an additional eight weeks until its spines develop. During this time it feeds on milk flowing from the mammary ducts onto tufts of hair within the pouch.

When the youngster emerges from the pouch, it is hidden by its mother in a protected spot. It appears that the young echidna then begins a short period of hibernation, during which continued development occurs. Echidnas are reproductively mature at one year of age.

—Kerry L. Cheesman

See also: Beaks and bills; Fauna: Australia; Lactation; Mammals; Reproduction; Reproductive strategies; Reproductive system of female mammals; Reproductive system of male mammals; Reptiles.

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MOOSE

Types of animal science: Anatomy, classification, reproduction
Fields of study: Anatomy, systematics (taxonomy), zoology

Moose, the largest species of deer, are herbivorous ruminants. Once hunted almost to extinction, they are now a protected species.

Principal Terms

ARTIODACTYLS: hoofed mammals, including cattle, pigs, goats, giraffes, deer, and antelope
GESTATION: the term of pregnancy
HERBIVORE: an animal that eats only plants
KERATIN: a tough, fibrous protein which is a major component of hair, nails, hooves, and the outer covering of true horns
RUMINANT: a herbivore that chews and swallows plants, which enter its stomach for partial digestion, are regurgitated, chewed again, and reenter the stomach for more digestion

Moose are artiodactyls of the family Cervidae (deer). Almost all artiodactyls walk on two toes. Their ancestors had five, but evolution removed the first toe, and the second and fifth toes are vestigial. Each support toe—the third and fourth toes—ends in a hoof. Artiodactyls are herbivores and many, especially the Cervidae, are ruminants. This means that they chew and swallow vegetation, which enters the stomach for partial digestion, is regurgitated, chewed again, and reenters the stomach for additional digestion. This maximizes nutrient uptake from food.

Moose are the largest of deer. Like all cervids, male moose have solid, bony, branched antlers, which are shed and regrown each year. Moose live in northern Europe, eastern Siberia, Mongolia, Manchuria, Canada, Alaska, Wyoming, and the northeastern United States.

Physical Characteristics of Moose

Moose—called elk in Europe—have long, solid bodies. Males can be eight feet tall at the shoulder, ten feet long from muzzle tip to rump, and weigh up to 1,800 pounds. Females are 25 percent smaller overall. Moose heads, antlered in males, are angular, long, and have large muzzles. Their large eyes, as in other deer, are set back on their faces and on the sides of their heads. This optimizes their vision. Moose also have thick necks, humped shoulders, and long, strong legs that allow running speeds of up to forty miles per hour. Moose

Moose Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Artiodactyla
Family: Cervidae (deer)
Genus and species: Alces alces
Geographical location: Northern Europe, eastern Siberia, Mongolia, Manchuria, Canada, Alaska, Wyoming, and northeastern United States
Habitat: Mountains, forests, and near lakes or marshes
Gestational period: Seven to eight months
Life span: Fourteen years, but some live up to twenty years
Special anatomy: Antlers

Moose have palmate antlers, shaped like a fingered hand, rather than the spiky antlers of most other cervids. (Digital Stock)

fur is brownish-black, fading to grayish-brown on the belly.

Moose antlers are large and palmate, holding up to twenty branched points, which look like fingers on a hand. Antlers are important during mating, when a male lacking them would lose fights for mates and a chance for offspring. Antlers differ from true horns, which are pointed, permanent, bony structures often seen on heads of male ruminants. Horns have bone cores which are extensions of the skull's frontal bone. Atop the core is a skin layer, rich in a tough, fibrous protein, keratin. The high keratin content in this skin makes it tough and durable. Horns range from straight spikes to elaborately curved varieties. Animals having horns keep them for life Antlers are horns that are shed yearly and regrown. Like true horns, antlers grow out of skull bones. They arise from permanent frontal bone structures called pedicles. At first antlers have soft, velvetlike skin coverings. Instead of hardening, as in horns, the covering dies off and is rubbed away by the animal. Antlers function like horns, serving for self-protection and allowing males to develop ascendancy.

Moose are often found on mountains, in forests, and near lakes and marshes. They are herbivores lacking upper incisor and canine teeth, but having pads in their upper jaws to help lower teeth grind vegetable food. Adults eat up to fifty pounds of vegetation per day, including water plants, branches, twigs, and leaves from aspen, willow and birch trees, berries, and bark. A moose often stands up against young trees and bends them over to reach leaves at their tops. In winter, moose dig through snow to find grass, twigs, and other vegetation. Moose eat during the daylight hours and at night.

The Life Cycle of Moose

Male moose are solitary animals during spring and summer. In September and October, they fight for mates. A successful male may lead several females and babies all winter. In the spring, the male leaves his harem, returning to a solitary life. Moose gestation, seven to eight months, yields one or two offspring which nurse for four months and stay with the mother until she is ready to give birth again. A moose can mate when it is two years old. The life spans of moose can be up to twenty years.

Moose are so large and strong that they have few enemies. Bears and wolves may prey on them. However, they usually attack young, old, or sick moose and males weakened by hunger or mating battles. Human hunters are the greatest threat to moose. For example, during the moose mating season, male moose seek females. Moose hunters lure moose into shooting range by imitating the love call of a cow through a horn or cupped hands. At one time, hunters killed off almost all moose in the eastern United States. Currently, they are protected by law in the United States and Canada.

—*Sanford S. Singer*

See also: Antelope; Deer; Elk; Fauna: Asia; Fauna; Europe; Fauna; North America; Horns and antlers; Molting and shedding; Reindeer.

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MORPHOGENESIS

Type of animal science: Development
Fields of study: Cell biology, embryology, genetics

Morphogenesis is the process, operating during the development of the organism and appearing through evolutionary history, by which patterns of form come into being in genetically controlled systems. By studying this multifaceted process, it is possible to understand underlying factors that regulate the appearance of patterns of structure in living organisms.

Principal Terms

BIFURCATION: the division of a Y-shaped and connected mesenchymal structure into a single proximal chondrogenic focus and two distal chondrogenic foci; this can lead to the formation of separate chondrification centers in a developing digit

CHONDRIFICATION: the process by which undifferentiated connective cells transform into chondrocytes (cells that make cartilage) and begin forming extracellular matrix

EPITHELIUM: the tissue that covers and lines all exposed surfaces of an organism, including internal body cavities such as the viscera and blood vessels

LIMB BUD: thickened epithelial cells along the lateral body fold that are underlain by mesoderm, creating a paddle-shaped extension from the trunk

SEGMENTATION: the division of a structure into linearly arranged segments; it can lead to the formation of somites, or it can lead to the formation of separate chondrification centers in a developing digit

ZONE OF POLARIZING ACTIVITY (ZPA): a region at the posterior base of the limb bud that seems to influence the distal development of pattern in a developing limb

Morphogenesis is the process that leads to the appearance of form in specific patterns, through the differential reproduction, growth, and movement of cells and tissues and interactions between tissues. Such movements are controlled by a variety of factors, including cell adhesion molecules (CAMs), the nature of the extracellular matrix (ECM), and the size of the cells themselves.

Most multicellular organisms begin their lives as fertilized eggs. Although this seemingly simple cell is really quite highly organized, it is still relatively uncomplicated when compared to the structural complexity of the parent. As each egg cell divides, the daughter cells become structurally and functionally distinct. This is the beginning of the process of cell differentiation, which can lead to complex multicellular organisms. As new cells appear, grow, mature, and divide, there is a point at which the eventual fate of these cells is determined. That is, at some point the eventual location, structure, and function of the descendants of such cells are fixed. This fate determination frequently takes place very early in the development of an organism. After a particular fate is determined, it is the process of morphogenesis that allows the potential fate to be realized. Also through the process of morphogenesis, patterns of form develop that increase the structural and functional complexity of an organism.

The Rules of Morphogenesis

Fate determination, morphogenesis, and pattern formation are not haphazard. In fact, these events are highly constrained, extremely stereotyped, and very predictable—so much so that models of morphogenesis have been formulated that rely on rules of development to establish the probabilities of particular forms developing. These rules take into account two types of conditions—initial and boundary conditions—that work together to produce pattern formation in a cascading process. Initial conditions are simply the cellular conditions that prevail in a certain part of an organism, such as cell size and number and the chemical makeup of cell membranes. Boundary conditions are the conditions that exist at boundaries of different types of tissue.

Only a few phenomena are responsible for setting the initial and boundary conditions within which a morphogenetic system operates. A variety of cellular phenomena are involved, including cell migration, cell division (producing new cell lineages), the rate of cell division, cell number, cell density, the orientation of daughter cells relative to parent cells, and even the places in which cell death occurs. Tissue-level phenomena also have an important impact on morphogenesis. In these cases, specific tissues possess certain properties and a limited ability to respond differently within the constraints allowed by those properties. For example, sheets of epithelial cells can become folded, but they seldom form a solid mass of cells. Finally, there are interactions that take place between different tissues. Among these interactions is induction, wherein one tissue will induce a specific response in an adjacent tissue. Examples of such induction are numerous and well known; they include the mesenchymal induction of dental epithelium during the formation of teeth.

Limb Morphogenesis

Although far from completely understood, one of the most thoroughly studied morphogenetic systems is the development of the tetrapod limb. (A tetrapod is a vertebrate with two pairs of limbs.) Because amphibians (such as frogs and salamanders) and chickens have large, easily obtainable eggs, they have been studied most. It will be useful to summarize the course of limb development, since it exemplifies many of the common features of morphogenesis and pattern formation.

Early in the formation of the limbs, a ridge forms along the flank of the embryo. Along this ridge, the apical ectodermal ridge (AER) develops as a thickened layer of epithelial cells. Undifferentiated connective tissue cells, called mesenchyme cells, accumulate underneath the AER and form the limb bud. These mesenchymal cells are derived from mesoderm that migrates into the limb bud following pathways of the ECM that are laced with CAMs, especially fibronectin. The AER is responsible for the formation of pattern in the proximodistal axis, which is a line from the base of a limb (the proximal end) to the outer end of the limb (the distal end).

Another focus of pattern formation also appears quite early in limb development; it is called the zone of polarizing activity (ZPA) and has influence over the anteroposterior axis of limb development. Together, the AER and the ZPA regulate a pattern of form that is shared by all tetrapods.

Under the influence of these pattern-generating centers, three types of mesenchymal chondrogenic foci will form: de novo condensations (which are unconnected), bifurcations, and segmentations. Segmentations and bifurcations both show recognizable connections, and they appear in a consistent and stereotyped fashion. Linear series of mesenchymal condensations showing connections with one another are called segmentations; a Y-shaped condensation with a single proximal focus connected to two distal foci is called a bifurcation.

In all tetrapods, a bifurcation leads to the formation of two skeletal elements in the region between the proximal bone in the arm (or leg) and the hand (or foot). In frogs and amniotes, the condensations at the base of the putative fourth digit, showing connection to the bone in the forearm (or lower leg), are the first to appear as the result of a bifurcation event. Each subsequent proximal digit condensation appears as a bifurcation. All distal condensations, after the proximal digital element forms, appear as the result of segmentation events. Thus, the development of limb elements is asymmetric and always emanates from the axis of the first digit to form chondrogenic foci.

The morphogenetic control of this pattern, which has been conserved throughout the long evolutionary history of tetrapods, is both simple and complex. It is simple in that only a few morphogenetic processes are responsible for generating the complex pattern of limb structure, so different in all the various tetrapods. It is complex in that so many phenomena can influence the ultimate structure of any particular limb. For example, the number of somites that contribute mesoderm to the limb bud mesenchyme can dictate the number of limb elements that will eventually form.

Studying Morphogenesis

There are two general methods for studying morphogenesis. In the older—but still widely used—approach, tissues are removed from an organism in order to be examined under a microscope. Tissues are often stained (a variety of staining materials may be used) to make them more readily visible, and they are usually cut into thin slices called sections. The purpose is to determine the position of individual tissues. If carefully staged materials have been used, it is possible to get some ideas about whether cells have moved and, if so, approximately how far they have moved. There are problems with studying morphogenesis in this way: Details can be missed, or, more worrisome, preconceived notions can bias observations. For example, a small set of sections may support a theory, but, because thin sections of tissue can vary greatly, many sections of the material under study may contravene a pet theory of development. One could simply reject the many conflicting sections, claiming them to be poorly prepared or somehow damaged material. Indeed, many sections are so rejected. With the advent of transmission electron microscopy (TEM) and scanning electron microscopy (SEM), more detailed observations could be made. New problems, however, accompany these methods. In TEM, the thinner sections which must be used increase the occurrence of variation, also increasing the chances of biased observations. SEM allows for the magnification of surfaces and a great increase in the depth of field, but it requires that materials be very carefully staged. In none of these methods is it possible actually to see individual cells move.

A second approach seeks to document cellular movements. Understanding such movements requires that individual cells be "marked." Marked cells are then grafted onto an unmarked host organism and followed. Both natural and artificial markers can be used. Pigment granules such as melanin and stained glycogen are examples of natural markers. These markers, however, can be affected by cellular activities, making it hard to follow the cells. Fortunately, there are other natural markers not so affected. For example, chick and quail cells stain differently, so the cells of one can be followed when they are transplanted into the other. One of the more frequently used artificial markers is tritiated thymidine. When it is introduced, this radioactive substance is permanently incorporated into the deoxyribonucleic acid (DNA) of the selected cells. Tritiated thymidine has several advantages: It works in any cell, it follows along with the cells, and it will be in all the offspring of the cell to which it was originally introduced. Unfortunately, as cells continue to divide, the concentrations of tritiated thymidine eventually approach undetectable levels.

Many systems have been studied using these methods, including the development of the tetrapod limb and vertebrate head, somite differentiation, and the appearance of the primary germ layers that eventually yield all other tissues.

Morphogenesis is the reflection of all the interactions that take place during the formation of a living organism and of the patterns of structure that characterize this organism. The study of morphogenesis is motivated by the desire to understand the appearance of patterns of structure. Such patterns are often conserved through evolutionary history. It is hoped that a clear picture of how these patterns are formed and regulated will show how the origin of novel morphologies is constrained. Thus, it will be possible to understand both the origin of novel forms and the maintenance of unchanging form.

—*Charles R. Crumly*

See also: Cell types; Determination and differentiation; Development: Evolutionary perspective; Growth; Histology.

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MOSQUITOES

Type of animal science: Classification
Fields of study: Anatomy, ecology, entomology, invertebrate biology, physiology, zoology

There are about 3,500 known species of mosquitoes, all of which are placed in the family Cuicidae of the insect order Diptera. The importance of mosquitoes to humans lies with their ability to feed on vertebrate blood and transmit organisms that cause disease.

Principal Terms

LABIUM: the sheath that contains the slender stylet-like mouthparts of the mosquito, including the mandibles, maxillae, and hypopharynx

SALIVA: the liquid containing enzymes secreted by the salivary glands that is injected into the host when the adult mosquito feeds

SIPHON TUBE: tube that extends from the rear of the larval abdomen at the air-water interface and allows the larva to breathe air

Although mosquitoes are found all over the world, as far north as the Arctic Circle, the vast majority of them live in the tropics and subtropics. The adults have wings and are able to fly, but the immature stages, or larvae, are wormlike and are confined to small bodies of water. Adult male mosquitoes do not have mouthparts that are capable of penetrating skin, so they feed primarily on nectar from flowers. However, adult females have piercing mouthparts that easily pass through the skin of larger animals so they can feed on their blood. About 200 million years ago they probably evolved from other insects that used their mouthparts to feed on plants.

The Life Cycle of Mosquitoes

Female mosquitoes lay their eggs in water or in areas that will be flooded with water after rainfall accumulates or the snow melts. The eggs hatch after a few hours of being submerged, and this is the reason for the usually large numbers of mosquitoes in the wet spring months. The larvae that hatch from the egg must remain in the water to develop, but they are only able to breathe when they come to the water's surface. At the end of the larval abdomen is a strawlike siphon tube that allows air to enter. By hanging with its head down and its siphon tube at the surface, the larva can continue to feed underwater and breathe at the same time. The larvae feed by filtering out small particles of food from the water and grow by periodically producing a new skin and molting the old skin. After three larval molts over the course of about one week, the larva changes into a comma-shaped pupa that does not feed but is transformed into the adult. The pupa comes to the water surface when its development is complete and the adult mosquito escapes from the pupal skin and flies from the water surface.

Adult mosquitoes often mate shortly after they emerge. The males of many mosquito species form swarms over trees and bushes into which the female enters. When she enters the swarm of males, her wingbeats produce a tone that attracts the male. Most females only mate once during their lives and store the sperm in a special sac that is used to fertilize the eggs just before they are laid. Males live only about two weeks and feed on sugars from plants. Female mosquitoes live for about a month. Unlike the males, they have needlelike mouthparts consisting of two elongated maxillae, two long mandibles, a labium, and a hypopharynx

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that has a hollow tube running its length. When the mosquito feeds, the sheathlike labium that encloses the other mouthparts folds away and the six needlelike mouthparts then penetrate the skin. The tube within the hypopharynx is connected to the salivary glands and allows saliva to be injected into the animal being fed upon. The saliva prevents the blood from clotting in the mouthparts and may also lessen the pain so the mosquito can feed without being detected. The saliva that is injected also produces the common symptoms of itching and redness that usually follow the mosquito bite. Feeding on blood is necessary if the female is to develop her eggs. By using the protein contained in the blood, she is able to mature about one hundred eggs within two days of feeding. She can take another blood meal and develop another egg batch every two days. Feeding behavior usually occurs at dusk or during the evening hours, when its hosts are asleep and less likely to defend themselves. A few mosquito species do not feed on blood at all and acquire the protein they need to develop eggs from the larval stage.

Adult female mosquitoes have special sensory receptors on their antennae that can detect the odors of potential hosts. The carbon dioxide that animals give off as they breathe is one of the major signals the female uses to locate a host for a blood meal, but other chemicals produced by the skin are also important. The female mosquito may also use body heat and the visual image of the host to locate it. Darker colors are generally more attractive than are lighter colors. Common mosquito repellents are believed to act as chemical masks that disrupt the pattern of host stimuli so the female no longer recognizes the host.

Mosquitoes and Disease

Mosquitoes are not just nuisances when they feed on humans. Female mosquitoes are able to acquire parasites, such as viruses and protozoa, when they feed on an animal that already has an infection in its blood. Some of these parasites are able to infect the tissues of the mosquito and then invade its salivary glands. Once the salivary glands contain the parasites, they can be transmitted to an uninfected host the next time the mosquito injects its saliva and feeds. Many diseases of humans and other animals are transmitted by mosquitoes when they feed on blood. Malaria is the most important of these, causing over one million human deaths each year. Other important mosquito-transmitted diseases include dengue, yellow fever, and viral encephalitis, all caused by viruses. Heartworm is an important disease of dogs that is caused by a nematode worm transmitted by mosquitoes. Filariasis is a similar disease in humans that produces grossly enlarged limbs.

The best way to control mosquitoes is to limit the places larvae can breed. This involves preventing water from collecting in small containers and channeling water runoff so it does not accumulate in puddles that might last long enough for the larvae to develop into adults.

—Marc J. Klowden

See also: Antennae; Diseases; Ingestion; Insects; Metamorphosis; Molting and shedding.

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MOUNTAIN LIONS

Type of animal science: Classification
Fields of study: Anatomy, wildlife ecology

Large animals, usually classified in the small cat Felis *genus, mountain lions once ranged across the New World. However, human predation and habitat destruction have greatly reduced or eliminated many regional subspecies.*

Principal Terms

CARNASSIALS: pairs of large, cross-shearing teeth on each side of jaw
CREPUSCULAR: active at twilight or before sunset
EPIHYAL: presence or absence of this hyoid bone determines if a cat generally purrs or roars
HYOID BONES: series of connected bones at base of tongue
PAPILLAE: sharp, curved projections on tongue

Mountain lions, also known as American lions, catamounts, cougars, deer tigers, Florida panthers, and pumas, are classified in the genus *Felis* with small cats because they share a solid epihyal bone that restricts their ability to roar. Mountain lions purr and during mating emit harsh, frightening screams.

Among American felines they are second in size only to the jaguar. Adult male mountain lions weigh from eighty to over two hundred pounds, and are often nine feet long from nose to tip of tail, and up to thirty inches high at the shoulder. Females are about a third less in size. Cats in the equatorial regions are smaller and have thinner coats than those in the extreme north and south of the mountain lion range.

Mountain lion coats are uniform in color, varying from reddish bronze to brownish yellow or gray, with black markings around the mouth and eyes and on the tip of the tail. Kittens are born spotted, but these marks soon fade. Thirty subspecies of mountain lions, varying slightly in head shape, coat color, and size, occupy separate geographic regions.

Behavior

Kittens remain with their mothers for eighteen months to two years. Otherwise, mountain lions live solitary lives. Each female has a distinct hunting range; where such areas intersect, cats avoid each other. Males hunt over much larger tracts, sometimes covering hundreds of square miles. Each territory overlaps several female ranges, which the males check frequently for breeding opportunities. Older males face challenges from younger cats seeking to establish their own territories.

Mountain lions are nocturnal or crepuscular hunters; they are almost invisible when silently stalking their victims in dim light. Except for mothers and kittens, there are few reports of cats aiding each other during hunting. Deer are the major prey in North America, capybara and peccary the preferred quarry in equatorial America. When larger animals are unavailable, mountain lions eat rodents, rabbits, and beaver. Blending into their surroundings, cats creep slowly toward intended prey, closing with a furious forty-five mile per hour rush, sometimes leaping as much as forty feet to surprise their target. Sharp claws hold victims, as canine teeth sever their spinal column or windpipe. Powerful jaws, containing scissorslike carnassials and tongues with rasplike papillae, permit cats to harvest every speck of meat from their prize.

Relations with Humans

Native Americans, carrying carved cat images as fetishes, revered the mountain lion as the greatest of all hunters. Native rituals used lion skins and paws to ensure hunting success. Europeans were less respectful, treating big cats as dangerous vermin to be destroyed. From the seventeenth century through much of the twentieth century, governments offered bounties for lion skins. Humans were the only species consistently preying upon adult mountain lions. Hunters set iron traps, dug pits, and used dogs to chase and tree the cats.

As expanding human settlement made wild prey scarce, mountain lions found cattle, sheep, and horses irresistible. The cats tended to avoid humans, but rare attacks and killings frightened people and led to calls for the cats' extermination. John James

Mountain Lion Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Subclass: Eutheria
Order: Carnivora
Family: Felidae (cats)
Genus and species: Felis concolor
Subspecies: F. c. cougar (eastern cougar), *F. c. coryi* (Florida cougar)

Geographical location: Original range was southern British Columbia to the Straits of Magellan and from the Atlantic Ocean to the Pacific Ocean

Habitat: Mountains, forests, deserts, and jungles

Gestational period: About three months

Life span: Up to twelve years in the wild, twenty or more years in captivity

Special anatomy: Large eyes with excellent night vision; jaws adapted to seizing and gripping prey, teeth designed for tearing and slicing flesh

Mountain lions prefer to stalk their prey during the twilight or early morning hours. (Corbis)

Audubon noted that by the 1840's, man had nearly eliminated mountain lions east of the Mississippi. By 1900, few mountain lions existed in North America east of the Rocky Mountain states.

Attitudes toward mountain lions began changing in the last decades of the twentieth century. Laws in western states banned or strictly limited hunting. However, as human intrusion into the mountain lion's habitat increased, cats occasionally attacked solitary hikers, joggers, and skiers, stimulating calls for removal of the predators. With great effort and expense, conservationists maintain a relict population of some seventy Florida panthers (*Felis concolor coryi*) in southwest Florida—a subspecies originally ranging from Louisiana to Florida. In Central and South America, where significant populations of mountain lions remain, destruction of habitat by expanding settlement has greatly reduced surviving numbers. Outside Florida, mountain lions are not technically an endangered species, but their long-term future remains precarious.

—Milton Berman

See also: Carnivores; Cats; Cheetahs; Fauna: Africa; Fauna: Asia; Groups; Jaguars; Leopards; Lions; Predation; Tigers.

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MOUNTAINS

Types of animal science: Ecology, geography
Fields of study: Conservation biology, ecology, environmental science, wildlife ecology, zoology

Mountains cover one fifth of the earth's terrestrial surface, and are one of the most extreme environments in the global ecosystem. They are globally significant landforms that function as storehouses for irreplaceable resources such as clean air and water, and biological and cultural diversity, as well as timber and mineral resources.

Principal Terms

ASTHENOSPHERE: the region below the lithosphere where rock is less rigid than that above and below it

BIOCLIMATIC ZONE: a zone of transition between differing yet adjacent ecological systems

ENDEMISM: the occurrence of species only within narrow environmental ranges

LOCAL RELIEF: the elevation difference between the lowest and highest points in an area

SUCCESSION: directional change in communities of vegetation or animals

TECTONIC PLATE: tectonic plate theory suggests that the earth's surface is composed of a number of oceanic and continental plates which have the ability to move slowly across the earth's asthenosphere

Mountains are the most conspicuous landforms on earth. They are found on every continent, and have been defined simply as elevated landforms of high local relief, with much of the surface in steep slopes, displaying distinct variations in climate and vegetation zones from the base to the summit. The earth's mountain ranges have been created by the collision of tectonic plates. Associated with many of these mountain ranges are volcanoes. If the solidified magma of a volcano builds up, it can become a mountain; likewise, if the collision involves two oceanic plates, a string of volcanic mountains, called an island arc, can form on the ocean floor.

Mountain Habitat

Mountains are globally significant reservoirs of biodiversity. They contain rich assemblages of species and ecosystems. Because of the rapid changes in altitude and temperature along a mountain slope, multiple ecological zones are stacked upon one another, sometimes ranging from dense tropical jungles to glacial ice within a few kilometers. Many plant and animal species are found only on mountains, having evolved over centuries of isolation to inhabit these specialized environments. Mountains can also function as biological corridors, connecting isolated habitats or protected areas and allowing species to migrate between them. These extraordinary ecological conditions, coupled with many bioclimatic zones, have resulted in an extremely high number of ecological niches available for habituation in mountain ecosystems.

Mountain Fauna

Because of the great diversity in habitats within mountainous regions, with each region showing a different combination of environmental factors, total mountain fauna is relatively rich and the variety of small communities very great, in spite of the general severity of the mountain environment as a whole. Likewise, this diversity has resulted in a wide range of endemic species that have evolved over centuries of isolation from other genetic material. Rocky Mountain National Park typifies this diversity as a home to 900 species of plants, 250 species of birds, and 60 species of mammals. Some are easily seen and others are elusive, but all are part of the ecosystem in the park. On a global scale, mountain fauna diversity includes many species of ungulates, including elk, bighorn sheep, moose, and deer. Also included in mountain communities are many species of rodents. Rodent species may include beaver, marmots, squirrels, and chipmunks. Other mammalian animal life includes bear, canids, including coyote and wolf, and many species of felids, such as mountain lions and bobcats. Mountain avian fauna includes many families of hummingbirds, bluebirds, hawks, falcons, eagles, and many more.

Major Mountain Ranges of the World

Africa: Atlas, Eastern African Highlands, Ethiopian Highlands
Asia: Hindu Kush, Himalayas, Taurus, Elburz, Japanese Mountains
Australia: MacDonnell Mountains
Europe: Pyrenees, Alps, Carpathians, Apennines, Urals, Balkan Mountains
North America: Appalachians, Sierra Nevada, Rocky Mountains, Laurentides
South America: Andes, Brazilian Highlands

Mountain meadows provide habitats for many animal and bird species. (PhotoDisc)

Threats to Mountains

Mountains are threatened in a variety of ways. There are constant threats from human activities, such as camping, hiking, and other recreational activities. Hikers create tracks in the soil that form erosion gullies. Likewise, hikers may trample on vegetation that has taken many years to grow. Commercial harvesting of trees in the lower forest zones of mountains is having an increasingly detrimental effect on biodiversity. Many countries have replanted indigenous trees with fast-growing coniferous trees, in an ill-fated effort to supply a growing human population with wood products. These hybrid forests are not nearly as beautiful as the native forests, but more to the point, they do not offer an environment conducive to the ecosystem that the native species supported. This problem creates a loss of wildlife, which becomes even more rare in these forests because of the decline of native vegetation. Global warming is another threat to mountain ecosystems. Snowlines are receding, and eventually, continued melting of glaciers and polar ice caps could lead to drying of major river systems which feed from them. Without question, human settlement and activities constitute the biggest threat to the mountain ecosystem.

—Jason A. Hubbart

See also: Chaparral; Ecosystems; Grasslands and prairies; Food chains and food webs; Forests, coniferous; Forests, deciduous; Habitats and biomes; Lakes and rivers; Marine biology; Rain forests; Savannas; Tidepools and beaches; Tundra.

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MULTICELLULARITY

Type of animal science: Evolution
Fields of study: Cell biology, evolutionary science, paleontology

By studying the fossil record, scientists have found that the first multicellular life appeared on the earth about 1 billion years ago. Before that time, only single-celled organisms existed. The appearance of multicellularity paved the way for the evolution of all higher organisms.

Principal Terms

Ediacarian (Ediacaran) fauna: a diverse assemblage of fossils of soft-bodied animals that represents the oldest record of multicellular animal life on the earth

eukaryotic cell: a cell that has a nucleus with chromosomes and other complex internal structures; this is the type of cell which makes up all organisms except bacteria

fossils: the remains of ancient life preserved in sediment or rock

multicellular organisms: organisms consisting of more than one cell; there are diverse types of cells, specialized for different functions and generally organized into tissues and organs

Precambrian eon: the earliest chapter of the earth's history, covering the time interval between the formation of the earth, about 4.6 billion years ago, and the beginning of the Cambrian period, about 570 million years ago

prokaryotic cell: a primitive cell that lacks a nucleus, chromosomes, and other well-defined internal cellular structures; only members of the kingdom Monera (such as bacteria) are prokaryotic cells—all higher organisms have eukaryotic cells

Multicellular organisms are those consisting of more than one cell. Three of the five kingdoms of living organisms are multicellular: the plants (Plantae), the animals (Animalia), and the fungi (Fungi). The other two kingdoms consist of single-celled organisms: the bacteria (Monera), which have primitive prokaryotic cells, and the protists (Protista), which have complex eukaryotic cells. Prokaryotic cells lack a nucleus and other internal cell structures and are found today only among the bacteria. Eukaryotic cells, on the other hand, contain a nucleus, other complex internal cell structures called organelles (such as mitochondria, which perform respiratory functions), and sometimes chloroplasts (which contain chlorophyll and perform photosynthesis). All multicellular organisms are composed of eukaryotic cells, so the eukaryotic cell must have evolved before multicellular organisms could develop. It is generally accepted that simpler types of organisms evolved first, followed by more complex organisms.

The Multicellular Kingdoms

Plants are multicellular organisms that have chlorophyll (a green pigment used for photosynthesis), plastids (internal structures on the cell that contain chlorophyll), and a cell wall that contains cellulose. Plants are sometimes called "primary producers" because they can manufacture their own food from carbon dioxide and water through a process called photosynthesis, using sunlight for energy and producing oxygen and organic matter (carbohydrates) as by-products.

Animals are multicellular organisms that cannot produce their own food and must feed on other organisms. They are "consumers." Metazoans have many types of cells, which are organized into tissues, and groups of tissues, which form organs. There are two primary embryonic tissue layers present in all metazoans (except the sponges). These are the ectoderm (outer layer) and the endoderm (inner layer). More advanced metazoans also have a third embryonic cell layer, the mesoderm, which lies between the other two layers.

Fungi (mushrooms and their relatives) possess cell walls like plants, but unlike plants, they lack chlorophyll. Although fungi appear plantlike, they cannot produce their own food because of the absence of chlorophyll, so they must feed by ingesting organic material and therefore are consumers. Because they are neither plants nor animals, the fungi are placed in a separate kingdom (Fungi).

Advantages and Origins of Multicellularity

Multicellularity probably evolved because it gave organisms some sort of advantage, assuring them of a greater chance of survival. Multicellularity allows organisms to become larger (which helps them to outcompete other organisms and provides a greater internal physiological stability), to have a longer life (because individual cells are replaceable), to produce more offspring (because many cells can be dedicated to reproduction), and to have a variety of body plans (which permits adaptation to various modes of life or environmental conditions). Specialization of cells for particular functions allows organisms to become more efficient.

Evidence for the origin of multicellularity comes from the fossil record, studies of the organization and biochemistry of living cells and organisms, and from studies of the embryonic and larval stages of animals. During the Archean eon (between 3.8 and 2.5 billion years ago), only single-celled, prokaryotic life (bacteria-like organisms) existed on the earth. Some of the prokaryotes were photosynthetic, including the cyanobacteria (or so-called blue-green algae). Some of these prokaryotes were colonial, with cells organized into structures such as chains, or filaments, or algal mats. These colonies differ from true multicellular organisms because they generally consist of only one type of cell rather than many types of cells. Colonies of blue-green algae formed moundlike structures called stromatolites, which were quite common during the Precambrian but are present only in a few areas today. Stromatolites appeared about 3 billion years ago but did not become abundant until about 2.3 billion years ago.

The Rise of Eukaryotic Organisms

Eukaryotic organisms appeared during the Proterozoic era. The eukaryotic cell probably evolved from prokaryotic ancestors some time before about 1.4 billion years ago. The oldest convincing fossils of eukaryotic cells are generally considered to be those from the 1.3 billion-year-old Beck Spring dolomite of California. Eukaryotic fossil cells have also been found in chert from the approximately 850 million-year-old Bitter Springs formation of Australia. The earliest eukaryotes were animal-like protozoans. This evolution occurred when photosynthetic prokaryotic cyanobacteria were ingested by protozoans and then developed a symbiotic (mutually beneficial) relationship with them. The evolution of the plantlike eukaryotes probably occurred by at least 1.4 billion years ago. (This date has been suggested because primitive multicellular algae fossils are present in rocks 1.3 billion years old.)

The eukaryotic cell was a prerequisite for the development of multicellular organisms. The plantlike eukaryotes are considered to be ancestral to the multicellular algae and higher plants. The protozoans are considered to be the ancestors of the metazoans (animals). The first multicellular organisms may have been algae. Fossils that appear to be primitive multicellular algae are known from the 1.3 billion-year-old sedimentary rocks of the Belt supergroup of Montana, and the 800 million- to 900 million-year-old Little Dal group of northwestern Canada. Multicellular algae can be found living today in both freshwater and marine environments.

Fossil fungi first appear in the fossil record in the 790 million- to 1,370 million-year-old Bitter Springs formation cherts of Australia. The fossil record of fungi is poor and not well known.

The Rise of Multicellular Animals

Multicellular animals evolved independently of the multicellular plants, probably arising from protozoan ancestors. The oldest evidence of metazoans (multicellular animals) in the geologic record is in the form of trace fossils. Trace fossils are imprints such as tracks, trails, or burrows made in sediment by moving animals. Over time, the sediment hardened into sedimentary rock as a result of compaction and cementation. The earliest trace fossils consist of simple trails and tubelike burrows. In some places, there is a succession of types of trace fossils from simple tubelike burrows in older rocks to more complex structures in younger rocks. This change suggests that the evolution and diversification of increasingly complex burrowing organisms occurred during the latter part of the Precambrian. The oldest trace fossils are less than one billion years old, and many scientists believe that it is unlikely that any trace fossils exist in rocks much older than about 700 million years old. The trace fossils appear in the geologic record just before the first appearance of soft-bodied metazoan fossils. Structures that resemble trace fossils, however, have been reported from much older rocks. Among these questionable traces are the one-billion-year-old Brooksella, which resembles a jellyfish. In addition, tubelike structures from the upper Medicine Peak quartzite in Wyoming have been dated at 2 billion to 2.5 billion years, at least 1 billion years older than the oldest known metazoans. The origin of these older traces is uncertain and may be a result of inorganic processes (such as dewatering of sediment), rather than of organisms.

One possible fossil metazoan that appears to be more than 850 million years old has been reported from the Tindir group of Alaska. This fossil is less than one millimeter long and appears to be a flatworm (phylum Platyhelminthes). Both the age and identification of this fossil have been disputed, but if valid, it is a very important find because some biologists theorize that the earliest metazoans would have been primitive flatworms.

The oldest unquestioned metazoan fossils are the imprints of a diverse assemblage of relatively well-developed, soft-bodied marine animals. More than half of the organisms appear to be some type of cnidarian or coelenterate (related to jellyfishes), about 25 percent appear to be segmented worms (related to annelids), and a small percentage appear to be arthropods (related to insects, crabs, and lobsters). Trace fossils are also present. This assemblage of soft-bodied fossils is called the Ediacaran fauna. It was discovered in 1946 in sandstones of the Pound subgroup in the Ediacara Hills of the Flinders Range in South Australia. The exact age of the Ediacaran fauna is uncertain because there are no nearby rocks of the proper type for radiometric dating. The Ediacaran fauna is clearly Precambrian, however, judging from its position in the geologic sequence. The soft-bodied Ediacaran fossils are separated from the younger fossil shells of the Cambrian (570 million years old) by a thick section of unfossiliferous rock (up to several hundred meters thick). Since the 1950's, fossils similar to the Ediacaran fauna have been found in rocks of approximately the same age on virtually every continent on the earth (with the possible exception of Antarctica). In some of these other areas, it is possible to date radiometrically the rocks associated with the fauna. These radiometric dates indicate that the early metazoan soft-bodied fossils range from about 620 million to 700 million years old. It is likely that the metazoans evolved some time prior to 700 million years ago because these fossils represent well-developed, complex animals.

Skeletonized faunas (animals with shells or other hard parts) did not appear until approximately 580 million years ago. The skeletonized faunas are represented by microscopic scraps, cones, tubes, and plates made of calcium phosphate or a hard organic material called chitin. It is not known exactly what types of organisms produced these skeletal remains, but the tiny fossils are so diverse and complex that it is assumed that the organisms must have had a long history of evolution during the Precambrian. The origin of skeletons was advantageous to marine organisms because hard parts provide protection against predators as well as the mechanical functions of support and muscle attachment.

Theories of the Origin of Multicellular Life

There are a number of theories to explain the origin of multicellular life. Most of the theories are derived from studies of various types of cells and living organisms, including advanced protozoans, early developmental stages (embryos), and larval stages. Four types of cells are central to these theories, and they are grouped into two categories: motile (capable of movement) and nonmotile (not capable of movement). The motile protists include flagellate cells (those with a whiplike "tail," or flagellum) and amoeboid cells (those such as Amoeba, which move by pseudopodia, or fingerlike extensions of the cell membrane). The nonmotile stages include coccine cells (those with many nuclei, sometimes called multinucleate cells) and sporine cells (those that divide and stick together to form multicellular aggregates).

There are many theories that have been proposed to explain the origin of plants, fungi, and metazoans (animals). Formerly, it was thought that plants evolved from prokaryotic algae (cyanobacteria, or blue-green algae), but it is more likely that plants arose from a eukaryotic ancestor, such as a flagellate cell. Flagellate algae are similar to flagellate protozoans, but it is not certain whether the algae evolved from the protozoan or vice versa. The presence of plastids (such as the chloroplasts that contain chlorophyll used for photosynthesis) may be the key feature separating plants from protozoans, fungi, and animals. According to a theory proposed by Lynn Margulis, plastids evolved from prokaryotic blue-green algae that were captured by eukaryotic cells. The sporine cell is another possible ancestor of the plants. Sporine cells appear to have had the capacity to evolve beyond the colony level and to produce complex tissue-level green algae and higher plants.

Fungi used to be considered as plants that had lost (or never evolved) chlorophyll. The discovery of a single-celled stage with flagellae among the more primitive fungi, however, suggests that fungi probably evolved from protozoans.

The ancestral multicellular organisms, which gave rise to all the more-complex living animals, are all extinct. The simplest multicellular animal living today is the sponge (phylum Porifera). The sponges are not considered to be ancestors of the more complex animals because their body organization and developmental history are very different. Sponges have no tissues, mouth, or internal organs. Instead, they consist of an aggregate of flagellate and amoeboid cells (and a few other types) roughly arranged in layers. The sponges may have evolved independently from the other metazoans. Sponges are classified as a distinct side branch of the animal kingdom (Parazoa), with a primitive multicellular grade of organization (no tissues). The remaining multicellular animals are grouped into the Eumetazoa.

Theories of Metazoan Origin

Several theories have been proposed to explain the origin of the metazoans. These theories can be placed into the following categories: evolution from single-celled protozoans; evolution from colonial protozoans; evolution from multinucleate coccine cells as a result of development of internal cell boundaries; and evolution from sporine cells. There are several versions of each of these theories, and there is no general agreement on which theory is best. Some researchers promote the colonial theory as the most widely accepted theory, whereas others claim no longer to take it seriously. Most experts agree that evolution of metazoans from colonial protozoans would seem to be easier than evolution directly from a single cell. Multicellularity may have arisen independently several times, in several different ways.

The colonial theory suggests that the metazoans evolved from flagellate or amoeboid protozoans that lived together in colonies, much like the modern green alga Volvox, which is shaped like a hollow sphere. From an original hollow spherical form, the shape of the ancestral metazoan changed as an indentation or invagination formed in the side. The indentation became larger, producing a double-walled "cup" (envision pushing one's thumb into the side of a deflated ball until that side becomes nested into the other side of the ball, forming a cuplike shape). The double-walled cup shape is referred to as a diploblastic body plan, meaning two layers of body tissue. These two layers are the ectoderm (outer layer) and the endoderm (inner layer). This process of indentation to produce a diploblastic (double-walled) form occurs in the embryos of many animals. The jellyfishes are a good example of animals with a diploblastic body plan. Nearly all groups of animals have ectoderm and endoderm (except the sponges), suggesting that nearly all groups of animals are related. Because the jellyfishes (phylum Cnidaria) have the simplest body plan, they are believed to be the most primitive. The diploblastic ancestral form has been called a gastrea. Ernst H. Haeckel, a prominent nineteenth century German biologist who studied animal embryos, believed that all bilaterally symmetrical animals evolved from a gastrea.

A second theory for the origin of metazoans suggests that the ancestral form was a bilaterally symmetrical animal resembling a flatworm. Some scientists believe that the complex organs and organ systems of metazoans are beyond the evolutionary potential of flagellate and amoeboid cells. The flatworm may have evolved from "cellularization" of a multinucleate coccine cell (formation of cell membranes around each of the nuclei) or from clumping of sporine cells. Most of the cells in the metazoans are sporine cells that stick together to form multicellular aggregates. Sporine protozoans do not exist, so it is hypothesized that sporine ancestors of the metazoans must have evolved from "preprotozoans." These hypothetical ancestors may have been solid balls of cells resembling the early stages of many embryos. At some point, the exterior cells may have developed (or redeveloped) flagellae and become specialized for locomotion, and the interior cells may have become specialized for digestion and reproduction. Such colonies of cells would have resembled the larval (immature) form of cnidarians, called a planula larva, and, hence, they are called planuloids. Planuloids are believed to have given rise to two groups of metazoans, the cnidarians (jellyfishes and their kin) and the flatworms. The primitive flatworms are believed to have been ancestral to all other bilaterally symmetrical metazoans.

Evidence from Rocks

Theories to explain the origin of multicellular life have been developed by biologists as a result of studies of various types of cells and living organisms, including advanced protozoans, early developmental stages (embryos), and larval stages.

Geologists (scientists who study rocks) and paleontologists (scientists who study fossils) have a variety of techniques that they use to search for the evidence of life in Precambrian rocks (older than 570 million years). These include searching for fossil remains and chemical analysis of organic residues that are probably the breakdown products of once-living organisms.

The first step in the search for Precambrian life is to locate rocks of the proper age. Geologic maps exist for virtually all parts of the world. From an examination of these maps, it is possible to identify areas that contain rocks of the proper age. (The age of a rock is determined by radiometric dating.) Age, however, is not the only consideration. For fossil remains to be preserved, the rocks must also remain little altered from the way they were originally deposited. Metamorphism (geologic alteration caused by heat and/or pressure) has deformed many Precambrian rocks to the extent that any fossils that may have been present can no longer be recognized.

Assuming that undeformed rocks of the proper age can be located, the search begins for fossil remains. Unfortunately, most Precambrian rocks are not fossiliferous. Precambrian multicellular fossils are found in only a few places in the world. In Australia, soft-bodied Precambrian metazoan fossils are restricted to a few thin layers of sandstone in a sequence of Precambrian rock more than one thousand meters thick. In most places in the world, however, there is a thick section of unfossiliferous rock separating the Precambrian metazoan fossils from the shelly faunas in the Cambrian rocks. This unfossiliferous sequence of rock is an interval for which there is little or no information on the types of life that existed.

Before multicellular organisms appeared (prior to perhaps one billion years ago), only microscopic, single-celled organisms existed on the earth. Microscopic fossils of single-celled organisms are found by careful examination of fine-grained, dark-colored rocks such as black cherts. The black color of the rocks commonly indicates the presence of carbon, which is present in all living organisms and which may be preserved in some fossils. Very thin slices of rock are prepared and mounted on glass slides so that the organic matter can be studied. These slices of rock, called thin sections, are so thin that light can pass through them, and they are examined with a microscope. Much of the carbon in these rocks is present as amorphous (indistinct or shapeless) patches, but in some places, microscopic structures are present that appear to be the fossilized remains of single-celled organisms. Pieces of rock can also be prepared for examination using a scanning electron microscope. The search for microfossils is difficult and painstaking. Among the problems involved are the possibility of contamination by modern-day organic matter in the laboratory and the possibility that the microscopic structures may really be inorganic in origin.

Chemical tests are used to search for the products of biological activity, which may be preserved in rocks. In principle, rocks that have been influenced by biological activity should contain certain characteristic isotopic ratios. There are a number of problems inherent in searching for organic residues. Organic material may have been preserved in the rock, but it could easily have been altered subsequently by heat and pressure or by circulating fluids. In addition, circulating fluids can contaminate the rocks by introducing organic material from much younger rocks.

Multicellularity in the Evolutionary Process

Studying the origin of multicellularity helps one to understand the conditions that led to the evolution of plant and animal life on the earth. As one begins to understand how multicellular life evolved, one may begin to wonder about why it was such a slow process. It is known that the earth formed about 4.6 billion years ago and that the first cells appeared about 3.5 billion years ago, but that the first multicellular life did not appear until approximately 1 billion years ago. In other words, it took more than 3.5 billion years for multicellular life to develop. More than three quarters of the earth's history had passed before multicellular life ever appeared.

One may also begin to wonder about the conditions that promoted the origin of multicellular life. Of all the planets in the solar system, the earth seems uniquely suited to life. Two of the most important factors involved are the presence of liquid water (which requires a specific temperature range) and the presence of an oxygen-rich atmosphere. None of the other planets in this solar system has either of these two characteristics. Interestingly enough, the earth originally did not have liquid water or an oxygenated atmosphere. Geologic evidence suggests that the earth's early atmosphere was the result of volcanic outgassing and that it consisted of gases such as carbon dioxide, carbon monoxide, ammonia, methane, hydrogen sulfide, nitrogen, and water vapor. As the planet cooled from its original molten state, the water vapor in the atmosphere condensed to form liquid water, which fell to the earth as rain and accumulated to form the oceans, rivers, and lakes. There is abundant geologic evidence that the earth's early atmosphere lacked the free oxygen that is breathed today. In the absence of free oxygen, chemical evolution in the oceans or lakes led to the formation of organic compounds, or what has been called the "primordial soup." The first living cells, the prokaryotes, evolved in this organics-rich water. As time passed, some of the early prokaryotic cells became photosynthetic, which allowed them not only to produce their own food from water and carbon dioxide but also to produce oxygen as a waste product. Oxygen was toxic to these early organisms. In order to survive, the cells had to develop a mechanism to adapt to the presence of increasing levels of oxygen. The buildup of oxygen led to the development of the ozone layer in the atmosphere and to the appearance of the eukaryotic cell. As the percentage of oxygen in the atmosphere increased, it is believed that some threshold level was reached, and it became possible for the environment to support multicellular organisms. That allowed a rapid diversification of life on the earth.

Hence, it appears that multicellular life on the earth appeared as a result of some prehistoric accident that resulted in global atmospheric change—the buildup of a toxic waste product (oxygen) as a result of photosynthesis by early life-forms. One might also speculate on the possible global effects of the increasing waste products that humans are now producing. The thinning of the atmospheric ozone layer is but one manifestation of the way that life is presently changing the earth's fragile environment. Knowing that the formation of the ozone layer was probably essential to the appearance of multicellular life on the earth, it is alarming to speculate on the consequences of its destruction. Life as humans know it depends on an earth with environmental conditions in a precarious balance.

—Pamela J. W. Gore

See also: Adaptive radiation; Cell types; Cleavage, gastrulation, and neurulation; Development: Evolutionary perspective; Evolution: Animal life; Evolution: Historical perspective; Protozoa.

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MUSCLES IN INVERTEBRATES

Type of animal science: Anatomy
Fields of study: Histology, invertebrate biology

Invertebrates, animals whose name means "without a backbone," make up more than 95 percent of all animal species. The internal organization of each of the invertebrate phyla differs drastically from one to another and from the vertebrate body plan. Variables such as skeletal elements and lifestyle affect the activity and survival of the group, but all invertebrates use muscles built on the same plan as those of vertebrates.

Principal Terms

ACTIN: one of the two major types of contractile proteins; it forms the thin myofibrils of the sarcomere

FAST MUSCLE: muscle cells that respond quickly to nervous impulses; in invertebrates, these muscle fibers have short sarcomeres and a low ratio of thin to thick myofibrils

MYOSIN: one of the two major contractile proteins making up the thick myofibrils

PARAMYOSIN: a structural protein associated with myosin myofibrils and thought to support them

SLOW MUSCLE: muscle cells that respond slowly to nervous impulses; in invertebrates, these muscle fibers have long sarcomeres and a high ratio of thin to thick myofibrils

TROPOMYOSIN: a double-stranded protein that lies in the grooves of actin myofibrils, blocking actin from attachment to myosin

TROPONIN: a globular protein composed of three subunits; one subunit binds calcium ions, and another draws tropomyosin away from actin, which allows myosin to form crossbridges constituting the third subunit

The most obvious characteristic of animals may be movement. Movement requires a mechanism. The mechanism allowing multicellular animals of all kinds to change position or posture is a muscle cell.

The Mechanism of Movement

A muscle cell, also called a muscle fiber, is specialized for contraction. Muscle is composed of many muscle fibers, and each muscle cell contains contractile molecules permitting the cell to shorten and thereby change its shape. Each muscle fiber moves by drawing its ends together or by contracting.

The contractile molecules are common to muscles of invertebrates and vertebrates. There are several kinds. Actin and myosin are the most prominent contractile molecules. Each actin molecule is rounded and forms myofibrils by assembling repetitive monomers to form a helix, a springlike shape. Two of these helices are coiled around each other like two intertwined strings of pearls.

Myosin is a more complex myofibril. Each myosin molecule is composed of a head and a tail. The tails of two myosin molecules are wound around each other helically, while the heads project from the same end but in different directions. In the presence of calcium ions, each head can swivel. If an actin molecule is exposed, the myosin head can attach to it, forming a crossbridge. Since they lie parallel to each other in the cell, when the myosin

Image Not Available

returns to its original position, it pulls the actin myofibril. The ends of the contractile unit move closer to each other, shortening the muscle cell.

Myosin tails lie parallel to each other, but at the opposite ends of the myosin myofibrils, the heads project in opposite directions. The heads lie close to the two end walls that attach the actin myofibrils. There is a small central area where only the oppositely facing tails of the myosin myofibrils are found.

A contractile unit is called a sarcomere. A sarcomere is a repeated unit within a muscle cell consisting of overlapping thick myofibrils (myosin) and thin myofibrils (actin). Since there are areas in which there is no actin and areas in which there is no myosin, some light stripes are seen crossing the myofibrils in a microscopic preparation of certain muscle fibers. Actin myofibrils connect to thick walls that mark the ends of a sarcomere. The myosin myofibrils are connected across the center of the sarcomere. During relaxation, actin is absent from the center, producing a light band. The regular pattern of light and dark areas along the length of the muscle fiber is characteristic of striated or skeletal vertebrate muscle. This vertebrate muscle type is the most studied in physiology and, therefore, is the best known.

The Specifics of Invertebrate Muscles

Invertebrate muscles have similar components, but the arrangement is less regular, the alignment of sarcomeres often being oblique. Actin and myosin myofibril arrangement is not readily delineated, but similar structures exist. A sarcoplasmic reticulum, similar to the endoplasmic reticulum of ordinary cells, is characteristic of vertebrate and invertebrate muscle fibers. It is arranged in a series of flattened sacs over a sarcomere's myofibrils. The sarcoplasmic reticulum can quickly absorb calcium ions, keeping their concentration around the sarcomere low. Without calcium ions, the myosin heads cannot be cocked.

Transverse, or T, tubules extend along the thick end wall of each sarcomere. They conduct the nerve impulse throughout the sarcomere to initiate contraction rapidly and simultaneously. When the impulse reaches the sarcoplasmic reticulum, stored calcium ions are released. This release begins contraction. Contraction ceases only if adenosine triphosphate (ATP) is present. Because they no longer make ATP, dead animals' contracted muscles do not relax; the muscles become stiff (exhibit rigor mortis).

Other molecules are also typically found in muscle cells. Tropomyosin is a strand of molecules that lies in a groove of the helically wound actin myofibrils. It blocks the attachment of myosin heads to actin molecules. Troponin is a three-part molecule that rests along the actin myofibril. One subunit attaches calcium ions. This changes troponin's conformation so that another subunit attracts the tropomyosin molecule, unblocking the actin myofibril so that the cocked head of myosin molecules can attach to the actin.

Paramyosin is a molecule similar to myosin found in invertebrates. It seems to act as a "filler" for myosin, keeping the myosin myofibrils aligned so that they can interact with the actin. It may be the contractile protein of some invertebrate muscle types. It is prominent in the "catch" muscles of mollusks.

Muscle Response Rates

Muscles may vary in their response rates even though they look the same. "Fast" muscle fibers contract rapidly in response to a nerve impulse. "Slow" muscle fibers contract several times more slowly. Although both types use the same contractile machinery, the slow muscle cells have less sarcoplasmic reticulum. This means that the calcium ions necessary to initiate contraction are not released as quickly everywhere along the contractile fibrils and are not pumped away from them as quickly as they are in the fast muscle cells.

Most invertebrate muscles are synchronous. This means that each contraction is initiated by a nerve impulse. The rate of contraction of synchronous muscles is determined by the rate of passage of nerve impulses. Even in flight, these muscles usually contract only about thirty-five times per second. Synchronous flight muscles are connected directly to the wings and are found in insects such as grasshoppers, moths, butterflies, and dragonflies.

True flies and bees, as well as beetles and true bugs, have a specialized kind of flight muscle called an asynchronous muscle. In asynchronous muscles, every contraction is not initiated by a nerve impulse. The contraction rates, up to one thousand times per second, are so rapid that nerve impulses could not be received and acted on quickly enough to produce that contraction rate. In these muscles, contraction is initiated by a nerve impulse received and transmitted by the T tubules, but there is no sarcoplasmic reticulum. Even fibrils removed from the cell and placed in a solution containing calcium ions and ATP contract and relax in an oscillatory fashion. The rates seem to be regulated by the myofibrils rather than by the calcium concentration. The T tubules seem to signal the contraction to begin and later turn off the cycling behavior of the myofibrils.

Asynchronous muscles are not directly attached to the wings of the insect. Elevator muscles are attached to the roof of the thorax. Their contraction pulls the roof of the thorax down and elevates the wings. Contraction of the wing depressor muscles pulls down the wings, but this stretches the wing elevators, stimulating them to contract and allowing the thorax roof to "pop up." Raising the thorax shortens the wing depressor muscles and terminates the active state of the depressors. They relax until stretched again by the elevation of the wings. The elevator and depressor muscle contractions follow the same sequence of stretch → contraction → shortening → relaxation → stretch, but are out of phase with each other. The frequency of wing beats depends upon the mechanical properties of the thorax and wings and not upon the frequency of nerve impulses.

Unlike vertebrate animals, there is a correlation between sarcomere length and speed of contraction. Rapidly contracting arthropod muscle fibers have short sarcomeres and relatively low ratios of thin to thick fibrils. Slowly contracting muscle fibers have long sarcomeres and high ratios of thin to thick fibrils. Intermediate types of fibers can exist within the same muscle.

Variations of Invertebrate Muscle Types

Because invertebrates are so varied, there is no generalization to which an exception cannot be found. For example, lobsters and crayfish have two separate muscle fiber types in their tail musculature. The tails are important in swimming and, particularly, in escape maneuvers. They must flex and extend rapidly to evade predators or aggressors. The bulk of the tail muscles consist of short sarcomere, rapidly contracting flexors and extensors. Thin sheets of long sarcomere—slowly contracting flexors and extensors—lie near the carapace. They are used for postural adjustments and for slow movements.

Flexors and extensors are good examples of another principle of muscle action. Muscles contract and they shorten. This shortening moves a body part. Relaxation allows the muscle fibers to lengthen. The force needed to lengthen the relaxed muscle comes from the contraction of its antagonist, a muscle that produces movement in the opposite direction from that of the first muscle. For example, flexing the tail of a lobster or crayfish is performed by the tail flexors. Relaxation does not return the tail to its extended position. Contraction of the extensor muscles moves the tail away from the body and extends the tail again. Relaxation of the extensors may allow the tail to be less rigid in its extension, but the tail will not flex until the flexor muscles are contracted. Muscles work in antagonistic groups to produce opposite movements (flexion and extension) and to produce postural changes that allow a lobster or crayfish to maintain its position when the current changes direction or speed.

Studying Invertebrate Muscles

Numerous methods are used to study the muscles of the invertebrates. Initially, the contraction patterns of whole muscles were studied by electrically stimulating muscles and their nerves. As in all biology, however, work is being done on the molecular level.

Glycerinated muscle is a preparation used to study the molecular elements necessary for contraction. Soaking muscle cells in glycerin removes the cell membrane and sarcoplasmic reticulum, but leaves the contractile fibrils intact. These can be used to determine the effect of presence or absence of ATP, calcium, magnesium, or other factors that might influence the working of the fibrils. They are used much the same as a whole muscle preparation. The ends of the fibrils are attached to one point that does not move and to another that does move when the muscle fibrils contract and relax. The movement can be recorded on paper or on an oscilloscope screen. The tension generated, or the length of shortening, can be calculated.

Microscopic analysis of the structural organization of invertebrate fibers also adds to the store of knowledge. Most invertebrate muscles do not have the striated appearance of vertebrate skeletal muscles. The myofibrils vary in their arrangements and are often difficult to discern. Microscopic analysis shows that rapidly contracting fibers have low ratios of thin to thick fibrils and slowly contracting fibers have larger ratios of thin to thick fibrils.

Muscles do not function without the coordination of the nervous system. Its contribution is different from that in vertebrates. Invertebrate muscle fibers do not exhibit the all-or-none response characteristic of vertebrates. Invertebrate muscle fibers receive innervation from several nerve fibers. A single nerve may serve many muscle fibers. Any muscle fiber is served by more than one nerve. The contraction strength of invertebrate muscle fibers depends upon the number and types of nerves sending impulses to that muscle cell at any time.

The study of the biochemical composition of myofibrils is also important. Actin and myosin are similar in all species. Vertebrate myosin occurs in two forms. One form has a higher intrinsic ATPase activity and responds quickly; the other has a slower intrinsic ATPase activity and twitches slowly. Invertebrate muscle fibrils have no such differences between myosin molecules. Paramyosin is a molecule peculiar to invertebrates. It is thought to be part of a supporting structure for the myosin tails. Some invertebrate muscles have been found not to have troponin and to have different forms of tropomyosin.

Electrophysiological studies have shown that invertebrate muscle fibers receive excitatory and inhibitory nerve fibers. Excitatory nerve fibers secrete acetylcholine and cause contraction. Inhibitory nerve fibers secrete serotonin and dopamine. The relaxation produced by these fibers is thought to be mediated by cyclic adenosine monophosphate (cAMP), a derivate of ATP. The relaxation may be a result of the breaking of crossbridges stabilized by paramyosin.

Simple and Complex Arrangements

Invertebrate neuromuscular systems are organized along the same general principles as in vertebrates: They coordinate body movements. All muscle cells shorten after receiving a stimulus, but the shortening will produce motion only if there is a skeleton, a structure to which the muscle fiber is anchored and another part to which force can be applied.

Sedentary sea anemones are relatively simple coelenterates that escape from threats by withdrawing their soft tentacles and contracting toward the substrate protected by thick body walls. Their body wall is a cylinder composed of two layers of cells separated by mesoglea, a jellylike material that allows diffusion of nutrients, wastes, and gases. Two groups of muscles are embedded in the body wall. In the outer body wall, longitudinal muscles parallel the long axis of the body. Their contraction shortens the body wall and draws it downward toward its base; its attachment is to the substrate. The circular muscles ring the inside layer of the body wall. Their contraction lengthens the body by squeezing the contents inward and narrowing the cylinder like a Chinese finger puzzle.

More complex invertebrates have more complex arrangements of muscles and skeletal parts. Their movements become more complex also. The best-known examples come from the larger and more numerous invertebrate phyla, the annelids, mollusks, and arthropods.

Annelids and Mollusks

Annelids have a hydrostatic skeleton like that of the sea anemone. Their bodies are divided into discrete segments, each with a fluid-filled cavity. Circular muscles of a segment contract, pressing against the fluid in the cavity extending it. This contraction of the circular muscles stretches the longitudinal muscles and sets the tiny bristles along the side of each segment into the substrate. The contraction of the longitudinal muscles squeezes the fluid into a shorter segment which stretches the circular muscles and widens the segment. The body is pulled forward by the bristles that had been set in the substrate.

One of the few examples of the use of hydrostatic pressure in place of muscles occurs in some spiders. The hind legs of jumping spiders have flexor muscles that bring the legs toward the body. They have no extensor muscles. Rapidly increased body fluid pressure straightens the legs, causing the spider to jump forward.

Mollusks include bivalves—sedentary clams, mussels, and oysters; gastropods—the slowly moving snails and slugs; and cephalopods—some of the quickest, most intelligent, and largest invertebrates, the octopods and squid. The muscular systems of these animals are as varied as their lifestyles.

The bivalves settle as adults in one place. They are unable to move about. Whenever a predator threatens them or environmental conditions change (for example, if the tide goes out), they must close their shells to shield their delicate body tissues. “Catch” muscles protect them by closing tightly without using much energy. These obliquely striated adductor muscles can maintain their contracted state for a long period. A short train of nerve impulses initiates a contraction that may last hours or days with no further nerve impulses. The catch muscle does not stretch readily, so prolonged pressure by a predator, such as a starfish, does not lengthen the muscle. The catch muscle remains contracted until a relaxation mechanism is activated by neural impulses in separate neurons. These catch muscles contain paramyosin surrounded by myosin molecules.

Arthropods

The arthropods are characterized by an exoskeleton, the joints of which allow movement. The skeleton is outside the body. It is composed of the cuticle, a hardened covering of chitin, with a thin, pliable hinge in the joints. Muscles cross the gap covered by the hinge. In arthropods, muscle tension is controlled largely or entirely by gradation of contraction within a motor unit. The degree of depolarization of these muscle fibers depends upon the frequency of impulses transmitted in motor neurons. Each fiber is a part of several motor units. In addition, inhibitory factors to arthropod muscles can prevent depolarization and, hence, contraction of the muscle (unlike vertebrate muscles). The neurons fire in short bursts to produce rapid movements.

Most rapidly contracting, short-sarcomere fibers are innervated by a phasic axon capable of producing rapid movements. The slowest, long-sarcomere muscle fibers are supplied only by the tonic axon that is active most of the time. These fibers provide for slow movements and postural adjustment. Muscle fibers with intermediate contraction times are innervated by both phasic and tonic axons. A muscle can, therefore, contract over a range of speeds and durations. An extreme example of this is the crustacean claw-opener muscle and the stretcher (extensor) of the proximal leg segment, which are both innervated by a single excitatory neuron. Separate inhibitory neurons supply each muscle so that they can be controlled independently.

In lobsters, the differentiation of the claws into a large crusher and a small cutter is correlated with muscular and neural activity. In their younger states, juvenile lobster claws have the same shape. Either claw can develop into the crusher. In the cutter claw, all the muscle fibers transform to fast fibers. In the crusher claw, all the muscle fibers become slow fibers. The change in shape and muscle type depends upon the presence of a manipulable environment and on the animal having unequal neuromuscular feedback to the central nervous system. The presence of a crusher on one side prevents the development of a crusher on the opposite side. Few generalizations describe invertebrates. Their muscles exhibit the same variety as the organisms that make up this diverse assemblage.

—Judith O. Rebach

See also: Anatomy; Arthropods; Crustaceans; Echinoderms; Exoskeletons; Histology; Insects; Invertebrates; Locomotion; Mollusks; Muscles in vertebrates; Physiology; Worms, segmented.

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MUSCLES IN VERTEBRATES

Type of animal science: Anatomy
Fields of study: Histology, zoology

Vertebrate muscle tissue provides for many vital bodily functions. For these purposes, there are three major types of vertebrate muscle tissue: skeletal, cardiac, and smooth.

Principal Terms

INVOLUNTARY: functioning automatically; not under conscious control

MOTOR NEURON: a nerve cell that transmits impulses from the central nervous system to an effector such as a muscle cell

MOTOR UNIT: a motor neuron together with the muscle cells it stimulates

TISSUE: a group of similar cells that executes a specialized function

TWITCH: a rapid muscular contraction followed by relaxation that occurs in response to a single stimulus

VOLUNTARY: capable of being consciously controlled

The ability of vertebrates to move their bodies and many of the contents of their bodies is a feature of major importance for their survival. The movements result from the contractions and relaxations of tissues specialized for the active generation of force: the muscles. Although initially it may seem sufficient to have only one type of muscle tissue, reflection on the functional requirements makes it clear that more than one type of muscular tissue is probably necessary. For example, the movement of the limbs should be under the conscious, voluntary activation and control of the animal. Otherwise, unwanted and uncoordinated random limb movements would result, or desired and possibly vital movements would not be forthcoming. In addition, the control of the limb movements should be precise, with as wide a range as possible for the forces which can be generated.

On the other hand, consider the movement of the blood through the circulatory system. This job must be continuously performed every minute of the animal's life. It would obviously be better to have this function run automatically, without the need for conscious, voluntary activation and control. The need for precise control of the forces generated here is also not as great as for the limb movements, nor is the need for a wide range of forces as great. The flow of blood to the various organs can be much better regulated by varying the diameter of the blood vessels at or near their entrance to the organs, thereby varying the flow into the organs, while the pumping forces generated to propel the blood remain relatively constant.

For the functions of controlling blood flow into organs and the mixing and passage of food through the digestive tract, it is again most reasonable to have automatic operation of the muscles involved, without the need for conscious, voluntary activation and control. To control the huge number of such muscles consciously is an impossible task in any case. Also, these muscles need to be able to change their lengths greatly, and sometimes, to maintain a maximal contraction for very extended periods; however, very rapid actions are not as important.

The preceding considerations make it appear necessary to have three fundamentally different types of muscle tissue. In fact, vertebrates do have three types of muscle tissue, whose different characteristics match these three sets of operational requirements: skeletal muscle tissue, cardiac muscle tissue, and smooth muscle tissue.

Skeletal Muscle

The skeletal muscle tissue occurs in the form of muscles that are usually attached to bones and cause movements of the skeleton. Some skeletal muscles are attached to the skin or to other skeletal muscles. They are under the animal's conscious, voluntary control. Skeletal muscle cells are long, cylindrically shaped cells with rounded ends and, when viewed under a microscope, are seen to have thousands of alternating light and dark bands oriented perpendicular to their long axis. Because of this appearance, skeletal muscle cells are said to be striated. The cells of a muscle are arranged in a parallel fashion, with their long forms mostly following the long axis of the parent muscle.

When a nerve signal stimulates a skeletal muscle cell, the muscle cell contracts relatively quickly and then, just about as quickly, relaxes (a muscle twitch). The contraction results in a shortening and thickening of the cell, which pulls the two ends of the cell, and whatever is attached to them, toward each other. The duration of a skeletal muscle twitch varies from muscle to muscle. For example, a muscle cell from one of the muscles controlling eye movements may complete a twitch in about ten milliseconds, while a cell from the soleus muscle (found in the calf of the leg) will complete a twitch about ten times more slowly.

The strength of the overall contraction of a skeletal muscle depends on two factors: the number of individual muscle cells in the muscle which become stimulated and therefore contract (called multiple motor unit summation, or recruitment); and the frequency at which the stimulations, and therefore the contractions, occur (called temporal summation). Since most skeletal muscles are composed of hundreds of individual muscle cells, and since each of the nerve cells (motor neurons) which can stimulate the muscle makes contact with only a relatively limited number of the muscle cells (each motor neuron and the muscle cells it contacts forming a motor unit), it is possible to regulate the strength and precision of the muscle's contractions, voluntarily, over a very wide range. This is accomplished by varying the summations—multiple motor unit (number of motor units activated) and temporal (the frequency of motor unit activation)—to meet the demands of a particular situation.

When two muscle twitches occur in rapid succession, it is possible for the muscle to begin the second twitch before it has completely relaxed from the first twitch. In this case, the contraction of the second twitch adds its strength to the force developed as a result of the first contraction; therefore, the second contraction develops more force than the first contraction. The result of continuing the frequency of such twitch-evoking stimuli is a somewhat jerky, oscillating contraction called incomplete tetanus. At high frequencies of stimulation (for example, about fifty twitches per second), there is no evidence of the muscle relaxing from any one twitch before the following twitch takes place, and the muscle makes a very smooth and sustained contraction called complete tetanus. If, following an initial single twitch-evoking stimulus of a skeletal muscle cell, a second stimulus is applied too quickly, there will be no further contraction of the muscle cell, regardless of how strong the second stimulus may be. The cell's ability to respond to this second stimulus is absent until enough time has passed to allow the cell to recover its excitability. The period during which the cell's excitability is absent is referred to as its refractory period. The refractory period of skeletal muscle cells is quite short (about five milliseconds). Skeletal muscles are responsible for the movements of the skeleton (skull, limbs, fingers, toes, and trunk) and for the variety of facial expressions that humans can produce. They also permit speaking, eye movements, breathing, chewing, and swallowing.

Cardiac Muscle

The second type of muscle tissue found in vertebrates is called cardiac muscle. It is the muscle tissue found in the heart. Microscopic examination of cardiac muscle cells reveals them also to possess striations similar to skeletal muscle; however, cardiac muscle is not under voluntary control. Hence, cardiac muscle is referred to as involuntary striated muscle. Cardiac muscle cells also differ from skeletal muscle in that the cardiac fibers branch and form interconnections with one another, forming a network of cells. The individual members of a network are joined by special types of cellular junctions called intercalated disks. The intercalated disks permit the excitation of a single cell, which must occur for the muscle cell to contract, to spread throughout the entire network of cardiac cells; therefore, the contraction of any one cardiac cell will result in the contraction of the entire network of cardiac cells. Thus, the heart's muscle tissue network operates as a functional unit, which is very important for the efficient development of the pressures necessary to push blood through the body's circulatory system. Another very important characteristic of cardiac muscle is its ability to contract in a spontaneous, rhythmical fashion without the need for neural or hormonal stimuli (although both nerves and hormones are present and function as modulators of cardiac activity, also at a subconscious level). This property is termed autorhythmicity, and it accounts for the involuntary nature of cardiac muscle. Cardiac muscle twitches are about ten to fifteen times longer than those of skeletal muscle, and the refractory period (about three hundred milliseconds) is about sixty times longer than that of skeletal muscle. The consequences of these traits are important. The long twitch maintains muscular pressure on the blood contents of the heart until most of it has been pumped out of the heart's chambers. The long refractory period prevents the development of tetanus, and allows the heart to relax between beats so that it can be refilled with blood.

Smooth Muscle

The third type of vertebrate muscle is called smooth muscle because of its lack of striations when viewed microscopically. Its basic and most important functions relate to the maintenance of stable internal conditions within vertebrate bodies. Examples of this are the regulation of blood flow to the various organs to supply them with the proper amounts of oxygen and nutrients, the maintenance of blood pressure during postural changes (such as from reclining to standing), the mixing and movement of ingested food within the digestive tract, and the directing of blood flow through or away from the skin to aid in body temperature regulation. Smooth muscle is also usually involuntary and often displays automaticity. Automaticity refers to the fact that smooth muscle often is stimulated to contract simply by being stretched, as, for example, occurs in the stomach following a meal, without the necessity of neural or hormonal stimulation. Nevertheless, involuntary nerves and hormones are both involved in regulating the actions of smooth muscle cells. The functions of smooth muscle are almost always such that contraction is the appropriate response to stretch of the organ containing the smooth muscle (as in the stomach example just mentioned).

Smooth muscle cells are very small: only about eight micrometers in diameter and between thirty and two hundred micrometers long. They are spindle-shaped, tapering toward each end. Although very small, these cells are able to contract to a length which is a much smaller fraction of their resting length than can either cardiac or skeletal muscle cells. Smooth muscle can also remain fully contracted for long time periods and consume very little energy. The speed of contraction of smooth muscle, however, is the slowest of all three muscle types.

Many smooth muscle cells are arranged as functional units which have the individual cells connected to each other by gap junctions. Gap junctions permit the passage of contraction signals from one cell to the next in the network in much the same way as it occurs in cardiac muscle. The result is that when one cell within the network begins to contract, a wave of contraction spreads throughout the entire network of smooth muscle cells.

Studying Vertebrate Muscle

Light and electron microscopes are frequently used to study muscle tissue. In particular, the electron microscope has made it possible to visualize the intricate and highly specialized internal structures of muscle cells, most of which are impossible to view with a light microscope, given their very small dimensions.

Many studies of muscle cells are actually studies of isolated parts of muscle cells. It is possible to break apart muscle cells and to separate many of their components from one another by the use of centrifugation. Centrifugation is the use of centrifugal force to separate objects by size and/or density. A centrifuge is a device in which samples of objects (in this case, muscle-cell structural components) that are to be separated are subjected to high centrifugal force generated by spinning the samples at great speed. The centrifugal force is the force that tends to impel an object outward from the center of rotation.

Once the various subcellular components are isolated, they can be subjected to a wide variety of biochemical tests to determine what type of molecules they contain (such as proteins, lipids, or carbohydrates), how much of each type they contain, and the exact chemical composition of these molecules (such as the amino acid sequence of a protein). In the case of muscle cells, much of the interest has centered on the large quantities of the proteins actin and myosin which they have been found to contain. Using isolated actin and myosin, scientists have learned much about their functions in muscle cells. In particular, it is now known that these two proteins are the molecules which generate the contractile forces which muscle cells are capable of producing. The precise molecular mechanisms are still unknown, but great progress has been made in discovering how actin and myosin accomplish the generation of contractile forces.

Studies of the electrical properties of muscle cells are performed using very sensitive amplifiers connected to fine glass pipette microelectrodes. These electrodes are formed from thin glass tubes which have been heated and pulled apart to produce a tapering of the wall of the tube. The final tip of the tapered tube is much smaller than a muscle cell. This makes it possible to insert the tip into the cell without killing it. When the electrodes are filled with a solution capable of conducting electrical signals, they can record the electrical activity that takes place in living, contracting, and relaxing muscle cells: their electrophysiological properties. These studies have revealed that all muscle cells possess an electrical voltage difference between their interior region and the surrounding environment. Just before a muscle cell begins to contract, this voltage difference decreases toward a zero value extremely rapidly. Combining such electrophysiological studies of muscle cells with simultaneous biochemical studies can be very rewarding.

Other techniques used in the study of muscle tissue include the observation of the relationships that various muscles have with other muscles, with nerves, and with bones, and the use of strain gauges to measure the strength of muscles when different experimental conditions occur (such as temperature changes, blood-flow variations, and pharmacological treatments). Even high speed X-ray motion pictures have been applied to the study of muscle tissue.

The Importance of Muscle

Vertebrate muscle tissue is involved in almost every bodily function. In particular, any function requiring the movement of some body part or parts needs to have a source of motive power. For this purpose, evolution has resulted in the development of the specialized muscle tissues found in all vertebrates, which account for up to 50 percent of their total body weight.

Because of the muscle-tissue characteristics of excitability (the ability to respond to stimuli), extensibility (the ability to be stretched), contractility (the ability to shorten actively and thereby generate force for the production of work), and elasticity (the ability to return to original length following extension or contraction), vertebrates have a wide range of important capabilities available which assist them in their survival.

For the muscular system, disease states or disorders resulting from improper nutrition, injury, or toxic substances are very often life-threatening conditions. This is most obvious for disturbances of the respiratory muscles or of the muscles involved in eating and swallowing; however, muscular disorders involving the heart, the circulatory system, the digestive tract, or any major group of skeletal muscles may also prove to be life-threatening.

The most common heart problems are caused by reduction or blockage of the blood supply to the heart muscle. Reduced blood supply usually is the cause of a reduced oxygen supply. The insufficient oxygen supply weakens the heart-muscle cells, causing the condition of ischemia. Complete interruption of the blood supply to an area of cardiac muscle tissue usually results in necrosis (death) of the affected muscle cells; the condition is referred to as myocardial infarction. The dead muscle cells do not regenerate but are replaced by scar tissue, which is not contractile. This results in decreased pumping efficiency by the heart. Depending on the size and location of the dead area, the result may range from barely noticeable to sudden death.

As a consequence of some bacterial infections, it is possible for the lining of the heart muscle to become inflamed. This can then result in abnormal irritation of some of the heart-muscle cells. These cells can then disrupt the normal autorhythmicity of the heart. Irregular heartbeats and/or uncoordinated contractions among the heart-muscle cells ensues. These conditions are very serious and can lead to death.

—John V. Urbas

See also: Amphibians; Anatomy; Bone and cartilage; Endoskeletons; Fish; Flight; Heart; Histology; Locomotion; Mammals; Muscles in invertebrates; Physiology; Reptiles; Vertebrates.

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MUTATIONS

Types of animal science: Development, evolution
Fields of study: Biochemistry, cell biology, developmental biology, embryology, evolutionary science, genetics

Mutations have been used to work out metabolic pathways, define genes and their controlling sites, understand how multicellular organisms develop, and study how organisms evolve.

Principal Terms

- ALLELE: one of many possible sequences of a gene
- CONTROLLING SITE: a sequence of nucleotides generally fifteen to sixty nucleotides long, to which a transcriptional activator or repressor binds
- GENE: a sequence of one thousand to ten thousand nucleotides, which usually specifies a protein
- MUTATION: a change in the nucleotide sequence of a gene or of a controlling site; changes in genes alter the protein, whereas changes in controlling sites determine where and how much of a protein is produced

In all living organisms, the hereditary information consists of two complementary strands of deoxyribonucleic acid, known as DNA. DNA strands are constructed of subunits called nucleotides that consist of a nitrogenous base, a deoxyribose sugar, and a phosphate. Generally, DNA strands consist of millions of nucleotides attached to each other like the rings of a chain. There are four different nucleotides. The two complementary strands are held together by hydrogen bonds between the bases. If there is an adenine (A) in one strand, it hydrogen bonds to a thymine (T) in the complementary strand. Similarly, if there is a guanine (G) in one strand, it hydrogen bonds to a cytosine (C) in the other strand. Thus, the amount of A is equal to T and the amount of G is equal to C. The order of nucleotides in a strand specifies the order of amino acids in proteins.

Genetics is the study of how the information in DNA molecules is expressed and how DNA molecules account for the heredity of an organism. Changes in the sequence of nucleotides in DNA may alter an organism's proteins, which in turn may change one or more of an organism's traits. DNA changes are called mutations, and the organisms that harbor mutations are known as mutants. The commonly encountered trait or organism is referred to as the wild-type. The characterization of mutations and mutants has been and still is one of the best ways of discovering the function of genes and determining how organisms maintain themselves, evolve, and develop. A study of mutations and mutants also has shed light on numerous genetic diseases.

Heat: The Cause of Most Spontaneous Mutations

Most mutations are caused by the instability of the nucleotide bases. Sometimes bases hit by rapidly moving water molecules briefly alter their chemistry. These chemical changes are known as tautomeric shifts. Tautomeric shifts alter the distribution of electrons and protons in the bases so that bases in the complementary strands no longer pair normally. The redistribution of electrons and protons in the bases causes abnormal pairings to occur. For example, an abnormal adenine (A*) pairs with C and an abnormal guanine (G*) pairs with T.

When a DNA molecule is being replicated, spontaneous tautomer shifts can result in permanent mutations. Spontaneous mutations occur, for example, when an A in the template strand undergoes a tautomer shift (A→A*) just as the DNA polymerase reaches it. A cytosine pairs with the A* and becomes part of the new strand being synthesized by the DNA polymerase. When this new strand, with a C in it instead of a T, functions as a template, the complementary strand will have a G in it rather than an A. This type of tautomeric shift during DNA replication converts what normally would have been an A = T base pair in "granddaughter" DNA to a G = C base pair.

Chemicals That Cause Mutations

Mutations are induced by many chemical and physical agents that are called mutagens. Many chemicals act as mutagens. Nitrous acid, for example, diffuses into cells and removes amino groups from DNA bases. These chemically altered bases no longer base pair normally. When DNA is replicated or repaired, incorrect nucleotides are inserted opposite the chemically altered bases. Nitrous acid changes adenine to hypoxanthine, which pairs with cytosine. It also changes guanine to xanthine, which pairs with T.

Base analogues are molecules that closely resemble normal nucleotides and consequently are incorporated into DNA that is being repaired or replicated. A base analogue to thymine, such as 5-bromouracil (5BU), is efficiently incorporated into DNA. 5BU spontaneously undergoes tautomeric shifts at a high rate. The abnormal form of 5BU pairs with G rather than A. Thus, 5BU introduces many base pair transitions in newly synthesized DNA molecules.

The most potent mutagens are alkylating agents, such as nitrosamines, methyl bromide, and ethylene oxide. These mutagens attach methyl or ethyl groups (alkyl groups) to A and G. This causes A and G to undergo tautomeric shifts at a higher than normal rate.

High-Energy Electromagnetic Radiation and Particles

Ultraviolet (UV) light is a powerful mutagen. It generally penetrates cells but is readily absorbed by thymine and cytosine bases in DNA. When two thymines or two cytosines next to each other in a strand absorb UV light, they often react chemically with each other to form thymine dimers or cytosine dimers that distort the DNA. These distorted regions stimulate a repair system that cuts out the

The Use of a Mutation to Determine a Catabolic Pathway

Sir Archibald Garrod (1857-1936) was an English physician who studied the effects of a mutation in humans and discovered a catabolic pathway. Garrod's research into the cause of alkaptonuria, a condition where the urine turns black upon exposure to the air, led to the idea that alkaptonuria occurred in persons with two defective genes for the enzyme that eliminates homogentisic acid in the urine. Homogentisic acid turns black when oxidized by oxygen.

In a paper published in 1902, Garrod analyzed a number of families where alkaptonuria occurred, establishing that the trait was recessive and followed simple Mendelian genetics. This was the first account of recessive inheritance in humans. When Garrod fed alkaptonuric patients homogentisic acid, their urine blackened upon exposure to air and contained nearly the same amount of homogentisic acid that they consumed. Normal individuals given homogentisic acid contained no detectable homogentisic acid in their urine. By feeding alkaptonuric patients various compounds that might give rise to homogentisic acid, Garrod discovered the metabolic pathway that led from the amino acids phenylalanine and tyrosine to homogentisic acid.

In his book published in 1908, *Inborn Errors of Metabolism*, Garrod concluded that alkaptonuria is caused by a block in the catabolic pathway that eliminates homogentisic acid. He reasoned that the catabolic block was caused by the lack of a specific enzyme. The fact that the trait followed Mendelian genetics suggested that a functional gene normally specified the enzyme involved in the breakdown of homogentisic acid. This was the beginning of the idea that genes specify enzymes.

Mutations Used to Determine an Anabolic Pathway

Between 1937 and 1941, George W. Beadle and Edward L. Tatum isolated fungal mutants that were unable to synthesize various vitamins and amino acids. They isolated these mutants to try to understand how genes control specific reactions in various metabolic (synthetic) pathways. The mutants would not grow on a simple medium unless supplied with the nutrient they were unable to synthesize. Beadle and Tatum induced large numbers of mutations in the fungus they were studying and isolated hundreds of mutants. Seven mutants were isolated, each carrying a defective form of a gene involved in the synthesis of the amino acid arginine. Using these mutants, Beadle and Tatum were able to order the chemical reactions by feeding the fungal mutants different metabolic intermediates. If the fungal mutants grew when a particular metabolic intermediate was provided, then the gene mutation affected a step leading to the synthesis of the intermediate. If the mutant did not grow, however, then the gene mutation affected a step that converted the intermediate into arginine. They concluded from their experiments that each gene controlled a different chemical reaction. They confirmed that a specific chemical reaction fails to take place in diploid organisms if both representatives of a given gene were defective. Beadle and Tatum's research strengthened the idea that genes specify enzymes. Their idea became known as the "one gene-one enzyme" hypothesis.

dimers and some DNA on either side and replaces the DNA with normal nucleotides. Excessive repair leads to an increased occurrence of spontaneous mutations. Sometimes a distortion in the template allows the DNA polymerase to add or to leave out nucleotides as it moves along the template during strand synthesis. This may explain how some additions and some deletions occur.

Very energetic electromagnetic radiation, such as X rays and gamma rays, as well as high-energy particles released from radioactive atoms, also induce mutations. These energetic mutagens easily penetrate cells and chemically alter many molecules in their path by stripping away electrons. Ions and radicals formed by these mutagens react with the DNA, causing bases to be released and DNA to break. DNA deletions, DNA transpositions, and DNA inversions may be promoted by DNA breakage.

When a gene is mutated, the protein the gene specifies generally becomes nonfunctional. In bacteria that have only one copy of each gene, traits are immediately altered by a mutation. On the other hand, in animals and plants that may have more than one copy of a gene, a mutation in only one gene may not produce a new trait because the wild-type (normal) gene often provides enough of the essential protein. When developing animals and plants are missing both genes, however, they may fail to develop or they may develop, but in a different way.

A few mutations are beneficial to the organism that acquires them and may make the organism better adapted to its environment. These beneficial mutations may make a protein work a little better or in a different way. Some mutations are also beneficial because they create diversity in a population. Diversity promotes the survival of a population by ensuring that some organisms survive if the environment drastically changes. A population that is too well adapted to a particular environment will not survive if there are significant changes in the environment. There have been at least five major mass extinctions during the history of life on earth, in some cases eliminating more than 85 percent of all species. The organisms that survived these mass extinctions were much less specialized than the organisms that did not.

Usefulness of Mutations

Mutations have been extremely useful in the study of organisms. Mutations allow scientists to understand what a particular gene and its product do. If the mutation eliminates the gene (and prod-

Mutations Used to Determine How Genes Are Regulated

In 1963, François Jacob and Jacques Monod published a classic paper in which they presented a model for how genes might be regulated. They used wild-type and mutant bacteria to demonstrate that certain enzymes are not produced when the genes that specified the enzymes are blocked by a repressor protein. Wild-type bacteria contain a repressor gene (R). A repressor specified by the repressor gene blocks DNA transcription (the synthesis of mitochondrial ribonucleic acid, mRNA) by binding to a controlling site (operator site, O) on the DNA that partially overlaps the ribonucleic acid (RNA) polymerase binding site (promoter site, P). If RNA polymerases are prevented from binding DNA, transcription is blocked. When transcription of a gene is inhibited, no enzyme can be synthesized. Jacob and Monod demonstrated that certain mutations (O) in the operator site could block repressor binding to the DNA. These controlling site mutations result in the continuous synthesis of mRNA and the enzymes the mRNA specified. These operator constitutive mutations (O) were shown to prevent repressor binding. Certain mutations in the repressor gene (R-) would eliminate the repressor and result in continuous synthesis of the enzymes regulated by the repressor. Other mutations in the repressor gene would create a super repressor (R) that failed to disengage from the operator site. This blocked the synthesis of the enzymes regulated by wild-type operators (O). Super repressors do not respond to the organic ligand that may bind to them and causes them to disengage from operator sites. Nevertheless, super repressors are unable to bind to constitutive operator sites. Researchers have discovered that many genes are also regulated by protein activators. Some promoter site mutations (P) increase the level of transcription, whereas other promoter site mutations (P-) abolish transcription.

Controlling sites, such as O and P, can be differentiated from genes, such as R, since controlling sites only affect genes on the DNA molecule where they are located (*cis* effect). Genes specifying repressors and activators affect genes both on the DNA molecule where the regulatory genes are located (*cis* effect) and also on other DNA molecules (*trans* effect). This is how genes became known as cistrons.

uct), scientists can guess what the gene does by looking at the affected organism. For example, if a mutation changes eye color (red to white), the affected gene most likely has something to do with pigment synthesis or deposition of the pigment in the eye.

The study of mutations and mutant organisms has helped scientists unravel anabolic (synthetic) and catabolic (degrading) pathways, determine how parental genes combine to produce new characteristics in progeny, clarify what genes are and what they do, establish how genes are regulated, and even decipher how multicellular organisms develop and evolve.

Mutations in Development and Evolution

The study of mutations and mutant organisms at the end of the twentieth century led to an understanding of how multicellular organisms develop and evolve. One of the most useful organisms in unraveling the development problem has been the small fruit fly *Drosophila*. Thousands of mutations that affect development of this organism have been characterized. Scientist found that a hierarchy of genes are involved in development. First, maternal genes are expressed. These genes activate gap genes and these, in turn, activate pair-rule genes. All of these gene catagories are known to be involved in regulating the expression of homeotic genes. Maternal, gap, pair-rule, and homeotic gene products all function as transcriptional activators and repressors. For example, the maternal gene product called bicoid stimulates its own synthesis, whereas it inhibits the synthesis of another maternal gene product called nanos.

Maternal Genes→Gap Genes→Pair Rule Genes→Homeotic Genes

This gene hierarchy is responsible for the anterior-posterior segmentation seen in *Drosophila*. Edward B. Lewis, Christiane Nüsslein-Volhard, and Eric Wieschaus shared the 1995 Nobel Prize in Physiology or Medicine for their studies of the genes that control *Drosophila* development.

Thomas Hunt Morgan

Born: September 25, 1866; Lexington, Kentucky
Died: December 4, 1945; Pasadena, California
Fields of study: Genetics
Contribution: Morgan's studies popularized the use of the fruit fly *Drosophila* for the study of animal genetics. He is credited with discovering the first sex-linked trait in *Drosophila* and with demonstrating how new characteristics could be passed on to successive generations. Morgan and his students showed that chromosomes exchanged genes, a process known as crossing over. In 1933, Morgan was awarded the Nobel Prize for Physiology or Medicine for his work on *Drosophila* genetics.

In his classic paper of 1910, Thomas Hunt Morgan described very rare white-eyed flies that appeared spontaneously in a red-eyed population. Because these mutants were always males, Morgan suspected that the gene controlling eye color was linked to the X chromosome that influenced the development of sex. The observation that white-eyed females could be produced from certain matings, however, indicated that the white-eyed trait was not limited to males.

Morgan's experiments demonstrated for the first time that a gene controlling eye color was linked (or limited) to the X chromosome. Red and white eyes are caused by different alleles of the same gene. These alleles on the X chromosome are represented in the following manner: X and X. Any gene linked to the X chromosome is called a sex-linked gene. In *Drosophila*, two X chromosomes generally result in a female fly, whereas one X chromosome results in a male. Morgan found that the R allele inducing red eyes is dominant over the r allele that allows white eyes to develop when it is the only allele a fly has.

The Y chromosome that pairs with the X chromosome in males (XY) lacks sex-linked genes. Thus, mating red-eyed females (XX) to white-eyed males (XY) results in all first filial (F1) generation flies, XX females and XY males, having red eyes. Matings between the F1 flies demonstrated that the red-eye-inducing allele and the white-eye-promoting allele always remained associated with the X chromosome. This suggested that the alleles were linked to the X chromosome.

In 1913, A. H. Sturtevant, working in Morgan's laboratory, reported on mutations linked together on a fruit fly's X chromosome. Sturtevant demonstrated that recombination between two X chromosomes could separate genes controlling different traits. In addition to using the alleles that determined eye color, Sturtevant used alleles that influenced wing formation. A normal wing forms under the influence of the L gene, but a miniature wing is associated with the l allele of the L gene. Genes linked on the X chromosome may be shown as follows: XL. Sturtevant observed recombination when he characterized the offspring from certain crosses. A female fly with red eyes and normal wings, XlXL, usually produces two types of eggs. One type of egg has the Xl chromosome, whereas the other type of egg has the XL chromosome. Very infrequently, when there is a crossover between the X chromosomes, rare eggs are produced with recombinant X chromosomes, one type of egg has the Xl chromosome, whereas the other type of egg has the XL chromosome. When these recombinant eggs fuse with a sperm carrying only a Y chromosome, recombinant male flies result, those that have normal eyes and normal wings (XLY) and those that have white eyes and miniature wings (XlY). By using various mutant flies, Morgan and Sturtevant discovered that they could both order a number of different genes on the X chromosome and determine how far they were from each other. The farther a gene is from another gene, the greater the number of recombinant offspring. The pattern of offspring was used to determine the sequence of genes on the X chromosome. Finding flies with mutations in different genes was essential for determining the sequence of genes and the distances between them.

—Jaime Stanley Colomé

Thomas Hunt Morgan popularized the use of the fruit fly Drosophila melanogaster *for the study of genetic mutations.* (Library of Congress)

Homeotic genes are found in all multicellular organisms. Homeotic genes similar to those found in *Drosophila* control the development of segments most visibly exemplified by the vertebrae and the bones in animals' appendages. Mutations in homeotic genes or their controlling sites affect the development of segments. Segments can be eliminated or modified by homeotic gene controlling site mutations.

One well-studied homeotic gene in *Drosophila* is the gene antennapedia, *antp*. Certain mutations in the controlling sites for the antennapedia gene result in legs developing rather than head antennae. Another homeotic gene is ultrabithorax, *ubx*. Some mutations in the controlling sites for ultrabithorax gene result in a second pair of wings developing where the pair of halteres normally develop. Halteres are tiny, winglike appendages that all flies have, which promote stable flight. Other mutations in the controlling sites for *ubx* produce a second pair of winglike structures that are half haltere (anterior portion), half wing (posterior portion). By studying mutations and the altered traits, scientists have discovered that controlling site mutations change when and where proteins are synthesized. For example, if a protein is to be produced in seven segments along the anterior-posterior axis of an animal, there must be at least seven different controlling sites that can respond to the different activators and repressors produced in each segment.

Numerous studies suggest that antennapedia and ultrabithorax are transcriptional repressor-activators that not only repress the development of legs and wings, but also stimulate the development of antennae and halteres, respectively. The study of *Drosophila* mutants is beginning to clarify how antennae and mouth parts evolved from leglike appendages and how halteres evolved from wings. The study of genes and controlling sites has led to the understanding of their role in the maintenance, development, and evolution of every organism.

—*Jaime Stanley Colomé*

See also: Asexual reproduction; Breeding programs; Cleavage, gastrulation, and neurulation; Cloning of extinct or endangered species; Copulation; Courtship; Determination and differentiation; Development: Evolutionary perspective; Estrus; Fertilization; Gametogenesis; Hermaphrodites; Hydrostatic skeletons; Mating; Parthenogenesis; Pregnancy and prenatal development; Reproduction; Reproductive strategies; Reproductive system of female mammals; Reproductive system of male mammals; Sexual development.

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NATURAL SELECTION

Type of animal science: Evolution
Fields of study: Ecology, evolutionary science, genetics

Natural selection is the process of differential survival and reproduction of individuals resulting in long-term changes in the characteristics of species. This process is central to evolution.

Principal Terms

ADAPTATION: the process of becoming better able to live and reproduce in a given set of environments

EVOLUTION: any cumulative change in the characteristics of organisms or populations over many generations

FITNESS: the relative ability of individuals to pass on genes to subsequent generations

HERITABILITY: the extent to which variation in some trait among individuals in a population is a result of genetic differences

POPULATION: a group of individuals that occupy a common area and share a common gene pool

SPECIES: the group of all individuals or populations that interbreed or potentially interbreed with one another under natural conditions

Natural selection is a three part process. First, there must exist differences among individuals in some trait. Second, the trait differences must lead to differences in survival and reproduction. Third, the trait differences must have a genetic basis. Natural selection results in long-term changes in the characteristics of the population.

As one of the central processes responsible for evolution, natural selection results in both fine-tuning adaptations of populations and species to their environments and creating differences among species. The importance of natural selection was first recognized by Charles Darwin, who provided the first widely accepted mechanism for evolutionary change. Natural selection is one of several processes responsible for changing the characteristics of populations and leading to an increase in adaptiveness. Other processes include genetic drift and migration. These processes interact with the processes responsible for producing variation (mutation and development) and those responsible for determining the rate and direction of evolution (mating system, population size, and long-term ecological changes) to establish the path of evolution of a species.

The Process of Natural Selection

Natural selection occurs through the interaction of three factors: variation among individuals in a population in some trait, fitness differences among individuals as a result of that trait, and heritable variation in that trait. If those three conditions are met, then the characteristics of the population with respect to that trait will change from one generation to the next until equilibrium with other processes is reached. An example that demonstrates this process involves the peppered moth. It has two forms in the United Kingdom, a light-colored form and a dark-colored form; there is variation in color among individuals. Genetic analysis has shown that this difference in color is caused by a single gene; the variation has a heritable basis. The moth is eaten by birds that find their food by sight. The light-colored form cannot be seen when sitting on lichen-covered trees, while the dark-colored form can be seen easily. Air pollution kills the lichen, however, and turns the trees dark in color. Then, the dark-colored form is hidden and the light-colored form visible. Thus, differences in color lead to fitness differences. In the early nineteenth century, the dark-colored form was very rare. In the last half of the nineteenth century, however, air pollution increased, and the dark-colored form became much more frequent as a result of natural selection.

The characteristics of a population can be changed by natural selection in several ways. If individuals in a population with an extreme value for a trait have the greatest fitness on average, then the mean value of the trait will change in a consistent direction, which is called directional selection. For example, the soil in the vicinity of mines contains heavy metals that are toxic to plants. Individuals with the greatest resistance to heavy metals have the highest survivorship. Evolution leads to an increase in resistance. If individuals in a population with intermediate values for a trait have the greatest fitness on average, then the variation in the trait will be reduced, which is called stabilizing selection. For example, in many species of birds, individuals with intermediate numbers of offspring have the greatest fitness. If an individual has a small number of offspring, that parent has reduced reproduction and a low fitness. If the number of offspring is large, the parent will not be able to provide enough food for all the young, and most, or all, will starve, again resulting in reduced reproduction and a low fitness. Evolution leads to all birds producing the same, intermediate number of offspring. If individuals in a population with different values for a trait have the greatest fitnesses on average and intermediates have low fitness, then the variation in the trait will be increased. This is called disruptive selection. For example, for Darwin's finches, individuals with long, thin bills are able to probe into rotting cactus to find insects. Individuals with short, thick bills are able to crack hard seeds. Individuals with intermediate-shaped bills are not able to do either well and have reduced fitness relative to the more extreme types. Evolution leads to two different species of finch with different bills.

A Slow and Holistic Process

Natural selection is a slow process. The rate of evolution—that is, response to selection—is determined by the magnitude of fitness differences among individuals and the heritability of traits. Fitness differences tend to be small so that more fit individuals on average may have only a few more offspring than less fit individuals. Heritabilities of most traits are low to intermediate, meaning that most differences among individuals are not a result of genetic differences. So, even if one individual has many offspring and another has few offspring, they may not differ genetically and no change will occur. For example, if all the beetles in a population were between one and two centimeters in length and there was selection for larger beetles, it could take five hundred generations before all beetles were larger than two centimeters. Also, the direction of selection may change from one generation to the next, so that no net change occurs.

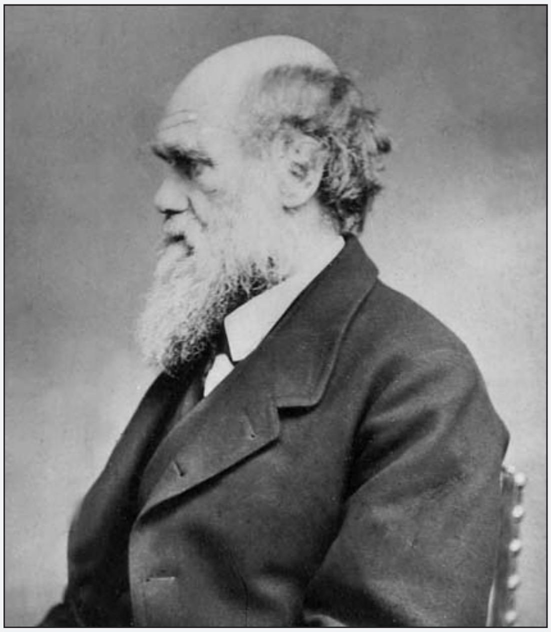
Natural selection does not act on traits in isolation. How a trait affects fitness in combination with other traits, called correlational selection, is important. For example, fruit flies lay their eggs in rotting fruit. Considered in isolation, a female should always lay as many eggs as possible. One fruit is not big enough for all the eggs she might lay, however, so she must fly from fruit to fruit. Flying requires energy, and the more energy that is used in flight the less that can be used to make eggs. So natural selection results in the division of energy between eggs and flight that yields the greatest overall number of offspring. This example demonstrates that the result of natural selection is often a trade-off among different traits.

By acting differently on males and females, natural selection results in sexual selection. This form of selection can explain differences in the forms of males and females of a species. In general, because male gametes, sperm, are much smaller and "cheaper" to produce than female gametes, eggs, more sperm than eggs are produced. As a result, it is possible for one male to fertilize many eggs, while other males fertilize few or no eggs. For example, a lion pride usually consists of

Charles Darwin

Born: February 12, 1809; Shrewsbury, England
Died: April 19, 1882; Downe, England
Fields of study: Entomology, evolutionary science, human origins, invertebrate biology
Contribution: Darwin was not the first philosopher or scientist to posit a theory of evolution, but his theories of natural and sexual selection provided much of the foundation for later scientific evolutionary theory.

Charles Robert Darwin had briefly studied medicine at the University of Edinburgh and attended Cambridge University, intending to prepare for the ministry, when he was offered a chance to sail on the HMS *Beagle* as a naturalist and companion to Captain Robert FitzRoy. The fifty-seven month voyage, from December 7, 1831, to October 2, 1836, allowed Darwin unique opportunities to explore fossils, fish and sea mammals, and coral reefs. Lengthy land excursions allowed him to examine land animals and fossils, primarily in South America.



Charles Darwin's theory of evolution through natural selection revolutionized not only the scientific view of the world but popular understanding as well. (National Archives)

Returning to England, he first published his findings as *Journal and Remarks*, volume 3 in the series *Narrative of the Surveying Voyages of H.M.S. "Adventure" and "Beagle" Between 1826 and 1836* (1839). This work was revised and published the same year as *Journal of Researches into the Geology and Natural History of the Various Counties Visited by H.M.S. "Beagle"* (1839). His findings caused him to question generally accepted assumptions about animal creation and to posit evolutionary change as occurring mainly through natural selection. In later works, he increasingly stressed the importance of sexual selection. Challenged by peers to examine individual species before generalizing about life as a whole, he began lengthy examinations of such life-forms as beetles and barnacles, which he published.

By the 1850's, despite his aversion to public controversy, he accepted the need to publish his general theories. They appeared in 1859 as *On the Origin of Species by Means of Natural Selection: Or, The Preservation of Favoured Races in the Struggle for Life*. Although he avoided discussion of human origin in this work, the controversy he dreaded was forthcoming. His ideas, however, were adopted by young scientists, most notably Thomas Henry Huxley, who sought to establish the natural sciences as disciplines separate from the natural theology that then prevailed in universities. These scientists became his spokespersons, as he continued his experiments at his estate; his theories gained widespread acceptance. In 1871, he dealt directly with the origin of human life in *The Descent of Man*; he followed this, in 1872, with *The Expression of Emotions in Man and Animals*. These works clearly placed man within the animal kingdom, not the product of a separate creation.

Darwin also published on narrower topics involving animal life and fossils, and extensively revised *On the Origin of Species*, ultimately producing six revised editions in the quarter-century after its initial publication. He wrote a brief autobiography, published posthumously in 1887. He was awarded numerous honors in England and on the Continent. At his death, his work was so widely respected that, despite his religious skepticism, England honored him with burial in Westminster Abbey.

—Betty Richardson

one or a few males and many females. Other males are excluded, and they live separately; larger males are able to chase away smaller males. The thick mane on male lions helps to protect their throats when they fight other males. Thus, larger males with thicker manes father more cubs than other males, leading to selection on these traits. Only males are under natural selection since all females, regardless of size, will mate. The result is that males are larger than females and have manes.

Group Selection

Natural selection can occur not only among individuals but also among groups. This process is generally known as group selection; when the groups are composed of related individuals, it is called kin selection. Group selection operates the same way as individual selection. The same three conditions are necessary: variation among groups in some trait, fitness differences among groups because of that trait, and a heritable basis for that trait. For example, in Australia, rabbits introduced from Europe in 1859 spread rapidly during the next sixty years. In order to control the rabbits, a virus was introduced in 1950. At first, the virus was very virulent, killing almost all infected animals within a few days. After ten years, however, the virus had evolved to become more benign, with infected rabbits living longer or not becoming sick at all. Virulent strains of the virus grow and reproduce faster than benign strains. So, within a single rabbit, virulent strains have a higher fitness than benign strains. The longer a rabbit lives, however, the more opportunity there is for the virus to be passed to other rabbits. Thus, a group of benign viruses infecting a rabbit are more likely to be passed on than a group of virulent viruses. In this example, group selection among rabbits resulted in evolution opposite to individual selection within rabbits; however, group selection and individual selection can result in evolution in the same direction. In general, natural selection can act at many levels: the gene, the chromosome, the individual, a group of individuals, the population, or the species.

Natural selection is the primary process leading to adaptation of individuals. It involves many traits acting together, differences among males and females, and differences among levels. The interaction of all these processes of natural selection determines the path of evolution.

Measuring Natural Selection

Natural selection is investigated in two ways: by use of indirect measurements and direct measurements. The indirect methods involve observing the outcome of natural selection and inferring its presence. The direct methods involve measuring the three parts of the process and following the course of evolution. Although the direct methods are preferred, as they provide direct proof of natural selection, in most instances, only indirect methods can be used.

Indirect methods involve three kinds of observations. First, comparisons are made of trait similarities or differences among populations or species living in the same or different areas. For example, many species of animals living in colder climates have larger bodies than those living in warmer climates. It is inferred, therefore, that colder climates result in natural selection for larger bodies. Second, long-term studies are done of traits, in particular changes in a group in the fossil record. For example, during the evolution of horses, their food, grasses, became tougher and horses' teeth became thicker. It is inferred, therefore, that tough grass resulted in natural selection for thicker teeth. Third, comparisons are made of gene frequencies of natural populations, with predictions from mathematical models. Gene frequencies are measured using various techniques, including scoring differences in appearance, as with light-colored and dark-colored moths; using electrophoresis to observe differences in proteins; and determining the sequence of base pairs of deoxyribonucleic acid (DNA). The models make predictions about expected frequencies in the presence or absence of selection. Indirect methods are best at revealing long-term responses to evolution and general processes of natural selection that affect many species. The indirect methods suffer from the problem that often many processes will result in similar patterns. So, it must be assumed that other processes were not operating, or other predictions must be made to separate the processes.

Direct methods involve two kinds of observation. First, there is observation of changes in a population following some change in the environment. There are many types of environmental changes, including man-made changes, natural disasters, seasonal changes, and introductions of species into new environments. For example, from the changes in the peppered moth following a change in pollution levels, one can measure the effects of natural selection. The second type of observation is the direct measurement of fitness differences among individuals with trait differences. For example, individual animals are tagged at an early age and survival and reproduction are monitored. Then, statistical techniques are used to find a relationship between fitness and variation among individuals in some trait. Alternatively, comparisons of traits are made between groups of individuals, such as breeding and nonbreeding, adults and juveniles, or live and dead individuals, again using statistical techniques. For example, lions that breed are larger than lions that do not breed. Direct methods are best at revealing the relative importance to natural selection of the three factors (variation, fitness differences, and heritability). The direct methods suffer from two limitations. It takes a long time for evolution to occur. So, although one can measure natural selection, it is often not known if it results in evolution. Also, for many species, it is impossible or impractical to mark individuals and follow them through their lives.

Many methods can be used to study natural selection and evolution. Each method provides information about different parts of the process. Only through the integration of these methods can the entire process of evolution be revealed.

Adaptation and Evolution

Natural selection is the central process in adaptation and evolution. By understanding how the process operates and where its limits lie, scientists hope to determine why evolution has proceeded in the fashion that it has. Historically, it was only after Darwin presented his theory of natural selection that the idea of evolution became widely accepted in the nineteenth century. In the twentieth century, much of the work of evolutionary biologists during the 1930's, 1940's, and 1950's was to integrate the fields of genetics, ecology, paleontology, and systematics, using natural selection and evolution as the unifying concepts.

Knowledge of natural selection is still growing; many questions proposed by Darwin and others are yet to be answered. It is still not known to what extent organisms are well adapted to their environments or whether the evolution of the parts of the chromosome that are not translated into proteins are a result of processes that do not involve natural selection. Of the many theories of how natural selection works, it is still unknown which ones are the most important in nature and to what extent evolution is caused by natural selection at the level of the individual, the group, and the species.

Genetic engineering requires knowledge of natural selection. The addition of a new gene into an organism will result in natural selection on that gene and change selection on other genes. Efficiency will be gained if successful and unsuccessful outcomes can be predicted beforehand. If genetically engineered organisms are to be released into nature, scientists need to be able to forecast their fates, such as whether the organism will remain benign or will become a pest. Genes added to one organism could possibly spread to other, native species. The solutions to these dilemmas involve predictions of the outcome of natural selection.

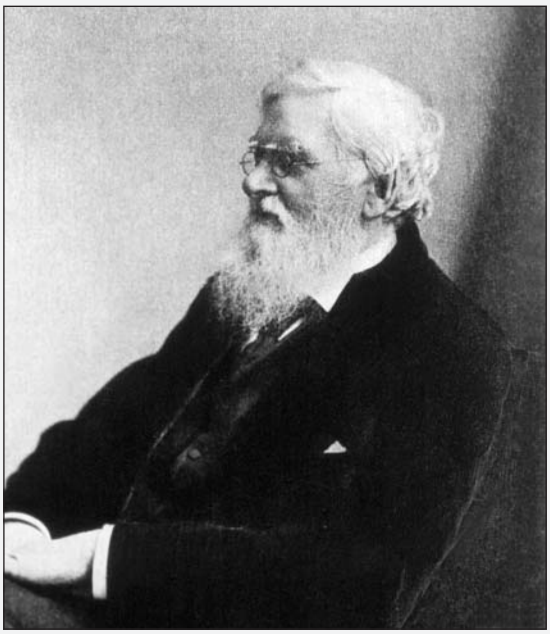
An understanding of natural selection is critical for conservation biology. During the twentieth century, the rate at which natural areas are being destroyed and species are becoming extinct has accelerated tremendously. Conservation biology attempts to stop that destruction and preserve species diversity. For extinction of endangered species to be halted, it must be understood how

Alfred Russel Wallace

Born: January 8, 1823; Usk, Monmouthshire, Wales
Died: November 7, 1913; Broadstone, Dorset, England
Fields of study: Entomology, evolutionary science, population biology, zoology
Contribution: Wallace, a pioneer of the science of zoogeography, proposed a theory of evolution by natural selection in 1855 that predated and stimulated the publication of Charles Darwin's *On the Origin of Species* (1859).

Alfred Russel Wallace grew up in rural Wales and then in Hertford, England. His formal education was limited to six years at the Hertford Grammar School. From 1837 to 1844 Wallace worked in his brother William's surveying business. In 1844, Wallace taught at the Collegiate School in Leicester, England.

In 1848, Wallace and the entomologist Henry Walter Bates embarked on an expedition to Brazil. Wallace and Bates planned to collect and identify biological specimens and then pay for their trip by selling their collections. Wallace spent a total of four years exploring the Amazon River basin, collecting birds, butterflies and other insects.



Alfred Russel Wallace independently proposed a theory of evolution very similar to that of Darwin. (National Library of Medicine)

Unfortunately, on the return voyage Wallace lost his precious collections when his ship caught fire and sank. Nevertheless, the expedition led to the publication of several articles and two books (*Palm Trees of the Amazon and Their Uses* and *Narrative of Travels on the Amazon and Rio Negro,* 1853). These reports attracted the attention of the Royal Geographical Society, which helped to fund his next expedition. For eight years (1854-1862) Wallace continued his research in the Malay Archipelago (Indonesia). Wallace's research on the geographic distribution of animals among the islands of the Malay Archipelago provided crucial evidence for his evolutionary theories and led him to devise what became known as Wallace's Line, the boundary that separates the fauna of Australia from that of Asia. By the time Wallace returned to England in 1862 he had collected over 125,000 animal specimens.

During an attack of a tropical fever, Wallace experienced a flash of insight in which he realized that natural selection could serve as the mechanism of evolution. Within a few days he completed his essay "On the Tendency of Varieties to Depart Indefinitely from the Original Type" and sent it to Charles Darwin for review and possible publication. Darwin was shocked to find that Wallace had developed a theory of evolution identical to that outlined in his own unpublished 1842 essay. Darwin's friends Charles Lyell and Joseph Hooker arranged for a joint presentation of the papers written by Wallace and Darwin and simultaneous publication in the August, 1858, *Proceedings of the Linnean Society.*

Graciously allowing Darwin to claim priority for the discovery of evolution by means of natural selection, Wallace continued to publish works on natural history and travel, including *The Malay Archipelago* (1869), *Contributions to the Theory of Natural Selection* (1870), *Geographical Distribution of Animals* (1876), and *Island Life* (1880). It was Wallace who called evolution by means of natural selection "Darwinism" in order to distinguish this theory from its predecessors. Unlike Darwin, however, Wallace continued to believe that natural selection could not account for the higher faculties of human beings.

—Lois N. Magner

natural selection will affect these species given massive environmental changes. By discovering how evolution is occurring under natural conditions, researchers will learn how to design nature preserves to maintain species.

—Samuel M. Scheiner

See also: Adaptations and their mechanisms; Clines, hybrid zones, and introgression; Development: Evolutionary perspective; Ecological niches; Evolution: Animal life; Evolution: Historical perspective; Extinctions and evolutionary explosions; Gene flow; Genetics; Human evolution analysis; Nonrandom mating, genetic drift, and mutation; Population analysis; Population fluctuations; Population genetics; Population growth; Punctuated equilibrium and continuous evolution; Sex differences: Evolutionary origin.

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NEANDERTHALS

Types of animal science: Anatomy, classification, evolution
Fields of study: Anthropology, archaeology, evolutionary science, human origins, physiology, systematics (taxonomy)

Neanderthals are the best-known extinct members of the human lineage. It is generally agreed that they were close relatives of modern humans, but the nature of the relationship is vigorously debated. They have been assumed to be a direct ancestor, a diseased member of the species, or an extinct side branch of the family tree.

Principal Terms

DEOXYRIBONUCLEIC ACID (DNA): the chemical that carries the instructions for all living things; closely related organisms have very similar DNA

GENUS: the first part of the scientific name of an organism; members of the same genus but different species are closely related, but cannot mate and produce fertile offspring

MITOCHONDRIA: subcellular structures containing DNA used to estimate the relationships between groups of organisms; the more similar the DNA, the more closely related the groups

SPECIES: the second part of the scientific name of an organism; members of the same species can mate and produce fertile offspring

SUBSPECIES: the third part of a scientific trinomial, assigned to one of two groups that can mate and produce fertile offspring, but that have some strikingly different characteristics

TAXONOMY: the science of classifying and naming living and fossil organisms, or the classification and scientific name of a living or fossil group

The fossil that gave the Neanderthals their name was found in a cave being quarried for limestone in Germany's Neander Valley in 1856. At least two Neanderthal fossils were discovered before the Neander Valley individual; however, neither was recognized as a member of an extinct human group until after the name "Neanderthal" was assigned. Many similar fossils have been found in scattered locations all over Europe and the Middle East since the Neander Valley discovery. Dates assigned to the various fossils indicate that the Neanderthals originated late in the Ice Age and became extinct a few thousand years before the last glacial retreat (from about 200,000 years ago to about 30,000 years ago). Thus the Neander Valley specimen lent its name to a fossil relative of modern humans that occupied Europe and the Middle East late in the Ice Age.

Though the Neanderthals were very similar to modern humans, they had several distinctive characteristics. Neanderthals were short and exceptionally stout-bodied with broad supportive bones and joints. This body form suggests a life filled with intense physical effort. Perhaps the compact body also helped them cope with cold stress under Ice Age conditions. Their brains were somewhat larger than modern human brains. That size may have compensated for the more massive total body size of the Neanderthals, since large-bodied organisms generally have larger brains. Their foreheads sloped up from their exceptionally heavy eyebrow ridges, their jaws extended forward beyond the plane of the face, and their chins were weakly developed. These and several other characteristics are used to define a fossil find as a Neanderthal.

Structure and Behavior

Rudolph Virchow's initial interpretation of the Neander Valley fossil as a diseased human was popular for a time. Virchow held that the fossil was a modern human whose unique features were the result of disease. However, as more fossils with the same characteristics were discovered all around Europe and the Middle East, this explanation became untenable. Later, misinterpretation of the characteristics of Neanderthal fossils led Marcellin Boule and others to interpret Neanderthals as stooped, bent-kneed, apelike subhumans with an animal nature to match.

Additional fossil discoveries, including evidence for toolmaking and burials, sometimes with flowers placed in the grave, caused anthropologists to rethink the presumed animal nature of the Neanderthals. Although the evidence for flowers has been challenged, the evidence for burials, presumably accompanied by mourning, is accepted by many anthropologists. In addition, fossils showed that some Neanderthals lived much of their lives with deformed limbs and other disabilities, which would have made it difficult or impossible for them to fend for themselves. Yet they apparently lived many years in that condition, suggesting the support of other members of a social group. Such behavior was not in keeping with Boule's picture of the Neanderthals as nonhuman animals.

Reinterpretation of the anatomic evidence also suggested that, instead of a bent-kneed, stooped posture, the Neanderthals walked on two rather straight legs and had hands capable of manipulating materials and making tools, much as modern humans do. All this indicated that the Neanderthals were more like modern humans than Boule's interpretation, and they came to be thought of in that light.

Taxonomic Relationship to Modern Humans

Neanderthals have always been recognized as close relatives of modern humans, but the specific taxonomy of the relationship is still a point of contention. They are placed in the same genus (*Homo*) as modern humans by almost all anthropologists, but researchers debate whether they were members of our species, *Homo sapiens* or belonged in their own species, *Homo neanderthalensis*. The discussion of the structure and behavior of Neanderthals bears directly on this question. If the Neanderthal characteristics were the result of disfigurement caused by disease, Neanderthals were simply aberrant humans and not especially interesting from the perspective of human evolution. However, if they were stooped, bent-kneed, and animal-like in behavior, they were probably a separate species, perhaps ancestral to modern humans, and therefore more interesting from the evolutionary perspective. On the other hand, if they were upright in stature, were skilled toolmakers, were supportive of their handicapped and elderly, and buried their dead with mementos such as flowers, they might earn the designation *Homo sapiens* and take on an even greater interest to the more modern members of that species.

Such arguments are part of the practical taxonomy of the Neanderthals, but the real key to species identification and species separation is (at least theoretically) interbreeding. If the members of two groups can mate with each other and produce fertile offspring, and if these offspring can produce fertile offspring, the two groups are generally considered to be members of the same species. Therefore, the real taxonomic question becomes: Could Neanderthals and early modern humans interbreed?

Because it is difficult to determine whether fossil groups interbred with one another, Neanderthal taxonomy has been primarily determined by anatomic and presumed behavioral characteristics, such as those already discussed. That taxonomy has vacillated with changing interpretations of those characteristics. Neanderthals have been placed in their own species (*Homo neanderthalensis*) for much of their history, but they have been identified as a human subspecies (*Homo sapiens neanderthalensis*) at other times. The latter designation implies that the Neanderthals and modern humans (*Homo sapiens sapiens*) were members of the same species and therefore could interbreed.

Determination of the Neanderthals' taxonomic position is an integral part of arguments over the mechanism of the origin of modern humans. There are two main hypotheses for that origin: the replacement hypothesis of Christopher Stringer and the multiregional hypothesis vigorously supported by Milford Wolpoff. The replacement hypothesis is also designated "out-of-Africa" because it assumes that a population of African origin expanded throughout Africa, Europe, and Asia and rapidly replaced the more primitive humanlike species living there, including the Neanderthals. Whether this replacement was by competition or by more direct and violent means is undetermined. The multiregional hypothesis suggests that the widespread, more primitive humanlike populations evolved into modern humans rather than being replaced by new immigrants. Both hypotheses hold that the more primitive populations also originated in Africa and spread to Europe and Asia at a much earlier date.

Because the Neanderthals are the best known and best understood early human group, an understanding of the Neanderthal relationship is critical to an understanding of the evolutionary history of humanity. A Neanderthal contribution to modern human ancestry would support the multiregional hypothesis, and the lack of such a contribution would be consistent with the replacement hypothesis.

Advances of the Late Twentieth Century

By the 1990's, the Neanderthals were well established as a group related to modern humans, but the questions remained: How close was the relationship? Did the two groups interbreed? Were Neanderthals a part of the evolutionary heritage of modern humans? During the 1990's, improved techniques and additional fossil discoveries led to greater understanding of the Neanderthals but little consensus on these questions. A few examples will illustrate the situation.

In a 1996 study, Jean-Jacques Hublin and several coworkers determined that Neanderthals found at an archeological site in France made bone tools and wore decorative emblems on their bodies, behaviors not uncovered with older Neanderthal fossils. They concluded that the Neanderthals were influenced by early modern humans who lived in the same area at the same time and that a reasonably elaborate cultural exchange must have occurred between the two groups. However, based on the strikingly different anatomy of the two groups' inner ears, they also concluded that the Neanderthals and modern humans did not interbreed. The investigators reasoned that if interbreeding had occurred, the two groups would have shared a common ear structure.

In 1997, Matthias Krings, Svante Paabo, and their colleagues isolated and engineered deoxyribonucleic acid (DNA) from the mitochondria of Neanderthal bones and compared it to DNA from modern human mitochondria. They found the Neanderthal DNA to be quite different from that of modern humans and concluded not only that the two groups were different species but also that Neanderthals were not ancestral to modern humans.

In 1998, Daniel Lieberman proposed that a reduction in the length of the sphenoid bone during embryology can explain most differences between the two groups' skulls. The sphenoid is a bone in the skull of both Neanderthals and modern humans, and Lieberman showed it to be shortened in modern humans but not in Neanderthals. He hypothesized that the impact of shortening the sphenoid resulted in the modern human skull characteristics, while the longer sphenoid resulted in the Neanderthal skull. Based on the fundamental nature of the change, he concluded that Neanderthals do not belong to the same species as modern humans and were probably not ancestral to modern humans.

In 1999, Cidàlia Duarte, Erik Trinkaus, and several colleagues discovered the buried remains of a four-year-old child in southern Spain. The skeleton was estimated to be about 24,500 years old, and they interpreted its anatomy to be a mixture of modern human and Neanderthal characteristics. Most anthropologists agree that southern Spain supported Neanderthal populations longer than other parts of the world, perhaps as late as 27,000 years ago, and that modern humans and Neanderthals coexisted in the region. Duarte, Trinkaus, and their group suggested that the skeleton they found demonstrated that the two groups did interbreed and that Neanderthals were part of the ancestry of *Homo sapiens*.

Significance

Consideration of this short list of studies in the 1990's demonstrates the state of knowledge about the Neanderthals' place in human evolution. Viewed alone, each study seems to clinch the position of its authors. In fact, the first three reinforce one another so well that Neanderthals would seem to be eliminated from direct participation in the evolution of modern humans. However, Duarte and Trinkaus's study would seem to clinch the opposite position, that Neanderthals were direct participants in the evolution of modern humans. This situation symbolizes the absence of consensus in the field. There are also established scientists with alternative viewpoints for each of these studies. Lieberman himself is a coauthor of a letter that criticizes his own conclusions about the sphenoid and points to the need for a better understanding of the development of primate skulls to help clarify the situation.

A number of anthropologists have pointed out that Krings and Paabo's conclusions are extrapolated from a single, short segment of the mitochondrial DNA and that more extensive studies, including studies of DNA from the nucleus, are necessary before definitive conclusions can be drawn. In fact, nuclear DNA studies of modern humans have suggested that modern human DNA comes from a number of sources rather than a single African source as in the out-of-Africa hypothesis. Clearly, extensive DNA comparisons would be helpful; however, DNA from fossils is difficult to find and difficult to work with, so an extensive collection of such studies is not likely to accumulate.

Ian Tattersall, who rejects the Neanderthals as direct contributors to modern human evolution, has criticized Duarte and Trinkaus's data and their interpretation of the data. The verbal exchange has been bitter, not an unusual circumstance for disagreements in this field.

Although anthropologists have learned an enormous amount about the Neanderthals, their relationship to modern humans continues to escape consensus. This is, without question, a result of the difficulty of the problem and the tentative nature of the evidence. Most agree that the Neanderthals were a successful group closely related to modern humans. Everyone's hope is that more fossils, improved technology, and fresh insight will clarify the question because understanding the Neanderthals is likely to contribute to an understanding of humanity.

—Carl W. Hoagstrom

See also: Apes to hominids; Baboons; Cannibalism; Chimpanzees; Communication; Communities; Evolution: Animal life; Evolution: Historical perspective; Gorillas; Groups; Hominids; *Homo sapiens* and human diversification; Human evolution analysis; Infanticide; Learning; Lemurs; Mammalian social systems; Monkeys; Orangutans; Primates.

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NERVOUS SYSTEMS OF VERTEBRATES

Type of animal science: Anatomy
Fields of study: Developmental biology, evolutionary science, neurobiology, physiology

The anatomy of vertebrate nervous systems determines many of the behaviors and adaptative capabilities of animals. Its study is a prerequisite to understanding how it functions.

Principal Terms

AXON: an extension of a neuron's cell membrane that conducts nerve impulses from the neuron to the point or points of axon termination

GRAY MATTER: the part of the central nervous system primarily containing neuron cell bodies and unmyelinated axons

INTERNEURON: a central nervous system neuron that does not extend into the peripheral nervous system and is interposed between other neurons

MYELINATED AXON: an axon surrounded by a glistening sheath formed when a supporting cell has grown around the axon

NEURAL INTEGRATION: continuous summation of the incoming signals acting on a neuron

NEURONS: complete nerve cells that respond to specific internal or external environmental stimuli, integrate incoming signals, and sometimes send signals to other cells

NUCLEUS (pl. NUCLEI): cluster of neuron cell bodies within the central nervous system

TRACT: a cordlike bundle of parallel axons within the central nervous system

WHITE MATTER: the part of the central nervous system primarily containing myelinated axon tracts

Animals must be able to coordinate their behaviors and to maintain a relatively constant internal environment, despite fluctuations in the external environment, in order to survive and reproduce. To do so, animals must monitor their external and internal environments, integrate this sensory information, and then generate appropriate responses. The evolution of the vertebrate nervous system has provided for the efficient performance of these tasks.

The Pattern of the Vertebrate Nervous System

Although the various vertebrates show differences in the organization of their respective nervous systems, they all follow a similar anatomical pattern. The nervous system can be partitioned conveniently into two major divisions: the peripheral nervous system (PNS) and the central nervous system (CNS). These divisions are determined by their location and function. The CNS consists of the spinal cord and the brain. The PNS, that part of the nervous system outside the CNS, connects the CNS with the various sense organs, glands, and muscles of the body.

The PNS joins the CNS in the form of nerves, which are cordlike bundles of hundreds to thousands of individual, parallel nerve-cell (neuron) axons (long tubular extensions of the neurons) extending from the brain and spinal cord. The nerves extending from the spine are called spinal nerves, while those from the brain are called cranial nerves. The elements of the PNS include sensory neurons (for example, those in the eyes and in the tongue) and motor neurons (which activate muscles and glands, thereby causing some sort of action or change to occur). Most nerves contain both sensory and motor axons.

Thus, the PNS can be divided into two major subdivisions: sensory (or afferent) neurons and motor (or efferent) neurons. There is very little information-processing accomplished in the PNS. Instead, it relays both environmental information to the CNS (sensory function) and the CNS responses to the body's muscles and glands (motor function). Sensory neurons of the PNS are classified as somatic afferents if they carry signals from the skin, skeletal muscles, or joints of the body. Sensory neurons from the visceral organs (internal organs of the body) are called visceral afferents.

The PNS motor subdivision also has two parts. One is the somatic efferent nervous system, which carries neuron impulses from the CNS to skeletal muscles. The other is the autonomic nervous system (ANS), which carries signals from the CNS to regulate the body's internal environment by controlling the smooth muscles, the glands, and the heart. The ANS itself is subdivided into the sympathetic and parasympathetic nervous systems. These are generally both connected to any given target and cause approximately opposite effects to each other on that target (for example, slowing or increasing the heart rate).

The CNS, where essentially all information-processing occurs, has two major subdivisions: the spinal cord and the brain. Virtually all vertebrates have similarly organized spinal cords, with two distinct regions of nervous tissue: gray and white matter. Gray matter is centrally located and consists of neuron cell bodies and unmyelinated axons (bare axons without the glistening sheaths called myelin, created by supporting cells wrapping around the axons). White matter contains mostly bundles of myelinated axons (white because they have glistening myelin sheaths around them). Bundles of axons in the CNS are called nerve tracts. Within the spinal cord, these are either sensory tracts carrying impulses toward the brain, or they are motor tracts transmitting information in the opposite direction.

Interneurons are neurons positioned between two or more other neurons. They accept and integrate signals from some of the cells and then influence the others in turn. Interneurons are particularly numerous within the gray matter. In the spinal cord, they permit communication up, down, and laterally. Most axons in the cord's tracts belong to interneurons.

The Vertebrate Brain

The brain of vertebrates is actually a continuation of the spinal cord, which undergoes regional expansions during embryonic development. The subdivisions of the brain show more variety among vertebrate species than does the spinal cord. The brain has three regions: the hindbrain, the midbrain, and the forebrain. Their structures are complex, and various systems of subdividing them exist. The major components forming the brain regions are the hindbrain's medulla oblongata, pons, and cerebellum; the midbrain's inferior and superior colliculi, tegmentum, and substantia nigra; and the forebrain's hypothalamus, thalamus, limbic system, basal ganglia, and cerebral cortex.

The hindbrain begins as a continuation of the spinal cord called the medulla oblongata. Most sensory fiber tracts of the spinal cord continue into the medulla, but it also contains clusters of neurons called nuclei. The posterior cranial nerves extend from the medulla, with most of their nuclei located there.

Also in the medulla, and extending beyond it through the pons and midbrain, is the complexly organized reticular formation. This mixture of gray and white matter is found in the central part of the brain stem but has indistinct boundaries. Essentially all sensory systems and parts of the body send impulses into the reticular formation. There are also various nuclei within its structure. Impulses from the reticular formation go to widely distributed areas of the CNS. This activity is important for maintaining a conscious state and for regulating muscle tone.

Prominent on the anterior (front) surface of the mammalian medulla oblongata are the pyramids: tracts of motor fibers originating in the forebrain and passing without interruption into the spinal cord to control muscle contraction. These tracts cross to the opposite side of the medulla before entering the spinal cord, which results in each side of the forebrain controlling muscle contraction in the opposite side of the body.

Many sensory fibers from the spinal cord terminate in two paired nuclei at the lower end of the medulla, the gracile and cuneate nuclei. Axons leaving these nuclei cross to the opposite side of the medulla and then continue as large tracts (the medial lemnisci) into the forebrain. Thus, each side of the brain gets sensory stimuli mostly from the opposite side of the body.

Immediately above the medulla is the pons. It contains major fiber pathways carrying signals through the brain stem, and a number of nuclei, including several for cranial nerves. Some pontine nuclei get impulses from the forebrain and send axons into the cerebellum, again with a majority crossing to the opposite side of the brain stem before entering the cerebellum.

On the dorsal (back) side of the medulla and pons is the cerebellum, an ancient part of the brain that varies in size among vertebrate species. The cerebellum forms a very important part of the control system for body movements, but it is not the source of motor signals. Its gray matter forms a thin layer near its surface called the cerebellar cortex and surrounds central white matter.

Vertebrates with well-developed muscular systems (for example, birds and mammals) have a large cerebellum, with several lobes and convex folding of its cortex. It is attached to the brain stem by three pairs of fiber tracts called cerebellar penduncles, which transmit signals between the left and right sides of the cerebellum and between the cerebellum and motor areas of the spinal cord, brain stem, midbrain, and forebrain. The cerebellum times the order of muscle contractions to coordinate rapid body movements.

The Midbrain and the Forebrain

The midbrain is the second major region of the brain. The midbrain's dorsal aspect, called the tectum, is a target for some of the auditory and visual information that an animal receives. The paired inferior colliculi form the lower half of the tectum. They help to coordinate auditory reflexes to relay acoustic signals to the cerebrum. The two superior colliculi, the other half of the tectum, assist the localization in space of visual stimuli by causing appropriate eye and trunk movements. In lower vertebrates, the superior colliculi actually form the major brain target for visual signals. Connecting fiber pathways (commissures) link the individual lobes of each pair of colliculi.

The midbrain's tegmentum contains several fiber tracts carrying sensory information to the forebrain and carrying impulses among various brain-stem nuclei and the forebrain. Two cranial nerve nuclei concerned with the control of eye movements are also in the tegmentum. The reticular formation extends through the tegmentum and regulates the level of arousal. It also helps to control various stereotyped body movements, especially those involving the trunk and neck muscles. Finally, the tegmentum contains the red nucleus, which, in conjunction with the cerebellum and basal ganglia, serves to coordinate body movements. The substantia nigra functions as part of the basal ganglia to permit subconscious muscle control.

The forebrain, the final major area of the brain, differs from the lower areas in the more highly evolved functions it controls. It has a small but extremely important collection of about a dozen pairs of nuclei called the hypothalamus. These control many of the body's internal functions (such as temperature, blood pressure, water balance, and appetite) and drives (such as sexual behavior and emotions). Immediately above the hypothalamus lies the thalamus, another collection of more than thirty paired nuclei. The two thalami are the largest anterior brain-stem structures. Their ventral (front) parts relay motor signals to lower parts of the brain. The dorsal (back) parts transmit impulses from every sensory system (except olfaction, the sense of smell) to the cerebrum.

The limbic system is organized from a number of forebrain structures mostly surrounding the hypothalamus and thalamus. It determines arousal levels, emotional and sexual behavior, feeding behavior, memory formation, learning, and motivation. In general, the limbic system exchanges information with the hypothalamus and thalamus, and receives impulses from auditory, visual, and olfactory areas of the brain.

The basal ganglia function with the midbrain's tegmentum and substantia nigra, the cerebral cortex, the thalamus, and the cerebellum. These paired structures' functions are unclear, but it is known that they are important for adjusting the body's background motor activities, such as gross positioning of the trunk and limbs, before the cerebral cortex superimposes the precise final movements.

The cerebral cortex, like the cerebellum, is an ancient brain structure; however, it shows even more variation among vertebrate species than the cerebellum. It is formed into two hemispheres, which have olfactory bulbs projecting from their anterior (front) ends. The olfactory bulbs receive impulses from olfactory nerves for the sense of smell. The gray matter of the cerebral cortex is at the surface, enclosing the white matter (fiber tracts) beneath. The white matter connects various parts of the gray matter of one hemisphere with others within the same hemisphere and with corresponding parts in the opposite hemisphere. It also connects the cortical gray matter with lower brain structures. The ultimate control of voluntary motor activity resides in the motor areas of the cortex, although this control is heavily influenced by all the previously mentioned motor-control areas of the CNS.

Corresponding to each of the major senses (touch, vision, audition), there are primary sensory areas. These areas get the most direct input from their sensory organs by way of the corresponding sensory thalamic nuclei. Surrounding each primary area are association areas that receive a less direct sensory input but also more inputs from other sensory cortical areas. In general, the more intelligent an animal is, the larger are its association areas.

Studying the Nervous System

Many methods are used in studying vertebrate nervous systems. The level of description desired often determines the methods employed. For example, the gross structure visible to the unaided eye is usually investigated using the entire brain or spinal cord of the animal under study. It will then be photographed or drawn, sliced at various points either parallel to its long axis or across its long axis, and again photographed or drawn, until a complete series of such "sections" has been assembled.

To see finer structural details requires microscopes and very thin slices of nervous tissue (less than a millimeter in thickness). Preparation of such thin slices of this soft tissue requires that it first be either frozen or embedded in a block of paraffin wax. A special slicing device called a microtome is then used to produce the thin sections. For easy observation of different structural details (such as nuclei and fiber tracts), various chemical stains can be applied to the slices of tissue. These stains specifically color particular structural features green, blue, or some other color, thereby making them more visible.

Nervous tissue can be selectively and painlessly destroyed in an anesthetized animal by cutting a nerve trunk, inserting a fine wire electrode into the CNS and destroying tissue with electricity, or inserting a fine needle and then either injecting a chemical agent that kills nervous tissue or using a suction device to remove areas of tissue. The precision and reproducibility of wire or needle placement within the CNS is possible with a device called a stereotaxic frame. This instrument positions the animal's head and brain in an exact standard position. Then, wires or needles are inserted a certain distance away from (for example, behind, below, or to one side of) common landmarks on the skull. Stereotaxic atlases are books published by investigators for specific animals, with the exact coordinates in three-dimensional space for most CNS structures.

Following such procedures, the animal may be immediately and painlessly sacrificed, its brain or spinal cord removed, and the previously described thin slices prepared and stained. It may be necessary to allow the animal to recover from its surgical treatment, since several days or weeks must sometimes pass for the severed fiber tracts to degenerate. Then, following a painless lethal injection, the nervous tissue is prepared as above using special staining techniques, which reveal the pathways of degenerating nerve fibers in the tissue sections studied later under the microscope.

Although new techniques are constantly being developed, the preceding methods have revealed that the hundred billion neurons of the vertebrate nervous system form the most complexly organized structure known. Through this knowledge of the structure of the nervous system, it has become possible to study intelligently its functions, to diagnose its diseases, and to devise methods of treatment when it becomes damaged or diseased.

A Complex Structure

The vertebrate nervous system is the most complex structure known to humankind. The human nervous system, for example, has more than a hundred billion cellular elements, and perhaps a hundred trillion points of information exchange between these elements. It is impossible to understand the details of such a structure in the same way that one can understand the structure of a radio; however, the general organizational plan can be discovered through the application of modern neuroanatomical techniques.

It is a widely accepted tenet of physiology that in order to comprehend the functioning of an organ or an organ system, it is necessary to have a critical understanding of its structure. In fact, physiology and anatomy are inseparable because function (physiology) always reflects structure (anatomy): It is impossible for an organ to perform in any other way than its architecture permits.

The nervous system is the ultimate control and communication system in the vertebrate body. Its complexity allows the vast range of vertebrate behaviors, as well as the rapid and precise regulation of the body's internal environment. The most complex vertebrate nervous systems display self-consciousness, reasoning, and language capabilities.

There are many reasons for studying the organization of vertebrate nervous systems, ranging from purely theoretical (such as determining the mechanisms of memory recall or clarifying the evolutionary relationships among vertebrate species) to very practical (such as treatments for mental illnesses, precisely defining brain death, or designing better computers).

For many, the ultimate goal is to obtain a better understanding of the relationship between the brain and the mind. It has been proposed that the mind and mental processes are emergent properties that appear when a certain degree of organizational complexity within the nervous system has been reached. The individual elements of the nervous system (the neurons) are not the constituents that think or possess consciousness. These unique capabilities are achieved as a result of the specific connections between neurons and sensory organs, and among neurons themselves.

It does not matter whether one performs an analysis of a machine or of a nervous system; it can never be expected to reveal its soul or its consciousness—if they exist. All that can be done is to admire the intelligence of its designer or the wisdom of nature.

—John V. Urbas

See also: Anatomy; Brain; Development: Evolutionary perspective; Habituation and sensitization; Physiology; Reflexes.

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NESTING

Types of animal science: Behavior, ecology
Fields of study: Conservation biology, ecology, environmental science, ornithology, wildlife ecology

Many animals build structures to house their eggs and their young. Egg-laying animals, such as birds, amphibians, reptiles, and fish, build temporary nests for each year's young, while social insects, such as bees, build nests, or hives, as permanent homes. The nests of mammals may be permanent or temporary, depending on species.

Principal Terms

INSECTIVORE: any animal that feeds on insects
MALLARD: a species of wild duck
ORNITHOLOGY: the scientific study of birds
PHEROMONES: chemicals excreted by animals into their immediate environments to identify their territorial influence to other organisms
TERRITORIAL BEHAVIOR: the combination of methods and actions through which an animal or group of animals protects its territory from invasion by other species
TERRITORY: any area defended by an organism or a group of organisms for purposes such as mating, nesting, roosting or feeding

Many animals build structures to house and protect themselves, their eggs, and their young. Nest sites include grasses, shrubs, and trees, but also cracks in trees, holes in the ground and banks, crevices in rocks, under the surface of the ground, within the nests of other larger animals, or even near wasp nests. The nests of birds are the most obvious and well known, but many amphibians, reptiles, fishes, social insects, and mammals also build nests of varying degrees of complexity and permanence.

Bird and Insect Nests

Larger bird nests are constructed of various kinds of material, such as mud, bark, roots, twigs, hair, feathers, grass, plant fibers, shed snake skin, spider webs, lichens, or even prey remains and human-made material such as shiny, light, metallic ornaments. Many nests are cup-shaped and open, while fewer are oval, round or ball-shaped, closed, with an entrance at the side or the roof. An example of the latter is the nest of the South American ovenbird (*Furnarius*), which is often built with mud on top of a fence or another exposed surface. Others build a domed, oven-shaped nest out of plant material (the North American ovenbird) or huge nests suspended from the ends of tree branches (thorn birds). Some oceanic gulls (*Rissa tridactyla*) nest on narrow cliff ledges. Grassland and tundra owls nest on the ground or on an elevated hummock.

Some birds utilize amazing skill to construct their nests. The weavers are capable of tying knots with strips of grass or palm leaves and can prepare an exceptionally tight and compact nest. Birds of the genus *Orthotomus* are known as tailorbirds due to their ability to manufacture nests that are built in a pocket made by sewing together the edges of one or more leaves, using plant fibers. Some others (the family Contingidae) prepare very primitive and weak nests in an apparent effort to avoid the attention of predators, since they are attended minimally by the parents. Finally, woodcreepers nest in holes, while vireos weave a cup between the arms of a forked branch.

Most bird species in an area construct a unique nest in a unique location but use specific construction materials transferred from a distance. Generally, female geese and robins build their own nests, but among several other species the nest is built only by the male, who may use it as a sexual attractant in courtship. In these species, the female chooses a nest and indicates her choice by adding the nest lining.

Woodpeckers create cavities in trees, thus supplying safe nesting sites for a large number of birds. These include owls, parrots, parids, and flycatchers. In some areas, forest managers protect pileated woodpecker cavity trees and employ strategies to encourage continued production of new cavity trees where even smaller woodpecker species may find a haven for nesting.

Bird nests are most often made of plant material such as grasses, providing temporary homes for eggs and hatchlings. (NOAA Central Library)

Some insects, such as termites and carpenter bees, excavate a tunnel through solid wood. When termite colonies accidentally separate from an original nest they may migrate or march to a new nesting site and develop supplementary reproductives.

Mammal Nests

Most rodents build underground residences with a central chamber, where they sleep, raise their young, and hibernate, and other chambers that serve as food storage quarters. Moles build the most complex shelters among all insectivores. The shelters have an underground nest chamber that is surrounded by concentric rings of tunnels that are interconnected by radiating ones. The presence of shallow surface tunnels allows the marking of their course and the accumulation of a large amount of earth indicates the location of the deep tunnel system. The mole uses its forefeet like a shovel to dig in a type of body movement that resembles that of a breaststroke swimmer. Shrews dig surface nests, but they also use the runs of other animals, such as rodents, and line them with plant material on which they place their offspring. Hedgehogs and solenodons construct nest chambers, usually during their breeding season, which warm them during low-temperature periods. Tree shrews build their nests of leaves and other vegetation among tree roots or in cavities of fallen timber, but they immediately desert them when they feel that their residence has been stalked or even detected by a predator.

Ground squirrels and kangaroo rats transport enough seeds and other food in their cheek pouches to last them for a whole season. Excavation of one rat den where a single five-ounce kangaroo rat resided produced nine underground storage chambers with a total of thirty-five quarts of seeds. Kangaroo rats also dig one-cubic-inch storage pits that they stuff with seeds. In one case, an area of fifty-five square feet adjacent to a den had close to nine hundred such pits. This can have a devastating effect on local crops, so-called rodent plagues. On the other hand, such underground activity tends to germinate seeds for wild grass in the arid steppe regions of Central Asia. Squirrels carry acorns and nuts to hollow trees and barns, as well as to holes in the ground. They also have an amazing memory of where the food is stored, which keeps them alive during the harsh winter. Finally, the North American pack rat or trade rat is attracted by bright, shining objects (like the magpie) and carries them home to its nest, where it stores them together with tree sticks and grass.

Cooperative breeding appears to exist in the form of communal nesting among several mammal species. Tree squirrels (*Sciuridae sciurini*), fox squirrels (*Sciurus niger*) and gray squirrels (*Sciurus carolinensis*) form kin clusters among unrelated members of their own species during all seasons, especially in winter. Gray squirrels have shown an intense female-female bond in the formation of groups.

Territorial Behavior and Nesting

Animals appear to have a distinct notion of nesting and territory. The dog's persistent trend to leave its own scent during its evening walk is an example of territorial behavior, whereby an animal or group of animals, including insects, vertebrates, and other invertebrates, protects its territory from the invasion of other organisms. The boundaries may be clearly defined by the animal through sounds, such as a bird song, or scents, created by pheromones, which are secreted by specialized glands. The animal is often fierce in claiming its territory and may even fight and chase intruders to discourage them. Generally, the closer the requirements different species have of their territory, the less likely it is that they can coexist in the same area. Thus, species with similar requirements can sometimes live in the same area only if they differ in behavioral ways, such as in feeding and nesting patterns, as well as activity periods. However, should the food resources be limited in areas, such as the desert, direct competition may lead to violent confrontations. Invaders may attack eggs or young offspring to suppress their hunger.

Territorial behavior secures the ability for an animal to mate uninterrupted, raise its young in a less harmful area and keep other animals from devouring the food intended for the young. Often territories are temporary, as in the case of birds or mammals that protect the immediate feeding area until the young become old enough to be self-sufficient. That territory may even be identified as the nest itself, a phenomenon common with most birds. Territorial claims are often successful since the inhabitants of neighboring or overlapping territories may avoid each other, especially during the nonmating seasons.

Artificial Nesting

Humans living in suburban and rural areas can provide the appropriate housing for cavity nesting birds, and people do have the ability to become backyard bird specialists. Artificial structures have been used extensively in the United States and Canada to increase waterfowl production, although the users of the artificial materials are not always the animals for which they were intended. During a study conducted in 1995, in which artificial nesting structures were intended for mallard use, redheads were found to be using them for normal nesting. It is believed that a combination of elevated water surfaces and subsequent limited nesting in the emergent vegetation may have made these nesting sites attractive to the redheads, which has thus provided a new alternative for nesting redheads.

Another study on the excavation and use of artificial polystyrene snags by woodpeckers was performed in Eastern Texas over a period of five years in the early 1990's. Only half of the monitored downy woodpeckers (*Picoides pubescens*) appeared to use the artificial snags for cavity excavation and later for nocturnal roosting, but not for nesting. None of the other six woodpecker species in the area excavated cavities in the artificial snags. Other animals, however, used these excavated cavities in the artificial snags. These include Carolina chickadees (*Parus carolinensis*), prothonotary warblers (*Protonotaria citrea*), southern flying squirrels (*Glaucomys volans*) and red wasps (*Polistes* sp.).

The human factor may affect, directly or indirectly, the breeding success of animals. Possible biological effects of electromagnetic fields attributed to high-voltage transmission lines are suspected to reduce the reproductive success of birds whose nests are nearby, as in the case of tree swallows. Similar effects have been postulated for the terns, gulls, and other birds that live in areas such as the Gulf Coast, where oil tankers, commercial fishing vessels, yachts, and other pleasure boats have degraded the environment. A debate and controversy occurred in the 1990's in the Pacific Northwest of the United States, where environmentalists lobbied for the preservation of the nesting habitat of the spotted owl to the detriment of the local logging industry.

—Soraya Ghayourmanesh

See also: Birds; Courtship; Displays; Habitats and biomes; Home building; Insect societies; Insects; Mammals; Reproductive strategies; Tool use.

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NEUTRAL MUTATIONS AND EVOLUTIONARY CLOCKS

Type of animal science: Evolution
Fields of study: Ethology, genetics

A neutral mutation is a change in the nucleotide sequence of a gene that causes no change in the function of the protein coded by that gene. If most molecular mutations are neutral, as has been hypothesized, then they can be used as "clocks," because the number of changes in the gene (or gene product) is positively correlated with elapsed time.

Principal Terms

ALLELE: one of two or more alternate gene forms of a single gene locus

AMINO ACID: an organic molecule with an attached nitrogen group that is the building block of polypeptides

ELECTROPHORESIS: a technique for separating molecules when they are placed in an electrical field; the separation is usually based on their charge and weight

GENETIC CODE: the three-nucleotide base sequences (codons) that specify each of the twenty types of amino acids; there can be more than one codon for a particular amino acid

NUCLEIC ACID: an organic acid chain or sequence of nucleotides, such as DNA or RNA

PHYLOGENY: the evolutionary history of taxa, such as species or groups of species; order of descent and the relationships among the groups are depicted

POLYMORPHIC: a genotype or phenotype that occurs in more than one form in a population

The hypothesis has been advanced, primarily by Motoo Kimura of the National Institute of Genetics of Japan and Masatoshi Nei of the University of Texas, that the vast majority of polymorphisms that occur at the molecular level are selectively neutral. Two major categories of polymorphisms are involved. The first is attributable to changes in the nucleotide sequences of deoxyribonucleic acid (DNA). The second is isozymic variation, detectable by protein electrophoresis. Isozymic variation is usually caused by changes in the amino acid composition of the protein. Since amino acids are determined by the genetic code, this type of variation also ultimately depends on changes in DNA. The proponents of the neutral theory admit that most of the evolution that occurs on the nonmolecular level, such as changes in morphological and behavioral traits, is attributable to natural selection. On the molecular level, however, they believe that most of the changes are caused by chance.

Selection Versus Chance

Extensive variability has been found for both DNA sequences and isozymes within the majority of natural populations. Isozymic polymorphism, in which two or more variants of an enzyme occur within the same species, ranges from approximately 15 percent in mammals to approximately 40 percent in invertebrates. Isozymic variation, even within the same individual, ranges from about 4 percent in mammals to 14 percent in some insects. Variability in DNA sequences among individuals of the same species is even higher than those found for isozymes. Proponents of the neutral hypothesis hold that these levels of variability are too high to be attributable to selection, but instead, most variability at the molecular level is attributable to chance. The result, they say, has been a large amount of enzyme and DNA variability that is selectively neutral. They are neutral in the sense that their contributions to an organism's fitness are so small that their occurrence is attributable more to chance than to natural selection. Neutralists do not believe that most molecular mutations are neutral; they assume that most are harmful and are eliminated by natural selection. Rather, they believe that those that currently exist are adaptively equivalent. Proponents of the neutrality theory believe that changes in DNA and amino acid sequences are for the most part neutral, consisting primarily of the gradual random replacement of functionally equivalent alleles.

Although the neutral theory is able to explain much about molecular evolution, there are some issues that remain subjects of intense debate. It is known that some protein and gene variation is not neutral but, instead, under certain conditions, conveys selective advantages or disadvantages. In some organisms (for example, the Japanese macaque), there also appear to be more rare alleles than would be predicted by the neutrality hypothesis.

The Hypothesis of a Molecular "Clock"

If the neutrality theory of molecular evolution is correct, then changes in base sequences of DNA could act as evolutionary "clocks." This theory holds that because mutations change the DNA in all lineages of organisms at fairly steady rates over long periods of time, a clocklike relationship can be established between mutation and elapsed time. The number of base substitutions in the DNA is directly proportional to the length of time since evolutionary divergence between two or more species. The idea of molecular evolutionary clocks was forwarded in the early 1960's by Linus Pauling and Emile Zuckerkandl.

The molecular clock postulated by the neutrality hypothesis is not like an ordinary timepiece, which measures time in exact intervals. Rather, molecular changes occur as a stochastic clock, such as occurs during radioactive decay. Although there is some variability for this type of clock (it is slower or faster during some periods than others), it would be expected to keep relatively accurate time over millions of years. A potential problem arises, however, because the rate of "ticking" for the molecular clock is not the same at every position along the DNA molecule. The rate has been shown to be slow for DNA sequences that directly affect the function of a protein (for example, those at an enzyme's active site), while the rate of change has been faster for positions on the DNA that are selectively neutral, that is, where they have little or no affect on the protein's function.

In a molecular clock, the number of changes in a DNA or protein molecule are the "ticks" of the clock. The number of "ticks," in turn, estimates the extent of genetic differences between two species. With this knowledge, scientists can reconstruct phylogenies. The phylogenies are usually depicted as branching patterns, which are based upon differences in DNA base-pair sequences or amino acid sequences. They depict not only the order of descent but also the degree of relatedness.

When choosing alternative phylogenetic hypotheses, biologists usually follow the principle of Occam's razor—the simplest theory is chosen over more complex ones. Thus, the phylogenetic tree that requires the fewest mutations is preferred over those that require more mutations. By "calibrating" the molecular clock with other, independent, events, such as those obtained from the fossil record, the actual chronological times of divergence can be estimated.

For example, humans and horses differ by eighteen amino acids in the alpha chain of the blood protein hemoglobin. It has been estimated from the fossil record that humans and horses diverged from a common ancestor approximately ninety million years ago. Other evidence suggests that half the substitutions took place since the time of divergence. Since nine amino acids have changed over a ninety-million-year period, the rate of amino acid substitution would equal approximately one every ninety million years.

Since mutation rates are known to be different for different genes, the ticking rate for different genes or proteins would not necessarily be the same. For example, the rate of substitution for the genes coding for the protein histone H4 is lower than that for the genes coding for the protein gamma interferon. Yet when nucleotide substitution rates are averaged for a number of different proteins, there does appear to be a marked uniformity in the rate of molecular change over time; the ticking of a number of clocks can be averaged, leading to more accurate estimates for divergence times.

Advantages and Disadvantages of the Theory

Much of the early work was done on sequence changes in proteins; however, there is a drawback to protein clocks. Their usefulness is limited because the genetic material itself is not being examined but, rather, a product coded by genes. This means that some of the changes in the genetic material may not be detected. For example, because of the redundancy of the genetic code, there could be a number of changes that occur in the nucleotide sequence of DNA that would not result in changes in the amino acid composition in a protein. Consequently, there has been great interest in directly examining the DNA itself.

Because of the advent of recombinant DNA techniques, molecular clocks can be based on changes in the genetic material. DNA-DNA hybridization also involves the comparison of DNA sequences, although on a broader scale. The DNA-DNA hybridization technique is attractive because it effectively compares very large numbers of nucleotide sites, each of which is effectively a single data point. One of the criticisms of molecular clocks is that most genes have not been found to "tick" with perfect regularity over long periods of time. During some periods, the rate of change (primarily because of mutation) may be fast, while at other periods it may be significantly slower. By comparing very large numbers of nucleotides, which represent many genes, DNA-DNA hybridization measures the average rates of change, which will produce more uniform estimates.

The concept of a molecular clock has been criticized on a number of grounds. First, it assumes that evolution in macromolecules proceeds at an approximately regular pace, whereas morphological evolution is usually recognized as occurring irregularly. It is also clear that the clock can tick at different rates among different macromolecules, whether they be proteins or DNA. Another problem is that the rate of the molecular clock varies among taxonomic groups. For example, the insulin gene has evolved much more rapidly in the evolutionary line leading to the guinea pig than in some other evolutionary lines. There are also notable differences among different parts of molecules. This variability was evident when sequences were compared among the first molecules examined in the light of the molecular clock hypothesis, notably hemoglobin molecules and cytochrome c. Another criticism is that a number of processes, known collectively as molecular drive, perturb the clock.

Recent data, however, suggest that nucleotide substitution rates in organisms as different as bacteria, flowering plants, and vertebrates are remarkably similar. For example, the average rate of substitution at "silent sites" (those at which mutation in the DNA produces no change in the amino acid encoded) is 0.7 percent per million years in bacteria, 0.9 percent for mammals, and 1 percent for plants. This relatively equal substitution rate across broad taxonomic categories would support the concept of the constancy of molecular clocks.

Testing the Hypothesis

A number of types of molecular clocks have been hypothesized. In the first group are techniques that directly estimate differences in the sequences of nucleic acids that make up DNA or in amino acid sequences (which are determined by DNA). Other methods are less direct, such as DNA-DNA hybridizations and immunological techniques. All the techniques ultimately assay genetic differences caused by base pair changes in DNA. Sequence comparisons and DNA-DNA hybridization techniques are now used more extensively.

In sequence comparisons, nucleic acid replacement in DNA or amino acid replacement in proteins are compared between species. Nucleic acid substitutions can be assayed by using restriction enzymes that only recognize specific base sequences or by direct sequencing. Amino acid substitutions can be assayed by traditional biochemical techniques, through automated sequencers, or by mass spectrometers. In both types of sequence analysis, the assumption is made that the greater the number of substitutions, the greater the evolutionary distance between the species. In DNA-DNA hybridization, DNA molecules from individuals from two species are separated into individual strands at high temperatures. The strands are then mixed at a lower temperature. This promotes joining of the strands from the different organisms. The extent of rejoining (how tightly they bond together) will be dependent on the degree of nucleotide pairing that occurs. If the nucleotide sequences between the two species are very similar, the DNA strands will bond very tightly; if there is little similarity, the bonds will be weak. The extent of bonding is measured by the temperature at which the new DNA duplex dissociates, or "melts." The higher the melting temperature, the greater the nucleotide similarity between the DNA strands from different species. The nucleotide similarity is presumed to be related to the evolutionary distance between the species.

Uses of the Theory

The use of molecules as clocks, in spite of their imperfect nature, has proven to be a valuable tool for inferring phylogenetic relationships among species and in estimating their times of divergence. Molecular data can be used independent of morphological and behavioral data for establishing evolutionary relationships. Similarly, divergence times estimated from the fossil record can be clarified through the use of molecular clock data. Molecular clocks have had a significant impact on evolutionary studies of organisms ranging from bacteria to humans, and molecular data have been instrumental in changing some long-held phylogenetic views. For example, the data obtained from DNA-DNA hybridizations in birds have forced a major revision in bird taxonomy. Molecular clocks have been used to assign time scales to a large number of phylogenies. Some of the phylogenies are wide-ranging; approximate times of evolutionary divergence have been assigned to vertebrate species as diverse as sharks, newts, kangaroos, and humans. Others are more specific. Some of the best-known (and most controversial) work has been done on primates. In one set of experiments, the amino acid differences of serum albumin (a blood protein) were measured among different species of primates. By comparing the albumins of species whose divergence times were known from fossil evidence, researchers were able to "calibrate," or calculate, the mean rate of change for serum albumin. Previously, most anthropologists believed that humans and apes had diverged approximately twenty-five million years ago; the DNA-DNA hybridization data suggest a much more recent date of approximately five million years. Subsequent DNA studies have confirmed the latter estimate. This had led to a reevaluation of the primate fossil record and of the way in which primates have evolved, including humans.

Another group of researchers has used DNA-DNA hybridization data to calculate the divergence dates among different primate species. After calibrating the molecular clock with dates previously established from the fossil record, they estimated the following approximate divergence dates: Old World monkeys, 30 million years ago; gibbons, 20 million; orangutans, 15 million; gorillas, 7.7 to 11 million; and chimpanzees and humans, 5.5 to 7.7 million years ago. In contrast to earlier work, they concluded that humans and chimpanzees are genetically closer to each other than either are to gorillas. As with the serum albumin data, these new estimates of times and order of divergence led to a reexamination of primate evolution.

—*Robert A. Browne*

See also: Evolution: Historical perspective; Gene flow; Genetics; Hardy-Weinberg law of genetic equilibrium; Population analysis; Population genetics; Punctuated equilibrium and continuous evolution.

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NOCTURNAL ANIMALS

Type of animal science: Behavior
Fields of study: Anatomy, behavior, physiology, zoology

Nocturnal animals are those active during the night. They are specially adapted to living where there is little or no light. Often, such creatures find their way, locate food, and detect danger in nearly total darkness.

Principal Terms

AUDITORY: pertaining to hearing
DIURNAL: awake and functional during the daylight hours
ECHOLOCATION: sonarlike determination, from sound echoes, of the positions of unseen objects
PINNA (pl. PINNAE): a term indicating the external ear of an animal
PIT VIPER: a poisonous snake, such as a rattlesnake, which detects its prey via paired heat-sensing pits in its head
TYMPANIC MEMBRANE: the eardrum

At nightfall, many animals are just beginning to waken and to function. All of these night creatures are called nocturnal animals. Folklore often brands them as evil, inimical creatures. This is not so; they are merely different from diurnal animals, which are active during the day. Their activity during the hours of darkness is usually due to a combination of factors. First, the nocturnal animals may make use at night, without having undue competition, of food sources and habitats also used by diurnal animals. Second, they may be safe from many predators who would hunt them during the daylight hours. Finally, nocturnal animals may be predators which, at night, have much less competition for prey, or have a better chance to capture it, than in daylight.

Most nocturnal creatures are highly adapted to living under conditions in which there is little or no light. These adaptations enable nocturnal animals to find their way through the world, locate food, and detect danger in almost total darkness. Although the diurnal species outnumber the nocturnal creatures, almost every type of creature living on earth has a nocturnal version.

Image Not Available

More on Bat Echolocation

An echolocating bat, needing to find prey or to navigate, emits ultrasonic waves of frequencies between twenty-five and eighty kilocycles per second. These sound waves bounce back from nearby objects. The patterns of the returning waves give a bat an accurate estimation of the size, shape, texture, and location of all objects scanned in this way. The process is very sensitive. Bats using echolocation can detect items one to two millimeters thick, located six to seven feet away.

Several adaptations of the auditory systems of bats optimize the effectiveness of its echolocation. One of them is the huge size—sometimes nearly as large as the bat's skull—and very complex folding of each of the bat's external ears (pinnae). This size, folding, and great pinna mobility collect returning sound echoes quite well and help the bat to pinpoint their sources.

Another feature of bat echolocation has to do with the muscles of the bat's inner ear, which contract briefly as the ultrasound emissions occur. The contraction is essential to counter the great intensity of the emitted ultrasound. If these muscles did not contract upon sound emission, the bat would deafen itself with its echolocation calls. Another aspect of the bat ear that aids echolocation is the light weight of the tympanic membranes and bones of the bat's middle ear. These auditory modifications, away from the norm in other rodents, allow faint echoes returning to the ear to cause vibrations that can be sensed and used.

Regular Senses and Special Senses

Diurnal animals survive as long as they have a combination of senses that enables them to fit, successfully, into a daylight ecological niche. This usually includes ability to see adequately, to hear well, and to have a useful sense of smell. The ability to see, hear, and smell falls within a fairly broad range among earth's many successful diurnal animals. Furthermore, weaknesses in one sense, such as the nearsightedness of the rhinoceros, may be compensated for by enhancement of one or more of the other senses. In rhinos, both the ability to hear and to smell are very well developed.

Nocturnal animals live under conditions that are skewed far away from the normal visual range of diurnal organisms. They must operate under conditions where there is either very little light or even no light at all. For this reason, all animals that are nocturnal have at least one sense, sight, hearing, smell, taste, or touch, that is very highly developed, compared to those who are diurnal. These powerful sense adaptations enable them to survive well in the dark hours. The extent of such special sensory development varies, depending upon the organism, its needs, whether it also functions during the day, and the extent to which it is subject to predation by other organisms. In some cases, senses not seen among diurnal animals operate in nocturnal animals.

The large, carnivorous felines, such as lions, tigers, or leopards, are not threatened by many other organisms. They survive well by using a combination of keen eyesight and hearing, as well as an excellent sense of smell. To further aid these big cats, their eyes face forward, allowing very accurate judgment of distances when they hunt. They also rely quite heavily upon very acute reflexes, great strength, and the ability to run down most prey hunted.

An extreme in visual development is seen in owls, which are the ultimate nocturnal avian raptors and which function and hunt almost exclusively at night. These birds are gifted with superb vision, fine hearing, and a very wide visual and aural range. For example, the night vision of many owl species is one hundred times more sensitive than that seen in humans. In addition, owl hearing is very acute, aided in some cases by the possession of asymmetric skulls with the two ears at different places, further enhancing their hearing. Another adaptation that optimizes owl vision and hearing is the ability to turn the neck through 270 degrees. This gives owls the widest aural and visual range of all birds. It is therefore unsurprising that owls hear even the tiniest squeak or rustle made by their prey on the ground below them, and then very efficiently locate the prey by vision.

Bats function only after the sun sets, most often feeding on insects captured while in flight. They have good hearing. However, their eyes are small and they possess relatively poor vision. Perhaps this is why they have developed a special sense, sonarlike echolocation, to pinpoint insect prey in the dark night skies and to navigate. In bat echolocation, sounds (often clicks) are emitted from the larynx or nose of the bat, depending upon species. These sounds then strike insects (and rocks or trees), and echoes bounce back to the bat's ears. The bat then uses the echoes to find its prey. Many bats have developed means to direct the sounds they make for echolocation. For example, bats with skin flaps on the nose often use them to direct sounds in the nasal passages. The excellent hearing found in bats is aided by their large, mobile, external ears. Bats are not "blind as bats." For example, they can use vision to navigate their way home, and often do. Some nocturnal birds, such as the nightjar, also use echolocation to capture their prey.

Rattlesnakes and many other snakes locate their prey in total darkness in another way that involves special sense organs. This process is most sensitive in poisonous snakes called pit vipers. These snakes have two heat-sensitive pits located on the sides of their heads. The pits help them to detect small animals which are their prey, such as rodents or birds. The detection is possible because the prey sought are warmer than their surroundings. The pit viper heat sensors are large groups of nerve endings so sensitive that they can detect the body heat of a rodent over a foot away. The heat discrimination of the pit nerve endings is huge and they can identify a temperature difference of less than one hundredth of a degree.

Nocturnal Animal Habitats

People generally think of nocturnal animals as living in the wild. However, many live cheek-by-

Nocturnal Animals

Bats sleep in caves or trees by day and seek food soon after sunset. Most eat insects, which they capture while in flight, via echolocation. Here, sound is emitted in flight, strikes insects, and then echoes bounce back. The bat uses the echoes to find its prey.

Gerbils, Jerboas, and other rodents burrow in the ground for safety from predators and to escape the heat of their desert environment. They come out at night to eat insects and plants. Their large eyes give them good night vision and their huge ears pick up very faint sounds.

Leopards and other big cats stalk herbivore prey in the dark. They depend on their ability to stalk prey silently or to ambush them, very acute hearing, good night vision, and their capacity for quick movement.

Nightjars are nocturnal insect-hunting birds. They fly with mouths open and eat bugs in their paths. They, like bats, use echolocation to find food.

Owls of woods, forests, and barns roost during the day. At night they hunt mice, voles, and small birds. First, an owl listens for tiny squeaks or rustling sounds from the ground. When these signals occur, the owl attacks silently. Its predation is aided by night vision one hundred times more light-sensitive than in humans, and a wide field of vision.

Scorpions and some Spiders are nocturnal, sleeping in burrows by day. At night they catch prey in similar ways. Scorpions await the close approach of insect prey. Then they move quickly, catch prey in their pincers, paralyze, and kill them. Trapdoor spiders speed out of partly open, sand-covered, silk burrow doors, seize, and kill insects that come close.

Tarsiers are small nocturnal primates. They sleep by day, and at night eat leaves, bugs, and frogs. Nocturnal existence protects them from predation. Large, sensitive, forward-facing eyes and very acute hearing via large, mobile ears help them to obtain food and to move effortlessly in dark trees.

jowl with humans in parks, gardens, and empty lots in urban and suburban areas. Just a few examples are badgers, raccoons, deer, and foxes. People often see them and view them as pests or problems because they raid gardens and garbage cans, and some kill pets. Another problem associated with nocturnal animals is that they can carry severe, contagious diseases (for example, foxes and raccoons may carry rabies) which can be fatal to people. Finally, many nocturnal species are on the verge of extinction. These range from insects to the big cats. A few nocturnal species, such as tigers, are finally being covered by international conservation agreements, perhaps just in time. The others should be helped to survive, too.

—Sanford S. Singer

See also: Adaptations and their mechanisms; Bats; Bioluminescence; Competition; Ears; Ecological niches; Ethology; Eyes; Habitats and biomes; Hearing; Owls; Predation; Rhythms and behavior; Sense organs; Sleep; Urban and suburban wildlife; Vision.

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NONRANDOM MATING, GENETIC DRIFT, AND MUTATION

Type of animal science: Evolution
Fields of study: Ecology, ethology, genetics, population biology

Nonrandom mating, genetic drift, and mutation are three mechanisms, besides natural selection and migration, that can change the genetic structure of a population.

Principal Terms

ALLELE: alternative forms of a gene for a particular trait

ASSORTATIVE MATING: a type of nonrandom mating that occurs when individuals of certain phenotypes are more likely to mate with individuals of certain other phenotypes than would be expected by chance

GAMETE: a haploid sex cell that contains one allele for each gene; sperm and egg cells are gametes that fuse to form a diploid zygote

GENETIC VARIATION OR DIVERSITY: the total number and distribution of alleles and genotypes in a population

GENOTYPE: the complete genetic makeup of an organism, regardless of whether these genes are expressed

HETEROZYGOTE: a diploid organism that has two different alleles for a particular trait

HOMOZYGOTE: a diploid organism that has two identical alleles for a particular trait

INBREEDING: mating between relatives, an extreme form of positive assortative mating

PHENOTYPE: the expressed genetic traits of an organism

Evolution is a process in which the gene frequencies of a population change over time, and nonrandom mating, genetic drift, and mutation are all mechanisms of genetic change in populations. These mechanisms violate the assumptions of the Hardy-Weinberg model of genetic equilibrium by increasing or decreasing the frequency of heterozygote genotypes in the population.

Nonrandom mating occurs in a population whenever every individual does not have an equal chance of mating with any other member of the population. While many organisms do tend to mate randomly, there are some common patterns of nonrandom mating. Often, individuals tend to mate with others nearby, or they may choose mates that are most like themselves. When individuals choose mates that are phenotypically similar, positive assortative mating has occurred. If mates look physically different, then it is negative assortative mating. Population geneticists use the term "assortative" because it means "to separate into groups," usually in a pattern that is not random. The terms "positive" and "negative" refer to the probability that mated pairs have the same phenotype more or less often than expected by chance. Two color varieties of snow geese (*Chen hyperborea*), blue and white, are commonly found breeding in Canada, and they show positive assortative mating patterns based on color. The geese tend to mate only with birds of the same color; blue mate with blue and white with white. Since a bird's color (phenotype) is determined by the presence of a dominant blue color allele, matings between similar phenotypes are also matings between similar genotypes. Matings between similar genotypes cause the frequency of individuals that are homozygous for the blue or the white allele to be greater, and the frequency of heterozygotes to be less than if mating were random and in Hardy-Weinberg equilibrium. Negative assortative mating increases the frequency of heterozygote genotypes in the population and decreases homozygote frequency. Assortative mating does not change the frequency of the blue or white alleles in the goose population; it simply reorganizes the genetic variation and shifts the frequency of heterozygotes away from Hardy-Weinberg equilibrium frequencies.

Inbreeding is the mating of relatives and is similar to positive assortative mating because like genotypes mate and result in a high frequency of homozygotes in the population. In assortative mating, only those genes that influence mate choice become homozygous, but inbreeding increases the homozygosity of all the genes. High homozygosity means that many of the recessive alleles that were masked by the dominant allele in heterozygotes will be expressed in the phenotype. Deleterious or harmful alleles can remain hidden from selection in the heterozygote, but after one generation of inbreeding, these deleterious alleles are expressed in a homozygous condition and can substantially reduce viability below normal levels. Low viability resulting from mating of like genotypes is called inbreeding depression.

Genetic Drift and Mutation

Genetic drift, like positive assortative mating, reduces the frequency of heterozygotes in a population, but with genetic drift, the frequency of alleles in a population changes. Nonrandom mating does not change allele frequency. Genetic drift is sometimes called random genetic drift because the mechanism of genetic change is random and attributable to chance events in small populations, such that allele frequencies tend to wander or drift. Statisticians use the term "sampling effect" to describe observed fluctuations from expected values when only a few samples are chosen, and it is easy to observe by tossing a coin. A fair coin flipped a hundred times would be expected to produce approximately fifty heads and fifty tails, plus or minus a few heads or tails. Yet, if the coin is flipped only four times, it is not too surprising to get four heads or four tails. The probability of getting either all heads or all tails on four consecutive flips is one out of eight, but the probability of getting all heads or all tails decreases to much less than one in a billion as the sample size increases from four to a hundred tosses. Similarly, it is much easier for nonrandom events to occur in small populations than in large populations. If a population has two alleles with equal frequency for a particular trait, then the result of random mating can be simulated by tossing a coin. The frequency of each allele in the next generation would be determined by flipping the coin twice for each individual, since sexually reproducing organisms have two alleles for each trait, and counting the number of heads and tails. In a small population, only a few gametes, each containing one allele for the trait, will fuse to form zygotes. Chance events can cause the frequencies of alleles in a small population to drift randomly from generation to generation; often one allele is lost from the population.

In small populations with fewer than fifty mating pairs, alleles may be eliminated in fewer than twenty generations by random genetic drift, leaving only one allele for a particular trait in the population. Thus, all individuals would be homozygous for the remaining allele and genetically identical. Theoretically, in any finite population random genetic drift will occur, but it is usually negligible if the population size is greater than a hundred. Sometimes, disasters or disease may drastically reduce the population size, causing a bottleneck effect. The bottleneck in population size reduces genetic variability in a population because there are only a few alleles and results in random genetic drift. Many islands and new populations are established by a small group of founders that constitute a nonrandom genetic sample because they have only a fraction of the alleles from the original large population. Founder effects and bottleneck effects are phenomena that result in a loss of heterozygosity and decreased genetic variability because of the chance drift in allele frequency away from Hardy-Weinberg equilibrium values in small populations.

Mutations are any changes in the genetic material that can be passed on to offspring. Some mutations are changes at a single point in the chromosome, while at other times, pieces of the chromosome are removed, extra pieces are added, or pieces are exchanged with other chromosomes. All these changes could result in the formation of new alleles or could change one allele into a different allele. The random mistakes in the chromosomes occur at the molecular level, and only later are the changes in information or alleles translated into phenotypic differences. Thus, mutation is the ultimate source of genetic variability and is random with respect to the needs of the organism. Most mutations are lethal and are never expressed, but nonlethal mutations provide the necessary variation for natural selection. Even though mutations are very important for evolution, they have only a small effect on allele and genotype frequencies in populations because mutation rates are relatively low. If an allele makes up 50 percent of the gene pool and mutates to another allele once for every hundred thousand gametes, it would take two thousand generations to reduce the frequency of the allele by 2 percent. The net effect of mutations is to increase genetic variability, but at a very slow rate.

Studying Genetic Variability

Population geneticists use a wide variety of laboratory, field, and natural experiments to investigate genetic variability. Natural experiments are situations that have developed without a scientist intentionally designing an experiment, but conditions are such that scientists can test a theory. Researchers have used known pedigrees or ancestral histories of zoo animals and have found that mortality rates of inbred young are often two to three times higher than for noninbred young. Population geneticists use pedigrees to calculate the probability that two alleles are identical by descent; this research provides an index of the amount of inbreeding in a population.

The study of random genetic drift is usually carried out in the laboratory. Scientists often use small organisms that reproduce quickly, such as fruit flies (*Drosophila melanogaster*), to conserve space and save time. In a 1956 study of eye color conducted by Peter Buri, after only eighteen generations and sixteen fruit flies per population, more than half of the 107 populations started had only one of the two alleles for eye color.

Mutations are so rare that even fruit flies reproduce too slowly for scientists to study the effects of mutations on populations, even though much is known about the mechanism of mutation by studying *Drosophila*. Small bacterial growth chambers can hold many millions of bacterial cells, and, since they reproduce quickly, even mutations that occur in only one in a million cells can be detected. In 1955, it was found that mutation rates were very low in bacteria until caffeine was added to the growth chamber, whereupon mutation rates increased tenfold. Any chemical or type of radiation that can cause mutations is called a mutagen. Electrophoresis has also been a useful tool for the study of nonrandom mating, genetic drift, and mutations, because allele and genotype frequencies can be determined from samples of the population and unique alleles can be identified.

The Dangers of Inbreeding

Most governments and religions forbid marriages between close relatives because matings between first cousins result in a 20 percent decrease in heterozygosity; for those between brothers and sisters, there is an 80 percent decrease in heterozygosity. The decrease in heterozygosity and genetic variation and increase in homozygote frequency often result in inbreeding depression because deleterious recessive alleles are expressed. All inbreeding is not undesirable; many of the prizewinning bulls and pigs at state fairs have some inbreeding in their pedigrees. Most breeds of dogs were produced by breeding close relatives so that the offspring would have particular traits.

Zookeepers and others that breed and protect rare and endangered species must continually be concerned about the negative effects of both inbreeding and genetic drift. Most zoos are lucky if they have two or three pairs of breeding adults, and total population sizes are usually very small compared to those of natural populations. These conditions mean that inbreeding may reduce the vigor of the population and genetic drift will reduce the diversity of alleles in the population, thus reducing the chances of survival for the captive species. There is hope for rare and endangered species if independent inbred lines are crossed, thus reducing the effects of inbreeding depression, and if breeding adults from other zoos or populations are traded occasionally, thus increasing the effective population size.

Mutations are the ultimate source of genetic variation and so are very important in the study of evolution, but the population-level effects of one mutation are difficult to study because of the low frequency of natural mutations. Certain nonlethal mutations may have little evolutionary impact but may be important medically because spontaneous mutations result in hemophilia or dwarfism (achondroplasia) in more than 3 out of 100,000 cases. As exposure to background radiation and chemical levels increases, mutation rates are likely to increase, as well as the incidence of mutation-related diseases.

—William R. Bromer

See also: Convergent and divergent evolution; Evolution: Historical perspective; Hardy-Weinberg law of genetic equilibrium; Mutations; Population genetics; Punctuated equilibrium and continuous evolution; Reproduction.

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NOSES

Types of animal science: Anatomy, behavior, development, evolution
Fields of study: Anatomy, biochemistry, biophysics, cell biology, developmental biology, genetics, herpetology, histology, immunology, neurobiology, ornithology, pathology, physiology, zoology

The nose is the major access channel for the sense of smell. The nose signals danger by detecting the smell of spoiled food, smoke, or natural gas. The nose also warms and humidifies the air as it moves onto lungs. It filters out particles and bacteria found in the inspired air and so prevents these particles from entering the lungs.

Principal Terms

MUCUS: the watery material covering the internal nasal structures that aids in humidification, warming, and particle filtration
OLFACTION: the sense of smell
SEPTUM: the bony structure that divides the nose into two sections
TURBINATES: bony structures that define the internal nasal anatomy

In vertebrates, the back of the throat is connected to the outside air through a passageway called the nose. The outside opening of the nose is referred to as the external naris, whereas the opening from the nose to the back of the throat is called the internal naris. In reptiles and amphibians, air drawn into the lungs passes through the external naris and into a tubelike structure which is the simplest form of a nose. In animals like the salamander, the nasal air passageway is a straight tube. Air exits this tube via the internal naris where it proceeds into the back of the throat. In some amphibians, such as the bullfrog, the channel between the external and internal naris has a bony bump on the floor of the nasal passageway. This bump, called the ementia, apparently functions like a baffle plate, so that the incoming air stream is deflected. As a result of this deflection, air moving through the nose is turbulent. This turbulence likely increases the ability to detect smells as well as improves the efficiency of the other nasal functions.

In mammals, the internal anatomy of the nose is defined by bony structures called turbinates. These turbinates produce multiple and convoluted air flow paths for the inspired air. As in the frog, these convoluted flow paths facilitate the various nasal functions.

In mammals the nose is divided into two halves along the midline by a bony structure called the nasal septum. In some mammals, such as the rat, the septum is incomplete, and so there is some mixing in the nose of air that comes into the left and right nostrils.

Air entering the nose travels in the airspace between the turbinates and the nasal septum. The surface of these nasal structures has a very rich blood supply, and so blood flow to these areas can be quickly changed. By changing the amount of blood flow to the nasal structure, the diameter of the nasal airspace itself can be quickly changed. Because of the speed and amount of diameter change that can occur in these areas they are called nasal "swell spaces."

Heat, Humidity, and Purification

When cold air enters the nose, it causes the blood flow to the swell spaces to increase dramatically. This causes a swelling of the nasal tissue and so reduces the size of the airspace through which the incoming air must travel. Because the air passageways are now more narrow, more heat can be transferred from the blood stream to the incoming air. Thus, the cold air is effectively warmed before

All canids, including wolves, have exceptionally keen senses of smell. (PhotoDisc)

it enters the lungs. When air that is warmer than the body temperature enters the nose the reverse happens, and the nasal air passageways are made wider.

The material covering the turbinates and nasal septum is called the mucus. This mucus layer is mostly composed of water and serves to humidify the incoming air. When the air is dry, water is evaporated from the mucus into the inspired air. When the air is dry, a considerable quantity of water can be lost through the nose. For animals living in dry, desert conditions, the nasal humidification process is critical because it is necessary to save every drop of water while still humidifying the incoming air. When these animals take air into the lungs, the inspired air passes through the extensive turbinate structures of the nose where it is humidified by the evaporation of water from the nasal mucus. As evaporation takes place, the surface of the mucus is cooled. When it is time to discharge the air from the lungs, the expired air passes over the cooled surface of the mucus. As a result, water in the inspired air is now picked up by the cooled surface and so it is not lost in the expired air. This type of water conservation method has been seen in kangaroo rats living in the deserts of Australia and in certain birds, such as the cactus wren, which inhabit warm, dry areas.

In addition to supplying water for humidification purposes, the nasal mucus serves as a trap for particulate matter. Smoke and dust particles and even airborne bacteria are trapped in the mucus of the nose. Beneath the nasal mucus is a layer of cells that contain hairlike protrusions called cilia. As the cilia of these cells beat, they create a wavelike action in the mucus. The mucus is thus moved through the nose and to the back of the throat. Once in the throat the mucus is swallowed and the particles and bacteria are dealt with in the stomach. The movement of the nasal mucus is an ongoing process and so trapped particles are continually being removed from the nose. There are also white blood cells and enzymes found in the mucus that destroy bacteria.

When particles (and sometimes even air) touch parts of the nose a sneeze occurs. In this case, breathing is stopped and air is forcibly expelled from the lungs at a high flow rate. The sneeze is an attempt to expel the particles from inside the nose.

However, when the odorant is very foul or stings the nose, breathing may be temporarily stopped. This protects the lungs from potentially damaging chemicals. The detection of potentially harmful chemicals occurs both through the smell receptors as well as through pain receptors that are found in the nose.

—David E. Hornung

See also: Anatomy; Beaks and bills; Bone and cartilage; Brain; Circulatory systems of invertebrates; Circulatory systems of vertebrates; Claws, nails, and hooves; Digestive tract; Ears; Endoskeletons; Exoskeletons; Eyes; Fins and flippers; Immune system; Kidneys and other excretory structures; Lungs, gills, and tracheas; Muscles in invertebrates; Muscles in vertebrates; Nervous systems of vertebrates; Physiology; Reproductive system of female mammals; Reproductive system of male mammals; Respiratory system; Sense organs; Skin; Smell; Tails; Teeth, fangs, and tusks; Tentacles; Wings.

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NUTRIENT REQUIREMENTS

Type of animal science: Physiology
Fields of study: Biochemistry, physiology

All animals depend on external sources of nutritional raw materials for energy, growth, maintenance, and functioning.

Principal Terms

CARBOHYDRATE: an organic molecule containing only carbon, hydrogen, and oxygen in a 1:2:1 ratio; often defined as a simple sugar or any substance yielding a simple sugar upon hydrolysis

LIPID: an organic molecule, such as a fat or oil, composed of carbon, hydrogen, oxygen, and sometimes phosphorus, that is nonpolar and insoluble in water

MINERAL: one of the many inorganic elements other than carbon, hydrogen, oxygen, and nitrogen that an organism requires for proper body function

PROTEIN: an organic molecule containing carbon, hydrogen, oxygen, nitrogen, and sulfur and composed of large polypeptides in which over a hundred amino acids are linked together

VITAMIN: an organic nutrient that an organism requires in very small amounts and which generally functions as a coenzyme

Food, used to provide material for production of new tissue and the repair of old tissue as well as used as an energy source, is obtained from a variety of plant, animal, and inorganic sources. Regardless of the source, food must provide its consumer with a sufficient amount of the essential nutrients. A nutrient is any substance that serves as a source of metabolic energy, raw material for growth and repair of tissues, or general maintenance of body functions.

General Nutritional Requirements

Animals differ widely in their specific nutritional needs, depending on the species. Within any given species, those needs may vary according to variations in body size and composition, age, sex, activity, genetic makeup, and reproductive functions. A small animal requires more food for energy per gram of body weight than does a larger animal, because the metabolic rate per unit of body weight is higher in the smaller animal. Likewise, an animal with a cool body temperature will have less energy needs and require less food than an animal with a high body temperature. An egg-producing or pregnant female will require more nutrients than a male. In order for an animal to be in a balanced nutritional state, it must consume food that will supply enough energy to supply power to all body processes, sufficient protein and amino acids to maintain a positive nitrogen balance and avoid a net loss of body protein, enough water and minerals to compensate for losses or incorporation, and those essential vitamins that are not synthesized within the body.

Activities such as walking, swimming, digesting food, or any other activity performed by an animal require fuel in the form of chemical energy. Adenosine triphosphate (ATP), the body's energy currency, is produced by the cellular oxidation of small molecules, such as sugars obtained from food. Cells usually metabolize carbohydrates or fats as fuel sources; however, when these carbon sources are in short supply, cells will utilize proteins. The energy content of food is usually measured in kilocalories, and it should be noted that the term "calories" listed on food labels is actually kilocalories (1 kilocalorie = 1000 calories). Cellular metabolism must continually produce energy to maintain the processes required for an animal to remain alive. Processes such as the circulation of blood, breathing, removing waste products from the blood, and in birds and mammals, the maintenance of body temperature, all require energy. The calories required to fuel these essential processes for a given amount of time in an animal at rest is called the basal metabolic rate (BMR). For a resting human adult, the BMR averages from thirteen hundred to eighteen hundred kilocalories per day. As physical activity increases, the BMR increases.

Energy balance requires that the number of calories consumed for body maintenance and repair and for work (metabolic and otherwise) plus the production of body heat in birds and mammals be equal to the caloric intake over a period of time. An insufficient intake of calories can be temporarily balanced by the utilization of storage fats, carbohydrates, or even protein, and will result in a loss of body weight. On the other hand, an excessive intake of calories can lead to the storage of energy sources. Animals normally store glycogen, but when the glycogen stores are full, food molecules, such as carbohydrates and protein, will be converted to fats.

Nutrient Molecules

Proteins are composed of long chains of amino acids and serve a number of important functions in all living organisms, but they are primarily used as structural components of soft tissues and as enzymes. Proteins can also be utilized as energy sources if they are broken down into amino acids. Animal tissues are composed of about twenty different amino acids. The ability to synthesize amino acids from other carbon sources, such as carbohydrates, varies among species, but few, if any, animal species can synthesize all twenty required amino acids. Those amino acids that cannot be synthesized by an animal, but are required for the synthesis of essential amino acids, are the so-called essential amino acids, and must be included in the diet. Humans, for example, require nine essential amino acids. Both plant and animal tissues can serve as protein sources, but animal protein generally contains larger quantities of the essential amino acids.

Carbohydrates are primarily used as immediate sources of chemical energy, but they can also be converted to metabolic intermediates or fats. Some carbohydrates are also structural components of larger molecules. For example, the nucleic acids deoxyribonucleic acid (DNA) and ribonucleic acid (RNA) contain the sugars deoxyribose and ribose, respectively, as an integral component of their structure. Most animals can also convert proteins and fats into carbohy-

Feeding Mechanisms

Since most animals cannot absorb nutrients directly from their environments, they must exert energy in order to obtain food. Although animals show tremendous diversity in their methods of obtaining food, most feeding habits can be classified in one of three different types. Many animals, particularly those living in aquatic environments, feed on particulate matter, the free-floating material made up of plankton, microscopic aquatic life-forms, and organic remains of dead and decaying plants and animals. Some of the animals utilize a technique referred to as suspension feeding, in which the food material is drawn into the digestive tract by currents created by external structures, such as cilia or setae. Other particulate feeders feed on deposits of detritus (decaying organic matter) that accumulate at the bottom of lakes or oceans.

A second feeding method involves the consumption of food masses. Most of these animals utilize specialized adaptions that allow them to capture and manipulate solid food. Herbivores have special adaptions for cutting and crushing or grinding plant tissues, while carnivores such as predators must have the ability to capture, hold, and either swallow the prey whole or shred it into smaller pieces. Feeding on liquids is a third type of feeding habit. This method, which involves the sucking of fluids from a host plant or animal, is utilized primarily by parasites, but it can also be observed in certain insects.

drates. The principle sources of carbohydrates are the sugars, starches, and cellulose in plants and the glycogen stored in animal tissue.

Lipids are an important and essential component of all biological membranes. In addition, several animal hormones, such as the sex hormones, are lipoidal in nature. Fats and lipids are also especially suitable as concentrated energy reserves, because each gram of fat supplies twice as much energy as a gram of carbohydrate or protein and does not have to be dissolved in water. Hence, animals commonly store fat for times of caloric deficit when energy expenditure exceeds energy uptake. Some animals, such as migratory birds and hibernating mammals, store large quantities of fat to offset the times that they are not actively feeding. Lipid molecules include fatty acids, monoglycerides, triglycerides, sterols, and phospholipids.

All animals require an adequate supply of essential inorganic minerals. Carbonate salts of the metals calcium, potassium, sodium, and magnesium as well as some chloride, sulfate, and phosphate are important constituents of intra- and extracellular fluids. Calcium phosphate is present as hydroxyapatite, a crystalline material that gives hardness and rigidity to the bones of vertebrates and the shells of mollusks. Certain metals, such as copper and iron, are required for oxidation-reduction reactions and for oxygen binding and transport. The catalytic function of many enzymes requires the presence of certain metal atoms. Animals require moderate amounts of some minerals and only trace quantities of others.

Animals require a variety of vitamins, diverse and chemically unrelated organic substances. Vitamins primarily function as coenzymes for the proper catalytic activity of essential enzymes. As with amino acids, the ability to synthesize differ-

Functions of Essential Minerals and Vitamins

Minerals

Calcium: nerve and muscle function, blood clotting, bone and tooth formation

Chlorine: acid-base balance, gastric juice

Chromium: associated with glucose and energy metabolism

Cobalt: component of Vitamin B_{12}

Fluorine: maintenance of tooth structure

Iodine: component of thyroxine, a thyroid hormone

Iron: component of essential enzymes and electron carriers in energy metabolism

Phosphorus: transfer of chemical energy, bone and tooth formation, nucleic acid synthesis

Potassium: proper nerve function, acid-base balance, water balance

Selenium: component of essential enzymes and functions in association with vitamin E

Sodium: proper nerve function, water balance, acid-base balance

Sulfur: component of certain amino acids

Copper, Magnesium, Manganese, Molybdenum, Zinc: components of essential enzymes

Vitamins

Vitamin A (Carotene): formation of visual pigments, maintenance of certain membranes

Vitamin B_1 (Thiamine), Vitamin B_2 (Riboflavin), Niacin: coenzymes for certain enzymes in energy metabolism

Vitamin B_6 (Pyridoxine): coenzyme for amino acid synthesis and fatty acid metabolism

Vitamin B_{12} (Cyanocobalamin): required for nucleoprotein synthesis

Vitamin C (Ascorbic acid): vital to collagen formation, serves as an important antioxidant

Vitamin D (Calciferol): increases calcium absorption from gut, bone and tooth formation

Vitamin E (Tocopherol): maintains pregnancy in mammals; serves as an important antioxidant

Vitamin K (Naphthoquinone): required for synthesis of a protein necessary for blood clotting

Biotin: coenzyme for enzymes associated with protein synthesis

Folic acid: required for nucleoprotein synthesis and formation of red blood cells

Pantothenic acid: forms part of coenzyme A associated with energy metabolism ent vitamins from other carbon sources varies among species. Those essential vitamins that cannot be synthesized by the animal itself must be obtained from other sources, primarily from plants but also from dietary animal flesh or from intestinal microoganisms. Vitamin C (ascorbic acid) can be synthesized by many animals, but not by humans. Vitamins K and B are produced by intestinal bacteria in humans. Vitamins such as A, D, E, and K are fat soluble and can be stored in fat deposits within the body; however, water soluble vitamins such as vitamin C are not stored and are excreted through the urine. Hence, the water soluble vitamins must be consumed or produced continually in order to maintain adequate levels.

Although not commonly thought of as a nutrient, water is tremendously important and comprises up to 95 percent or more of the weight of some animal tissue. Water is replaced in most animals by drinking, ingestion with food, and to some extent, by the metabolism of carbohydrates and lipids.

—D. R. Gossett

See also: Biology; Cannibalism; Carnivores; Cold-blooded animals; Digestion; Digestive tract; Food chains and food webs; Herbivores; Hibernation; Ingestion; Metabolic rates; Migration; Osmoregulation; pH maintenance; Predation; Ruminants; Scavengers; Thermoregulation; Warm-blooded animals; Water balance in vertebrates.

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OCTOPUSES AND SQUID

Type of animal science: Classification
Fields of study: Marine biology, zoology

Octopuses and squid belong to the order Octopoda, members of which have eight tentacles covered with sucker pads. They have two eyes and a well-developed nervous system and are considered among the most intelligent of all invertebrates.

> **Principal Terms**
>
> INVERTEBRATES: animals without backbones
> TENTACLES: a long flexible arm or projection

Octopuses and squid belong to the order Octopoda, which is in the class Cephalopods, phylum Mollusca, which includes snails and clams. They are related to other mollusks but have no internal or external shell. There are more than one thousand species of octopuses and squid alive today. They have two eyes and eight (octopuses) to ten (some squid) tentacles that are attached directly to the head. The tentacles are covered with sucker pads that help the animal move along the ocean floor, its normal place of residence. They have the most complex brain of the invertebrates, and also have long- and short-term memories, much like vertebrates.

The genus *Octopus* contains several different species, which vary greatly in size. The smallest is *Octopus arborescens*, a species that averages two inches in length. The largest species, *Octopus dofleini*, commonly known as the giant Pacific octopus, can grow to sixteen feet in length and weigh up to three hundred pounds, with a tentacle span of thirty feet. The best known and most widely distributed species is *Octopus vulgaris*, a medium-sized octopus found in every ocean. This species is from two to three feet in length and lives in holes on the ocean floor. It feeds mainly on crabs, lobsters, and other crustaceans. It is very intelligent: One Japanese scientist taught an octopus how to open a sealed jar in order to get at its contents, a spiny lobster.

An octopus can change its skin color quickly when it is frightened or threatened. Its changed color provides camouflage to help it blend in with the background so that the octopus becomes almost invisible to predators. Scientists have discovered that octopuses change colors not only for defense, but also to reveal their moods and emotions. Angry members of the species turn a deep red in color, while during mating season, both males and females display stripes and colors that reflect their inner excitement. Some species squirt out clouds of a dark inky substance, which hangs in the water for several seconds. This inkblot has the same size and shape as the octopus, and while it draws the attention of the predator, the octopus escapes. When an enemy, such as a moray eel, attacks an octopus, it may lose one of its eight arms in the fight, and while the eel watches the twitching arm the injured octopus can swim away. The tentacle grows back very quickly.

Squid are cephalopods and belong to the order Teuthoidea (ten-armed), which has many species. They are found in every ocean and range in size from less than one inch to more than sixty-five feet in length. Adult squid of some species can race through the water at speeds of up to twenty-five miles per hour. They are aggressive hunters, equipped with two more tentacles than octopus. The squid use these extra arms to catch their food. Some squid hunt in packs and use their ability to change color to lure their prey. They are also bioluminescent, which means they can light up.

Cephalopod Facts

Classification:
Kingdom: Animalia
Subkingdom: Eumetazoa
Phylum: Mollusca
Class: Cephalopoda
Subclass: Nautiloidea (chambered nautilus), Coleoidea (octopuses and squid)
Orders: Sepioidea (cuttlefishes), Teuthoidea (squid), Octopoda (octopuses)
Suborder: Three suborders of Octopoda—Palaeoctopoda (finned), Cirrata (webbed), Incirrata (round bodied)
Geographical location: Every ocean, but mainly the Indian Ocean and the South Pacific
Habitat: The ocean floor
Gestational period: Varies by species from forty days to one year
Life span: One to three years for octopuses; five years for squid; fifteen to twenty years for chambered nautilus
Special anatomy: Eight to ten tentacles, usually with suction cups at the end; round, sacklike bodies for octopuses

Actually, bacteria living under their skin produce the light in squid that live close to the surface. Deep-water squid, on the other hand, living thousands of feet below the surface, make their own light. These species have light-producing organs called photophores that make two chemicals: a protein called luciferin and an enzyme known as luciferase. When the two chemicals are mixed, the enzyme breaks down the protein, releasing a pale, blue-green light. This is the same process used by fireflies. Some squid species can squirt out clouds of glowing bacteria when they are endangered. This light show distracts the predator and helps the squid escape.

Squid, Cuttlefish, and Nautilus

The giant squid, *Architeuthi*, is the largest invertebrate on the earth, having eyes the size of automobile headlights and weighing up to one thousand pounds. Despite their size, no one has ever seen one of these animals in its natural environment. Although these monsters of the deep have been found in the nets of commercial fishermen, in the stomachs of sperm whales, and washed ashore in Australia, no scientific information has been gathered on the species by direct observation. Perhaps the major reason so little is known about giant squid is that they live so deep in the ocean. Another reason is their enormous speed and rapid acceleration. Because of this speed they can easily evade their major predators, tuna and sharks. Some apparently even have the ability to leave the water for short periods and glide through the air like flying fish to escape their enemies.

The cuttlefish, genus *Sepia*, is a cephalopod that can eject clouds of ink to confuse enemies and can swim almost as rapidly as squid. It most remarkable characteristic, however, is its ability to change color, which biologists believe is used by the species as a method of communication. Cuttlefish can display thirty different color patterns that range from very light to very dark. They can also exhibit zebralike stripes and patterns that look like a pair of dice. They can change colors quickly to escape predators by blending into the background. Color changes are also used to attract mates and outshine rivals during courtship. Cuttlefish have ten arms or tentacles, with two longer than the other eight. Most of the time the two longer arms are tucked under their bodies, but if supper swims by they shoot out to grab the shrimp or fish and drag it to their mouths.

Next to the octopus, the cuttlefish is probably the most intelligent invertebrate in the sea. In experiments, cuttlefish have been taught to recognize which colored disks signal food and which do not. Baby cuttlefish know from the moment of birth how and when to bury themselves in the sand, how to squirt an inky substance to confuse predators, and how to get away quickly when they encounter larger animals. The ink of the cuttlefish, which is called sepia (the genus name) was the original dark pigment used in India ink. This ink was used in quill pens in England and France in the 1600's and is still used today by artists for drawing and lettering.

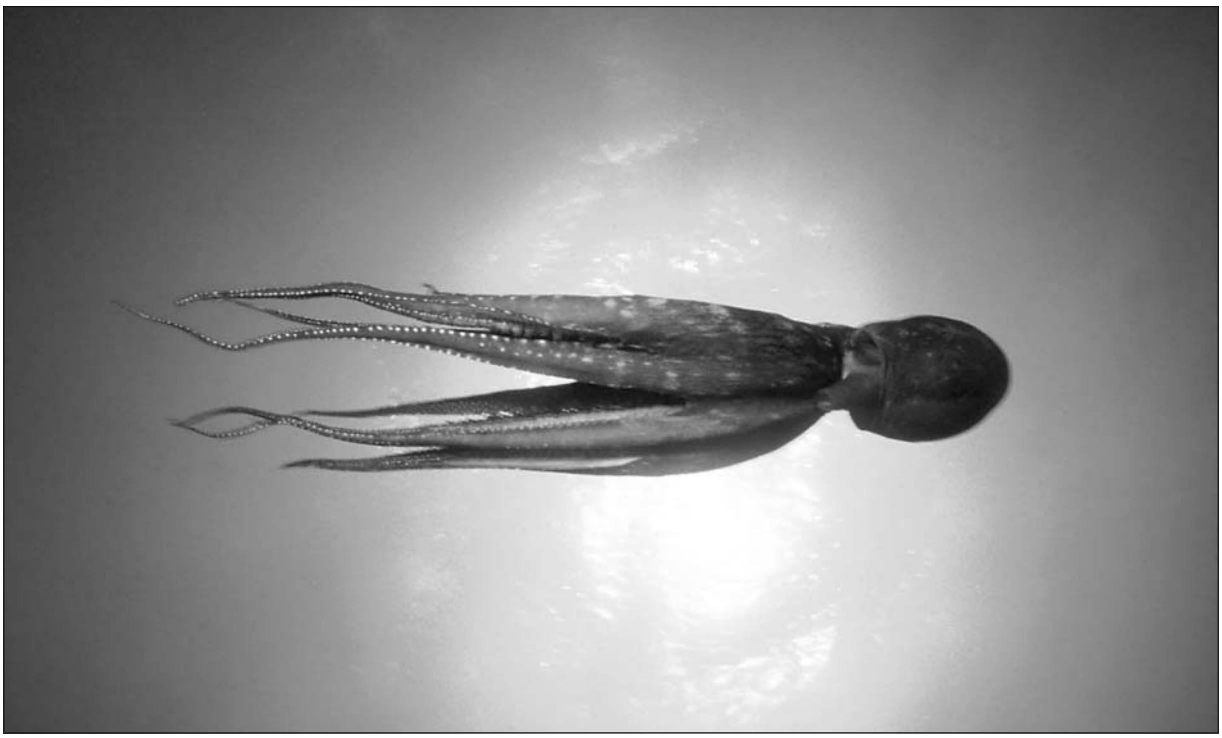
The chambered nautilus is one of five species in the genus *Nautilus*. It is a living fossil. The surviving species are found only 60 to 1,500 feet below the surface of the Indian and Pacific oceans. Five hundred million years ago, nautiloids were the masters of the sea. At that time there were more than 2,500 species, some with straight shells and others with coiled shells like the modern nautilus. They are nocturnal feeders, coming to the surface only on moonless nights to feast on small fish and shrimp. They are the only members of the class Cephalopoda to still have an external shell. They have eighty to one hundred arms surrounding their heads. Each arm can touch and taste food. The nautilus gets its name from the thirty to thirty-eight walled chambers that are found inside its shell. The animal lives in the outermost chamber and uses the others to float in the water.

The nautilus is an endangered species, mainly because of the beauty of its shell. Philippine Island fishermen catch about five thousand living animals every year to sell to shell collectors. They are also hunted extensively off the coasts of India and Indonesia.

Growth and Reproduction

Most cephalopods, including the giant squid, grow quickly and die after a short life. The great Pacific octopus, for example, which is only one-twentieth the size of the giant squid, lives just two to three years. It is estimated that the giant squid lives for no more than five years. This means that its growth to adulthood is extremely fast. When it is a baby, it is less than an inch long, but within three years it has reached almost sixty feet in length. Growing at such a rapid rate requires huge amounts of food. Giant squid eat enormous quantities of fish and other squid, which they catch with the suckers on their tentacles and crush in their massive mouths.

Octopuses and squid have separate sexes and reproduce internally. In some species, modified



The tentacles of an octopus are attached directly to its head, leading to the name "cephalopod," meaning "head-foot." (Digital Stock) sucker discs at the tip of one of its tentacles distinguish the male. This arm is used to remove a packet of sperm from within his body cavity and insert it into the cavity of the female. Within two months after mating, the female attaches strands of clustered eggs to the ceiling of her dwelling under the sand. The number of eggs laid varies greatly from species to species, with the common octopus laying anywhere from 200,000 to 400,000 very tiny eggs. Other species lay as few as 150 eggs. Once the eggs are laid, the mother gently caresses the eggs with her suckers to keep algae and bacteria from growing on them. She also squirts them with streams of water to keep them clean. As the baby inside the egg matures, the mother's gentle caresses become more violent to help the developing octopus break away from its egg house. Most mothers do not eat after laying their eggs and die shortly after their eggs have hatched. Baby octopuses in species like *Octopus vulgaris* are carried about in water currents for about a month before they settle to the bottom, where they start to feed. Babies in other species look just like a miniature adult and immediately sink to the bottom where they start living. On average, the survival rate for a baby octopus is extremely tiny. Only about one or two out of 200,000 eggs will survive to become an adult.

The chambered nautilus cements its eggs to rocks or coral on the seafloor. They take almost a year to hatch. A baby nautilus is only about an inch long when it hatches from its egg case but grows into an adult quickly. It is the longest-living cephalopod, with some adults living fifteen to twenty years. Unlike the octopus, the chambered nautilus does not die immediately after reproduction.

Cephalopods make up a large part of the diet of whales, seals, fishes, and seabirds.

Cephalopod Evolution

The earliest ancestors of octopuses and squid were mollusks with thick shells that protected them from their enemies. Of the estimated one thousand species of cephalopods still living, only the chambered nautilus and cuttlefish have remnants of an internal shell. Cephalopods began losing their shells in the Triassic period, 245 to 208 million years ago. The earliest squid appeared in the Jurassic period, 208 to 144 million years ago. The oldest known octopod, *Palaeoctopus newboldi*, now extinct, comes from the Cretaceous period and is at least 140 million years old.

—Leslie V. Tischauser

See also: Camouflage; Deep-sea animals; Defense mechanisms; Intelligence; Invertebrates; Learning; Marine animals; Marine biology; Mollusks; Shells; Tentacles.

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OFFSPRING CARE

Types of animal science: Behavior, reproduction
Fields of study: Ethology, ornithology, reproduction science

In most species, one parent alone or neither parent cares for the offspring. In some species, however, both parents jointly care for their offspring. In a few species, several adults share parenting duties or take turns "babysitting."

Principal Terms

ALLOPARENTING: performance of parenting duties by an individual not the parent of the offspring (though usually a relative)
ALTRICIAL: the condition of being weak and relatively undeveloped at birth (or hatching) and thus dependent upon parental care for a prolonged period
CUCKOLD: a partnered male who is helping his mate to raise offspring which are not genetically his own
NEST-PARASITE: also called brood-parasite; an individual (or species) that lays its eggs in the nest of another individual (or species) and does no parenting at all
PRECOCIAL: the condition of being strong and relatively well developed at birth (or hatching) and thus not particularly dependent upon parental care
SEX-ROLE REVERSAL: generally used to refer to species in which the male does most of the parenting
VIVIPAROUS: characterized by live birth (as opposed to egg-laying)

In the animal kingdom, there are species in which neither parent cares for offspring, species in which one parent cares for offspring, species in which both parents care for offspring, and species in which individuals other than parents help care for offspring. Patterns of caring for offspring relate to several key factors.

Precocial Species Versus Altricial Species

The most important factor determining the number of caretakers, as well as the quality and duration of parental care, is simply how much care the offspring need. In species in which young are born well developed and capable of surviving on their own, there is little reason for parents to provide help. Hatchling fish and baby turtles, for example, are born or hatched looking just like miniature adults, and are fully capable of moving about and feeding themselves. Young of such species are referred to as precocial, and usually get no parental care at all. Young of most invertebrate species as well are capable of surviving without help, and so are typically left to fend for themselves.

On the other hand, in species in which young are born or hatched quite helpless with no chance of surviving on their own, it should not be surprising that one or both parents are likely to stay around. Young of such species are referred to as altricial. Dogs and cats are excellent examples of species with altricial offspring; so are humans. Generally speaking, mammals are more altricial than most groups of animals, and all mammalian young initially depend upon their mother for food (milk), delivered by means of lactation.

Compared to other animals, birds, too, are relatively altricial—especially raptors (birds of prey) and songbirds. When altricial birds first hatch they are featherless and unable to regulate their own body temperature; one or both parents must regularly warm the hatchlings just as they earlier warmed the eggs. Furthermore, altricial birds hatch with their eyes closed and they are not strong enough or coordinated enough to leave the nest to feed or to flee from danger. Because baby birds need tremendous amounts of food and there are usually quite a few offspring, in most species of birds, both parents provide care.

Prey Species Versus Predatory Species

Although the young of birds and mammals are quite helpless compared to the young of animals in other taxonomic groups, there are variations. As a rule, prey species tend to be more precocial than predatory species and, therefore, to require less parental care.

Young of species which are herbivorous (vegetarian) but are in constant danger of being eaten by carnivorous (meat-eating) species cannot afford to be completely helpless even if they are dependent upon their mother for food. Grazing mammals, such as zebra and deer, are vulnerable to lions and wolves, so young of these species must be able to stand up and run just a few minutes after birth: they are born with open eyes, well-developed muscles, and a full coat of hair. Although mammalian young need to nurse from their mother, they are able to start grazing fairly quickly, so typically it is only the mother who provides support, and her care is not exceptionally prolonged.

Among birds the same pattern is found: Herbivorous species, such as ducks and chickens, that are preyed upon by mammalian, avian, or reptilian predators, hatch with open eyes, the ability to walk, run, or swim, and a coat of downy feathers so that even though they cannot yet fly, they can leave the nest without need of further incubation. Offspring of these species can usually eat on their own almost immediately after hatching, and therefore can often get by with only one parent to show them what to eat and to protect them until they can fly.

Compared to young of prey species, young of predatory species tend to be born in a much more altricial state, and therefore, to need more parenting. Lion cubs and wolf pups do not have open eyes or the strength and coordination to leave their nest, den, or lair until a few weeks after birth. Even after they can move about and are weaned from mothers' milk, they are still too uncoordinated to hunt successfully and must be fed by one or both parents. In fact, species such as lions and wolves, which not only have altricial young, but frequently have large litters, often re-

"Noncooperative" Breeding

In Australia, birds called choughs (pronounced "chuffs") live in extended family groups that cooperate to defend territories and raise young that may need provisioning for as long as two years. Some of the youngest helpers are not much older than their younger siblings, and when provisioning their charges, often cheat. If no older adult is looking, a young helper may pretend to feed its sibling, but at the last minute, swallow the food itself.

In the southwestern United States live acorn woodpeckers, a communal species in which a group of up to a dozen birds shares common nest-holes and food repositories for storage of acorns. Despite their seeming cooperation, when more than one female lays eggs in the same nest-hole, they initially take turns destroying or removing one another's eggs from the hole and placing them in the food repository for later consumption. Over a third of eggs laid get destroyed in this fashion.

Some birds lay their eggs in another bird's nest and do not do any parenting at all. Facultative or opportunistic nest-parasites (also called brood-parasites) are species such as ducks, which usually make their own nest and raise their own young, but which, in a good season, may lay extra eggs in a neighbor's nest or, in a bad season, may forego nesting but lay a few eggs elsewhere on the chance that another parent will manage better. Obligate nest-parasites are species such as the Australian and European cuckoos, which never make a nest and never raise their own offspring, but which lay their eggs in the nest of birds of a different species.

cruit other adults to help raise their offspring. Amongst African (but not American) lions, related females form groups called prides that hunt together and help take care of one another's offspring. Wolves form hunting packs, and all members (both male and female) help to feed the young. This behavior is called aunting when it is done by a female relative, or more generally, alloparenting. Alloparenting is also seen among some rodents and primate species.

As with mammals, carnivorous and insectivorous birds come into the world in a more altricial state than their vegetarian brethren, and therefore need more care. In the majority of bird species, both parents cooperate to raise young and, as with some of the most altricial mammalian species, if there is a large brood, parents of some species recruit helpers. In birds, helpers are usually the parents' offspring from a previous brood or season, and are thus siblings or half-siblings of the young they are helping to raise. Species that use this extended family system are referred to as cooperative breeders—although some are less cooperative than others.

Quantity Versus Quality Parenting

A third factor relevant to parenting is the number of offspring, either sequentially or in litters, that an individual produces. All individuals have a limited life span and a limited amount of energy, and during that life span they can allocate that energy either to producing a large number of offspring or to providing intensive care for a smaller number of offspring. Thus, while animals with altricial young that require intensive care do not have an option of producing huge numbers of offspring, species with precocial young do.

Most invertebrates and many vertebrates (other than birds and mammals) take the "quantity" strategy: They produce large numbers of offspring and provide no parental care at all. A large majority of the offspring of these species die before reaching adulthood, but a small percentage survive and reproduce. Extreme examples of taking a "quantity" strategy are the semelparous species, species that can only reproduce once in their lifetime. Salmon are well-known for this form of reproduction. Many spiders and insects, too, die before their only batch of young are even hatched.

At the other extreme is the strategy of having a small number of well-cared-for offspring, each of which has a high probability of survival. All altricial species are constrained to the "quality" strategy, but some precocial species opt for "quality" as well. Alligators and crocodiles are excellent mothers, protecting their eggs before they hatch, then transporting and protecting the young afterward. Some species of amphibians, fish, and even insects are devoted parents.

Maternal Care Versus Paternal Care

In mammals, if only one parent is necessary, it is always the mother who is committed to caretaking because she is the one who must provide the offspring with their first food through nursing. No other animals, however, nurse their young, so in other species, if only one parent is necessary, it does not necessarily have to be the mother who becomes the caretaker.

In single-parent species, whether it is the mother or father who becomes the caretaking parent depends, to a great extent, on parental certainty. In viviparous species (species that give birth to live young rather than lay eggs) the parent that gives birth is, for certain, one of the two genetic parents, and is therefore the parent most likely to care for the young if they need it. With rare exception, that means that mothers become the caretaking parent in viviparous species. In egg-laying (oviparous) species, parental certainty depends on whether fertilization was internal (as in birds and many invertebrates) or external (as in most fishes and amphibians). If fertilization is internal, then again, it is only the mother who is certain to be a genetic parent of the eggs she lays, and who is therefore most likely to take on the role of caretaker when only a single caretaker is needed. If, on the other hand, fertilization is external, then both parents are equally likely to be the genetic parent of any young that later hatch from eggs at the breeding site, and if parenting is needed, male and female are equally likely

Fathers Extraordinaire

Because mothers are the single parent in most single-parent species, those species in which the father does most of the parenting are referred to as sex-role-reversed. Typical of role-reversed species is a cluster of sex differences that are reversed in many ways other than just parenting: Females tend to be larger, more aggressive, and more flashy than the males, and they may be the more "promiscuous" sex, mating with a series of stay-at-home fathers in a mating system called polygyny.

Polygyny and exclusive paternal care have been best studied in birds. Other types of animals, however, also provide examples of exclusive paternal care. In several species of invertebrates, fish, and amphibians, females lay their eggs and leave, while males remain to guard the eggs after they have been fertilized, protecting them against the vagaries of weather, water currents, and predation. Even after the eggs hatch the male may continue to guard the young or to transport them: Some tiny Amazonian frogs carry their tadpole offspring on their back if the small pool of water where they hatched starts to dry up. In other species, males carry fertilized eggs on their back, in their mouth, or in a specialized pouch. In the case of pipefish, seahorses, and some frogs, the male's tissue actually provides nutrients to the developing embryos. In these rare creatures, one could truly say that it is the male that becomes pregnant.

to become the caretaker. The result is that while most species that have external fertilization do not remain with their eggs or provide any parental care at all, in those that do, factors other than parental certainty determine which sex becomes the guardian.

In species with internal fertilization, the probability that a particular male is the father (or one of the fathers) of a particular set of offspring depends upon how many males the female mated with and when. In the few species that have been closely studied, if a mother needs help to raise her offspring, males seem to expend effort in proportion to the probability that they are actually the genetic father. This is because males that are parenting or otherwise providing resources for offspring that are not genetically their own are wasting their effort in terms of reproduction.

A male that is caring for another males' offspring is sometimes referred to as a cuckold. In some human cultures, to call a man a cuckold (or the equivalent) is a huge insult. However, in humans and other animals, when a male provides care for a female's offspring even though they are not genetically his, he is sending her a signal that he is a good provider, and perhaps he is making it more likely that she will mate with him in the future.

The Spectrum of Parental Behavior

Most parents are good to most of their offspring most of the time. Parents provide food and sometimes shelter; they protect their offspring from danger and chase away predators; they may place their offspring in safe refuges; they may even teach their offspring necessary information or skills such as how to hunt, the location of productive feeding sites, or traditional migration routes.

At some point, however, there may be conflict between parents and offspring; conflict is especially common over how much care the parents provide versus how independent the offspring have become. Avian parents, for example, may displace their offspring from the nest to make way for a new brood; mammalian mothers may resort to force to wean their maturing offspring and so be able to nurse a new infant or litter. Alternatively, offspring may be sexually mature and ready to leave, but are manipulated by their parents to remain in the family acting as helpers.

The most extreme forms of parental manipulation involve neglect and what is called tolerated siblicide. In particularly bad times when resources are scarce, parents may provide care for only one or a few offspring, allowing the others to die. Even in good times, parents with very large broods or litters may neglect the smallest and weakest young. Parents of some species allow older siblings to kill, and perhaps eat, their younger siblings; in fact, this behavior is the norm in some species.

Humans tend to equate parenting with moral goodness; among other animals it equates simply to survival and reproduction. Different species provide parental care—or not—as it is needed, in order to maximize the probability that at least a few offspring will survive to maturity. In some vertebrate species parenting may be associated with intense emotions and bonding, as it is in humans, but across the animal kingdom there is no one right way to parent; what works is what works.

—Linda Mealey

See also: Asexual reproduction; Birth; Breeding programs; Cleavage, gastrulation, and neurulation; Cloning of extinct or endangered species; Copulation; Courtship; Determination and differentiation; Development: Evolutionary perspective; Estrus; Fertilization; Gametogenesis; Hermaphrodites; Hydrostatic skeletons; Mating; Parthenogenesis; Pregnancy and prenatal development; Reproduction; Reproductive strategies; Reproductive system of female mammals; Reproductive system of male mammals; Sexual development.

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OMNIVORES

Types of animal science: Anatomy, classification
Fields of study: Anatomy, entomology, ornithology, marine biology, zoology

Omnivores are animals that eat both plants and animals. They are found in all types of animals, including arthropods, fish, birds, and mammals. Omnivore diets may vary seasonally.

Principal Terms

CARNIVORE: a flesh-eating animal
CARRION: dead animals
DIURNAL: active during the day
HERBIVORE: an animal that eats only plants
HERMAPHRODITE: an organism having male and female reproductive systems
RADULA: a tonguelike, toothed organ for grinding food

Many animals are either herbivores, who eat only plant food, or carnivores, who eat only the flesh of other animals. The preference for one type of food or the other depends largely on the type of digestive system that the animal has, and the resources it can put into its "energy budget." Meat is generally easier to digest and requires a less complex digestive system and a relatively short intestinal tract. However, in order to get meat, carnivores have to invest a lot of time hunting their prey, and the outcome of a hunt is always uncertain. The food of herbivores is much easier to obtain, since plants do not move and all the herbivore has to do is graze on the grasses, leaves, or algae readily available around it. However, the cellulose that plants are made of is very tough to digest, and thus herbivores must have a much more complex and lengthy digestive tract than carnivores. Many herbivores are ruminants, with multipart stomachs, who have to chew and digest their food more than once in order to get adequate nutrition from it.

Carnivores and herbivores are also vulnerable to a loss of their food source. Herbivores whose digestive systems are specialized to process only one type of food will starve if that food becomes scarce due to drought or some other climatic change. Carnivores often have specialized hunting patterns that cannot be changed if the prey (usually herbivores) become scarce due to loss of their own food source.

Omnivores maximize their ability to obtain food by having digestive tracts capable of processing both plant and animal food, although they are usually not capable of digesting the very tough plant material, such as grasses and leaves, that many large herbivores eat. Omnivores may also be scavengers, eating whatever carrion they may come across. Omnivores often lack the specialized food-gathering ability characteristic of pure carnivores and herbivores. Many animals often thought of as carnivores are actually omnivores, eating both plants and animals.

Types of Omnivores

Omnivores can be found among all types of animals, living on land and in water. They include fishes, mollusks, arthropods, birds, and mammals.

Most insects are either herbivores, such as grasshoppers, or carnivores such as mantises. However some, such as yellow jacket wasps, are omnivores, eating other insects, fruit, and nectar. Omnivorous snails and slugs eat algae, leaves, lichens, insects, and decaying plant and animal matter. Their main organ for eating is called a radula, a tonguelike, toothed organ that is drawn along rocks, leaves, or plants to scrape off food; it

Raccoons eat everything they can get their paws on, including fish, insects, birds, plants, crustaceans, and carrion. (PhotoDisc)

is also used to bore holes through shells of other mollusks, to get to their flesh.

Omnivorous fish include the common carp, goldfish, catfish, eels, and minnows. Since a fish's food is often suspended in the medium through which the fish swims—water—being able to gulp up whatever comes into its mouth is an efficient way for a fish to eat. Similarly, bottom-feeders (fish that suck up material from the floor of whatever body of water they inhabit) also benefit from not needing to sort through the material before they ingest it.

Many birds are omnivores, such as robins, ostriches, and flamingos. The pink or red color of flamingos occurs because they eat blue-green algae and higher plants which contain the same substances that make tomatoes red. They also eat shrimp and small mollusks.

Mammal omnivores include bears, members of the weasel family, such as skunks, the raccoon family (raccoons and coatimundis), monkeys, apes, and humans. Raccoons and coatis, found only in the Americas, eat insects, crayfish, crabs, fishes, amphibians, birds, small mammals, nuts, fruits, roots, and plants. Like other omnivores, they also eat carrion. Bears eat grass, roots, fruits, insects, fishes, small or large mammals, and carrion.

—*Sanford S. Singer*

See also: Baboons; Bears; Carnivores; Chimpanzees; Digestion; Digestive tract; Ecosystems; Food chains and food webs; Gorillas; Herbivores; Hominids; Ingestion; Lemurs; Metabolic rates; Monkeys; Nutrient requirements; Orangutans; Plant and animal interactions; Predation; Raccoons and related mammals; Shrews; Skunks; Teeth, fangs, and tusks; Weasels and related mammals.

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OPOSSUMS

Type of animal science: Classification
Fields of study: Anatomy, zoology

Opossums are omnivorous mammals which are the only native marsupial in North America.

Principal Terms

ARBOREAL: living in trees
CARRION: rotting carcasses
MARSUPIUM: pouch
OPPOSABLE: positioned opposite of other objects
PREHENSILE: wrapping

Opossums represent the oldest surviving mammal family. Ancestors resembling modern opossums lived on earth at the same time as the dinosaurs. Scientists have located seventy-million-year-old opossum fossils. The Virginia opossums are found in the United States and Canada, while relatives representing seventy species of the Didelphidae family live in Central and South America.

Anatomy

The Virginia opossum is the largest species of the Didelphidae family. They are about the size of a domestic cat and measure from 0.3 to 0.8 meters (1 to 2 feet) in length, with a 22 to 50 centimeter (9 to 20 inch) long tail. Their weight varies from 2 to 5.5 kilograms (4 to 12 pounds). Other opossums are much smaller, averaging 7.5 centimeters (3 inches) in length with a 5 to 10 centimeter (2 to 4 inch) long tail.

Opossums have varying lengths and thicknesses of fur, in shades of white, gray, brown, and black. Some opossums have stripes. Opossum eyes are black, and their ears are usually hairless. Their faces have a mask or are white. They have a pink nose at the end of a long, pointed, whiskered snout which has fifty sharp teeth. Their four feet and tail are also pink and hairless. Each forefoot has five toes with claws. Opossums have an opposable, thumblike toe on their hind feet that can grasp objects and cling to branches. They are arboreal animals and agile climbers. Their prehensile tails are used for balance.

Life Cycle

Male opossums attain maturity at eight months, and females are sexually mature between six and nine months. Female opossums can produce two litters annually. As many as fifty-six offspring

Opossums have prehensile tails that allow them to hang from branches and other objects. (Corbis) may be in a litter, but, because female opossums can only nurse twelve to fifteen newborns in their marsupium, most newborn opossums die.

Born blind, each newborn opossum, which is almost embryonic and as small as a bean, crawls from the birth canal near their mother's tail and across her stomach to her pouch. They attach to nipples inside the pouch, where they nurse for two to three months. This nursing period provides them with immunities to diseases. The babies stay inside the pouch when the mother leaves the den to forage. As they grow and the pouch becomes full, the young opossums sometimes briefly leave the pouch, then return for nourishment. From the age of three to five months, the babies ride on their mother's back. While traveling this way, the young opossums gain scavenging and survival skills.

Opossum Facts

Classification:
Kingdom: Animalia
Subkingdom: Metazoa
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Subclass: Eutheria
Order: Marsupialia
Suborder: Didelphoidea
Family: Didelphidae
Genera: Didelphis (opossums, with three species); *Marmosa* (mouse opossums, with forty-seven species); *Monodelphus* (short-tailed opossums, with fourteen species); six other genera

Geographical location: North, Central, and South America

Habitat: Forests, grasslands, mountains, and swamps

Gestational period: Twelve to fourteen days

Life span: From one to three years in the wild, up to ten years in captivity

Special anatomy: Opposable thumblike toe on the hind foot, prehensile tail, pouch

Behavior

Opossums tend to be solitary, nomadic animals that can range over 30 to 96 acres (0.5 to 1.5 square miles) daily. They nest in hollow trees and other animals' burrows. Opossums are nocturnal, foraging at night. Because they are adaptable, opossums can live in a variety of habitats and are frequently found in urban areas which formerly were wooded. They adjust their scavenging and living habits to find food and shelter whether they are in a rural setting or in the middle of a city. Extremely cold weather is the primary environmental condition that deters opossums from otherwise suitable habitats. Opossums are hardy and immune to most diseases. They are the mammal most resistant to rabies.

Opossums are omnivorous and eat a variety of insects, especially crickets, beetles, and cockroaches. They also consume snails, slugs, snakes, worms, birds, and rodents in addition to carrion and eggs. Berries, fruit, and vegetables appeal to opossums, particularly when overripe. Opossums have keen senses of smell, vision, and hearing to locate sustenance and clean up organic wastes in their territories.

The life expectancy of opossums is one to three years in the wild and as many as ten years when kept in captivity. In addition to being preyed upon by wildlife and domesticated animals, opossums are killed by humans for sport, fur, and meat, or by accident with vehicles. Baby opossums often survive automobile impacts which kill their mothers. Opossums show a variety of defense mechanisms: They move more slowly than their predators and often spray a foul-smelling secretion to thwart attacks. Virginia opossums feign death by becoming limp when frightened and unable to escape. They sometimes hiss or growl, exposing their teeth. Opossums occasionally fight and bite. Opossums hide in brush-covered areas that are difficult for predators to access. They can make sounds, including screeches, but are usually quiet. Scientists have gauged opossums' ability to learn and distinguish objects as greater than that of dogs and almost equivalent to pigs.

The National Opossum Society (http://www.opossum.org) offers information about how people can rehabilitate injured opossums and raise orphans. The group also addresses the controversial use of opossums as laboratory research specimens.

—Elizabeth D. Schafer

See also: Fauna: Australia; Fauna: North America; Kangaroos; Marsupials; Omnivores; Reproductive strategies; Scavengers; Urban and suburban wildlife.

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ORANGUTANS

Type of animal science: Classification
Fields of study: Anatomy, conservation biology, wildlife ecology, zoology

Orangutans are large apes with orange to reddish-brown shaggy hair. They have very long arms and no tail. They survive solely in the jungles of Borneo and Sumatra, where their habitat has been destroyed to the point that they are listed as a threatened species.

Principal Terms

ARBOREAL: living completely or primarily in the trees
BIPEDAL: walking on only two feet, as humans do
QUADRUPEDAL: walking on all four feet
SEXUAL DIMORPHISM: the occurrence of anatomic and physiologic differences that distinguish males from females of a particular species

The name "orang-utan," commonly written in the hyphenated form, comes from two Malay words: *orang* meaning "person," and *hutan* meaning "forest or jungle." Thus, Malaysian *orang-utan* means "persons of the jungle." Since these animals are very humanlike and live secretive lives in the dense jungle, the origin of the name makes sense. Orangutans are considered to be a threatened species. Less than twenty thousand are believed left in the wild.

Orangutans are the second largest of the apes, and show marked sexual dimorphism. Males may grow to be 220 pounds (100 kilograms) and females about half that. The arms of a full-grown male may reach a span of 7 to 8 feet (2.1 to 2.4 meters), and their hands are longer than any other primate. These arms and hands are ideally adapted for the arboreal life. Comparatively, the legs are short and weak; there is no external tail. While adult males with arms extended (swinging through the jungle) may appear to be enormous, when standing erect on the ground they rarely exceed 4.5 feet (1.3 meters) in height. Females, by contrast, reach only 3.5 feet (1.1 meters).

Habitat

Two to three million years ago, orangutans lived as far north as China and as far south as Java. As land bridges formed during the Ice Age, orangutans moved south in search of a warmer climate. Today they can only be found on the Indonesian islands of Borneo and Sumatra.

Orangutans are the only truly arboreal apes, spending most of their life in forest trees. Their anatomy is well suited for this lifestyle. They walk

Orangutan Facts

Classification:
Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Primate
Family: Hominidae
Genus and species: Pongo pygmaeus
Geographical location: Sumatra and Borneo
Habitat: Dense rain forests, particularly lowland forests
Gestational period: Eight to nine months
Life span: Thirty-five years in the wild, fifty years in captivity
Special anatomy: Orange to red-brown hair; arm length exceeds torso length

up trunks using irregularities in the bark to give a grip to fingers and toes, and proceed silently through the middle stories of the forest. These middle stories are especially well suited for horizontal travel, where densely growing trees poke up into the canopy. Often vines are used for quickly moving up and down to get to the next horizontal branches. Orangutans do not jump; they climb and walk the branches on all four legs. They may also sit, recline, or hang in a variety of positions, including suspended from both feet or from one foot and one hand.

On the ground, orangutans are normally quadrupedal, although they occasionally walk in the bipedal position. Their weight is borne by clenched fists with the palm touching the ground (unlike gorillas and chimpanzees). Their walk is similar to that of a dog, with diagonally opposed limbs moving forward together.

Orangutans are very shy primates that spend virtually all of their lives in trees. (PhotoDisc)

Orangutans live alone, in pairs, or in small family groupings. They build nests in the trees from groups of small branches, bent or broken and laid across one another, then lined with smaller branches that are patted down into a circle of approximately three feet in diameter. Nests are placed ten to one hundred feet above the ground and are difficult to spot. Nests may be built new each night when animals are moving about, but may remain intact for several months after being built.

While moving and at rest in trees, the orangutan grasps vegetable and animal matter within its reach, testing each one as food. It prefers a variety of jungle fruits as its principal diet, but also eats or chews an infinite variety of buds and leaves, flowers, bark, epiphytes, canes and roots, honey, and even fungi. It forages and eats at leisure, picking fruits with cupped hands and spitting seeds and shells back out of its mouth.

Orangutans satisfy most of their need for water by taking it in with their moist food. When on the ground they drink from a stream or lake by bending over from a standing position. They have also been seen to squat down and use their hands to spoon the water into their mouths.

Reproduction and Development

Orangutans reach maturity at about ten years of age, and can begin breeding at any time thereafter. Mating begins with a male singing a song, a low hum that increases to a deep roar before decreasing again. Often playful wrestling, touching, and other acts precede mating. Mating occurs in trees, face to face, usually in a hanging position. Mating may occur repeatedly over a period of several weeks. The pair then separates and each goes its own way. Males play no role in parenting.

Female orangutans have a menstrual cycle similar to that of a human female. It lasts twenty-nine days, with a slight flow of blood for three to four days. Pregnancy lasts nearly nine months, and newborns generally weigh 2.25 to 3.25

Biruté Galdikas

Born: May 10, 1946; Weisbaden, West Germany
Fields of study: Conservation biology, systematics (taxonomy), wildlife ecology, zoology
Contribution: Galdikas has devoted her life to studying the endangered orangutan and preserving its rain-forest habitat. She is the world's leading authority on these mysterious apes, whom she has studied for nearly thirty years in the jungles of Borneo.

Biruté Galdikas was born in West Germany not long after the end of World War II. Her parents met at a refugee camp after fleeing their Lithuanian homeland during the war. Two years after her birth, her father moved the family to Canada so he could work in the copper mines. Galdikas grew up in Toronto and enjoyed visiting the zoo. She became particularly fascinated by the primates, and noted that the behavior and expressions of the orangutans reminded her of humans. She hoped that one day she could learn more about them.

Her family moved to Vancouver, and then to Los Angeles. Galdikas entered UCLA to study psychology and anthropology. She received her B.A. degree in 1966 and entered graduate school to study anthropology. It was while she was a student there in 1969 that she met the renowned paleontologist Louis Leakey. It did not take long for her to convince him to support her efforts to study the wild orangutans (Dr. Leakey already supported the work of Jane Goodall with chimpanzees and Dian Fossey with gorillas). With Dr. Leakey's support for her project, Galdikas set out for Borneo in 1971, and set up a jungle camp that she called Camp Leakey.

From Camp Leakey and various jungle outposts, Galdikas has studied the orangutan in its natural environment for thirty years. She has rescued many babies that were taken illegally from the jungle, restored them to health, and has released more than two hundred back to the wild. She has marveled at the mysteries surrounding orangutan social life, and has studied their behavior, speech, reproduction, and life cycle in the wild. She has collected enough data to radically update our understanding of the forces that shape the lives of orangutans in the wild. Galdikas and her colleagues have even taught sign language to orangutans in the hope of being able to learn what was important to them. By hiring many local people to help with her work at Camp Leakey, she has also helped the government and the peoples of Borneo to gain a greater respect for the orangutan and the need to preserve its habitat.

Amidst her studies in the jungles of Borneo, Galdikas wrote about her observations and prepared her doctoral thesis. In 1978, she received a Ph.D. in anthropology from UCLA. When not engaged in field work in Indonesia, she teaches at Simon Fraser University in British Columbia and at Indonesia's Universitas Nasional.

Biruté Galdikas formed and continues to run the nonprofit Orangutan Foundation International. Its purpose is to prevent the extinction of orangutans and their rain-forest habitat by raising money to fund research, conservation, and educational programs. She continues her scientific work to learn more about these solitary primates.

—Kerry L. Cheesman

pounds (1.1 to 1.6 kilograms). The infant clings to the mother's fur and the mother holds the infant with one arm, usually over the hip. This leaves three limbs for traveling and feeding. The youngster nurses for two to three years, with solid food (chewed up fruit) being added periodically. By the end of the first year the youngster begins to explore away from its mother, but remains within eyesight at all times.

By age four, a youngster is pretty much on its own, feeding itself and roaming freely. At that point, the mother is able to mate again. Offspring have only about a 50 to 60 percent survival rate in the jungle, with accidents and disease striking many young orangutans.

Orangutans are shy animals that have only one natural enemy: humans. Currently, orangutans are protected by law in all of their territory, but poaching and illegal logging continue to threaten the survival of the species. Unless large areas of undisturbed jungle are set aside as sanctuaries, the orangutan may have a hard time surviving in the future.

—Kerry L. Cheesman

See also: Apes to hominids; Baboons; Cannibalism; Chimpanzees; Communication; Communities; Evolution: Animal life; Evolution: Historical perspective; Fauna: Africa; Gorillas; Groups; Hominids; *Homo sapiens* and human diversification; Human evolution analysis; Infanticide; Learning; Lemurs; Mammalian social systems; Monkeys; Primates.

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OSMOREGULATION

Type of animal science: Physiology
Fields of study: Biophysics, cell biology

Osmoregulation is the ability an organism must have to adjust its internal concentrations of solutes and of water so that it can maintain an osmotic pressure appropriate to its functioning.

Principal Terms

EURYHALINE: the ability of an organism to tolerate wide ranges of salinity

HYPEROSMOTIC: describes a solution with a higher osmotic pressure, one containing more osmotically active particles relative to the same volume, than the solution to which it is being compared

HYPOOSMOTIC: a solution with a lower osmotic pressure, fewer osmotically active particles relative to the same volume, than the solution to which it is being compared

ISOSMOTIC: a solution having the same osmotic pressure, the same number of osmotically active particles relative to the same volume, as the solution to which it is being compared

OSMOCONFORMER: an organism whose internal osmotic pressure approximates the osmotic pressure of its environment; such an organism is also referred to as "poikilosmotic"

OSMOREGULATOR: an organism that maintains its internal osmotic pressure despite changes in environmental osmotic pressure; such an organism is also referred to as "euryosmotic"

STENOHALINE: the inability of an organism to tolerate wide ranges of salinity

Osmotic pressure of a solution is the measure of the tendency of water to enter a solution from pure water. Osmoregulation, the regulation of osmotic pressure, is vital to every organism. The phenomenon collectively is called "osmosis." It is the difference of hydrostatic pressure that must be created between that solution and pure water to prevent any net osmotic movement of particles in the water when the solution and pure water are separated by a semipermeable membrane. Hydrostatic pressure is a measuring device: It is a means of assessing the tendency of a solution to take on water osmotically.

Only dissolved solutes contribute to osmotic pressure. The number of individual particles determines the strength of osmotic pressure. Each particle makes a roughly equal contribution to osmotic pressure. The same number of molecules of a substance such as sodium chloride (table salt), which ionizes in water to release two ions (one sodium ion and one chlorine ion) display twice as much osmotic pressure as the same number of molecules of glucose, which retains its molecular form in water. Cells and other suspended materials do not contribute to osmotic pressure.

Several characteristics of solutions depend upon the number of particles in the solution. These are called "colligative properties." Increasing the number of particles of solute impairs the ability of the solvent to change state. The colligative properties are the freezing point, the boiling point, the osmotic pressure, and the vapor pressure. Only freezing point depression and vapor pressure are used to determine osmotic pressure.

Osmoticity refers to the osmotic pressure of solutions. Isosmotic solutions have equal osmotic pressures. A hypoosmotic solution has an osmotic pressure lower than the solution to which it is being compared; a hyperosmotic solution is one with a greater osmotic pressure than the solution to which it is being compared. These solutions can be body fluids, environmental liquids, or laboratory solutions.

The terms used to describe the changes in volume of cells exposed to solutions of differing concentrations are often confused with those comparing osmotic pressure. Changes of cell volume are described by the term "tonicity." Solutions isotonic to a cell cause no change in cell volume. Hypotonic solutions will cause the cell to swell as water diffuses into the cell; the cell may even burst. Hypertonic solutions will cause a cell to shrink as water diffuses across the cell membrane into the solution.

The Challenges of Osmoregulation

This discussion reveals some of the problems that an organism encounters in the environment as concentrations of water and salts vary. Most organisms attempt to regulate both their volume and their ion content. If volume is not regulated, the chemicals within the cell will become too dilute to react or too concentrated to interact. If ions are not regulated, chemical reactions will be affected by inappropriate levels of ions, which may change the electrochemical properties of the cellular solution. Thus, there are independent challenges to volume regulation, to ion regulation, and to osmotic regulation. The homeostatic physiological responses to all three types of challenges are interconnected but distinct.

Osmoregulation is the regulation of the ratio between all dissolved particles, regardless of their chemical nature as ions or molecules, and water. All organisms are exposed to osmotic stress. Any organism incurs obligatory water losses. These occur during respiration, urination, and defecation. The organs most often thought of as participating in osmoregulation are the kidneys. They are intimately concerned with the elimination or conservation of water. Some salts are also found in urine. The proportions of the salts excreted in urine may be different from those in the body fluids because the kidney can retain required ions while eliminating less desirable ones.

Freshwater organisms are in danger of dilution, and they excrete great quantities of dilute urine. Saltwater organisms usually produce small quantities of isosmotic urine, which preferentially excretes divalent ions such as magnesium and sulfate. Other surfaces lose water, causing desiccation. The composition of the diet also influences the need for excretion of urine. Nitrogenous wastes from protein metabolism must be eliminated in urine, often as urea, which requires water for its excretion.

Carbon dioxide released during metabolism of carbohydrates and fats is eliminated by the respiratory organs. In terrestrial organisms, air leaving the lungs is usually saturated and some water is lost on expiration. The respiratory organs of aquatic organisms are gills. Their surfaces must be permeable to water. Freshwater organisms gain water through them and hypoosmotic marine organisms lose water through them.

The metabolism of carbohydrates produces what is known as metabolic water, which can be used to prevent desiccation. Metabolic water produced from the metabolism of fats is lost because of the higher rate of respiration required to supply the oxygen needed in fat oxidation.

Salt Loss

Preformed water is present in any food. Even the driest seeds contain a small amount of water. The nutrients also always include salts. The presence of great quantities of salts may require urinary loss of water in excess of the preformed water found in the food.

Although feces may appear to be solid, they contain some water that was not absorbed in the gut. The presence of salts and other solutes in the digesta may also draw water from the hypoosmotic body fluids into the gut. One of the reasons that humans cannot drink seawater, in fact, is that the magnesium ions in ocean water increase the permeability of the gut and increase water loss, because the seawater is hyperosmotic to body fluids. More water is lost than can be gained.

Salts can be lost from the body by means other than urine formation and defecation. Marine reptiles and birds have salt glands located on the head. Since neither can produce hyperosmotic urine, these glands allow the elimination of salt with a minimum loss of water as the secretion may be four to five times as concentrated as body fluids. The cloaca of birds and the rectal glands of sharks also have the capacity to excrete salts.

One of the most fascinating mechanisms of osmoregulation is found in elasmobranch fish—the sharks, skates, and rays. Their body fluids are hyperosmotic but hypoionic to seawater. Blood salt concentrations are below those of seawater. Excess osmotic pressure is supplied by two molecules: urea and trimethylaminoxide (TMAO). Urea is toxic to most organs, but some organs resist its deleterious effects. Others would be harmed but are apparently protected by the TMAO. Retention of both urea and TMAO minimizes enzymatic disturbances by urea and allows the elasmobranchs to avoid the salt gain associated with hypoosmotic body fluids.

Organisms exposed to environmental variations have two choices: they can maintain internal constancy or homeostasis at the expense of metabolic energy, or they can allow their internal conditions to follow that of the environment. Organisms that maintain their internal osmotic pressure despite changes in external osmotic pressure are called osmoregulators. These euryosmotic organisms are protected from environmental changes. Their metabolism can continue to function, but much of the energy will be used to maintain their body fluids at the appropriate osmotic pressure.

Organisms that allow their osmotic pressure to follow that of the environment are called osmoconformers. These poikilosmotic organisms often have a limited tolerance for such changes. They are stenohaline. They may be less vigorous at salinities other than their optimal levels. The adults of such groups (for example, mollusks such as oysters and mussels) may be found in salinity extremes not tolerated by their young. These populations must be maintained by immigration of young spawned in more favorable salinity conditions.

Hormonal Regulation of Osmotic Pressure

The internal osmotic pressure is affected by the hormones present in the body fluids. In invertebrates such as annelids, mollusks, and arthropods, neuroendocrine changes are seen upon changing the osmotic pressure of the environment. These changes indicate that nervous and endocrine systems are at work regulating the osmotic pressure of the organism. In most invertebrates, the biochemical nature of these hormones is unknown. Some freshwater pulmonate snails, however, produce an antidiuretic hormone and a neurosecretory factor associated with electrolyte balance. Depending upon the demands placed on them, insects such as grasshoppers and cockroaches can synthesize diuretic or antidiuretic hormones.

The best-known hormonal factors in ion regulation are studied in vertebrates. The pituitary gland produces antidiuretic hormone (ADH), which promotes water retention in terrestrial vertebrates. In fish and amphibians, ADH may induce urine formation and increase water loss through diuresis.

The adrenal gland also produces hormones that influence ion retention. In mammals, aldosterone increases reabsorption of sodium in the kidney and promotes the excretion of potassium. In nonmammalian vertebrates, extrarenal glands maintain salt and water balance by affecting the gills and intestines of fishes, the urinary bladder and skin of amphibians, and the salt glands of elasmobranchs, reptiles, and birds.

Measuring Osmoregulation

Osmoregulation involves the balancing of water and solutes in the body so that the animal can continue to function. Because the presence of particles influences certain physical characteristics of the solution, these colligative properties can be used to determine osmotic pressure of solutions. Colligative properties change with increasing numbers of particles in solution: The osmotic pressure increases; the boiling point increases; the freezing point decreases; the vapor pressure decreases.

Freezing point depression and vapor pressure can be used to measure a solution's osmotic pressure. Freezing point is used most often. It works for the same reason that salt is spread on ice on sidewalks in winter. The salt lowers the freezing temperature of the water. Body fluids are much more dilute than the salt and water mixtures that melt ice, but the salinity of the ocean (approximately thirty-five parts salt for each thousand parts of solution) causes it to freeze as much as 1.6 degrees Celsius lower than pure water. Only marine organisms have body fluid osmotic pressures in that range. Terrestrial organisms have much less salt and therefore much lower osmotic pressures in their body fluids. Because most body fluids are so dilute, a large sample may be required to determine freezing point depression. When only small volumes of body fluid exist, the determination becomes more difficult.

Vapor pressure determinations are also used in osmometry. Usually, a small amount of the fluid being studied is tested in a capillary tube. In one ingenious method, the capillary tube is placed in a solution more concentrated than the experimental fluid. The higher osmotic pressure of the reference solution pushes a meniscus up the tube. The rate of movement of the meniscus depends upon the difference in concentrations between the experimental and the reference solutions.

Another ingenious method of using vapor pressure to determine the osmotic pressure of an experimental solution requires enough fluid to fill a depression. A glass plate with capillary tubes filled with reference solutions of known osmotic concentrations is mounted over the experimental fluid. The reference tube that exhibits no movement is at equilibrium with the experimental fluid. One of the rigors of this method is that all movement must stop.

Another method involves capturing a precise volume of experimental fluid in a capillary tube. The shape of drops of the same volume of reference solutions is compared to that of the experimental solution. Those of the same concentration will have the same shape because their vapor pressures are exerting equal force on the drop. Thermocouples are also used in vapor pressure determinations. This procedure is delicate and costly and is used infrequently. All these procedures are difficult and require patience. Now, electronic instruments analyze the constituents of solutions and allow easier calculation of the osmotic pressures of solutions than ever before.

Freshwater Versus Saltwater Environments

All organisms experience osmotic stress. There is no environment in which the osmotic pressure and the ion composition exactly match the requirements of the cells. Every organism must expend metabolic energy to maintain appropriate water and ion concentrations.

Freshwater organisms are hyperosmotic to their environment. They risk losing scarce ions through their permeable gills and in their urine and also tend to take up water through their gills or other surfaces and in their food. They face the problem of dilution of their body fluids by the environment.

Marine organisms are often isosmotic to the salt water they inhabit. They must change the concentrations of some ions, however, in order to attain this state. Magnesium is present in greater amounts in seawater than is desirable in their body fluids and must be eliminated. These organisms ion regulate even though they are not in danger of volume changes.

Marine organisms that evolved from freshwater or terrestrial ancestors are often hypoosmotic to seawater. They are in danger of desiccation as water from body fluids diffuses into the hyperosmotic ocean water. They also must regulate the types of ions that are retained and eliminated from their bodies.

Marine organisms may also be exposed to freshwater when they enter rivers, which dilute the salt content of the incoming tidal water. Under these conditions, the water is brackish—not as salty as the sea, but not as pure as freshwater. The criticality of this situation depends upon whether the organism is tolerant or intolerant of salinity changes. Organisms that can live in only a narrow range of salinities are called stenohaline. Organisms that are tolerant of wide ranges of salinities are called euryhaline.

Terrestrial organisms are always hyperosmotic to their environment, so they continually face desiccation in the air. They also must adjust the ion composition of their body fluids, because the foods that they eat may not have inorganic ions in the desired ratios and because some ions are always lost in urine.

One example of the influence of these effects concerns the interaction of oysters and the protistan parasite known as MSX. (MSX stands for "multinucleate sphere unknown," which refers to the protista *Haplosporidium nelsoni*.) The MSX organism survives in osmotic pressures greater than 0.4 osmolar. Oysters are osmoconformers which grow in saline, brackish, and nearly fresh water. At osmotic concentrations less than 0.4 osmole, oysters can survive and are unaffected by MSX. When rainfall is abnormally low, however, the salinity of brackish water increases, and oysters which were protected in low-salinity water are exposed to higher-salinity water, which allows the MSX organism to infect them.

Organisms exposed to tides may protect themselves from exposure to variations in osmotic pressure by sealing themselves off, the way snails and bivalve mollusks do. Others may move offshore to more saline waters or onshore, away from the increasing salinity. Worms that burrow in the sediments of salt water are protected from transient changes in salinity because there is little exchange of solutes with the overlying salt water.

The vertebrates adapted to their various environments by using hormones to regulate salt and water balance. Because of the differing demands of aquatic and terrestrial environments, in different groups, the same hormone may have opposite effects, but that effect is always to maintain the optimal osmotic pressure to ensure survival.

—Judith O. Rebach

See also: Kidneys and other excretory mechanisms; Lakes and rivers; Marine biology; Nutrient requirements; pH Maintenance; Thermoregulation; Tidepools and beaches; Water balance in vertebrates.

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OSTRICHES AND RELATED BIRDS

Type of animal science: Classification
Fields of study: Anatomy, ornithology, physiology, population biology

The ostrich and its relatives are famous for their exotic appearance and for being flightless birds. They are the oldest type of bird alive today, dating back eighty million years to the age of dinosaurs.

Principal Terms

MOLT: to shed old feathers and grow new ones
MONOGAMOUS: having only one mate
NOMADIC: travels distances in search of food
OMNIVOROUS: eating both animal and plant foods
POLYGAMOUS: having more than one mate
PRECOCIAL: in birds, those that are down-covered, fully developed, and active at birth

Ostriches belong to a striking group of flightless birds known as ratites, that also includes emus, cassowaries, rheas, and kiwis. Ratites have flat, smooth breastbones that lack a keel to which flight muscles could attach. They are thus unable to fly, and have weak wing muscles. They do use their wings, spreading them out to help them cool off, and also to splash water when bathing. Ratite feathers are different from those of flying birds. The individual strands are not interlocked, and thus they are soft and billowy and air passes right through them. Their plumes have long been admired by humans and used for decoration and adornment. As with other birds, their feathers function as protection from the elements, and ratites preen, spreading waterproofing oil to their feathers with their beaks. They also molt once a year. Ratites have heavy, strong bones and powerful leg muscles, and are able to run swiftly. They are omnivores, feeding on a variety of grasses, plants, seeds, fruit, insects, and small animals. There are many farms in the United States that raise ostriches, emus, and rheas for their feathers, hide, meat, and oil. In their native countries, ratites are hunted or raised for their feathers and as food. Ostriches have also been tamed for riding and for pulling carts.

Ostrich Characteristics

Ostriches have long necks and legs and are the largest living birds. Males stand eight feet tall, and weigh three hundred pounds. The ostrich can take strides of twenty-five feet and outrun pursuers at speeds of forty miles per hour. If cornered, the ostrich has a powerful kick that can maim an enemy. It has two toes on each foot, and a razor-sharp toenail that both grips the ground while running and can slash the flesh of its enemy.

Male ostriches are black with white plumes on their tail and wings. Females are grayish-brown. The head and legs are featherless. The neck is covered with down and is red or grayish. The ostrich has huge eyes with long protective lashes and has keen eyesight for spotting danger a long way off. It can make loud hissing and roaring noises.

Ostriches are native to Africa; they are nomadic and graze on open savanna. They often follow herds of zebras or antelope, catching insects and small animals stirred up by their hooves. They swallow sand and stones to help grind up their food. Contrary to popular belief, they require a regular water supply.

When mating, male ostriches make a booming call and perform a courtship dance for the females. They are polygamous, taking three or more

Ratite Facts

Classification:
Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Class: Aves
Orders: Struthioniformes (ostriches); Casuariiformes (emus, cassowaries); Rheiformes (rheas); Apterygiformes (kiwis)
Families: Struthionidae (ostriches, one genus, six species); Dromaiidae (emus, one genus, three species); Casuariidae (cassowaries, one genus, four species); Rheidae (rheas, two genera, nine species); Apterygidae (kiwis, one genus, seven species)
Geographical location: Southern Hemisphere—Africa (ostrich), Australia (emu and cassowary), New Guinea (cassowary), South America (rhea), New Zealand (kiwi)
Habitat: Semidesert and open plains (ostrich, emu, rhea); forests (cassowary, kiwi)
Gestational period: One breeding cycle per year; incubation varies from forty days (ostrich) to eighty days (kiwi)
Life span: Ostriches average forty years in the wild, up to eighty years in captivity; others average ten to twenty years
Special anatomy: Unkeeled breastbone, tiny wings, unbarbed feathers, solid bones, strong muscular legs

hens as mates. The male scratches a shallow pit into which each female lays up to a dozen eggs, for a total clutch size of up to thirty eggs. This communal nesting behavior is unusual among birds. The male shares incubation with one dominant female. The male sits at night and the female during the day. Ostriches lay the largest eggs of all living birds, seven inches long and three pounds. The eggshell is very tough and hard for predators to crack open. The parent will sometimes lay with its neck outstretched on the ground when danger threatens, giving rise to the legend that they bury their heads in the sand. They may also feign injury to lure predators away from the nest. Newborn chicks are precocial and instinctively know how to search for food. They are full adults by three years of age.

Ostrich Relatives

Rheas live in flocks on grasslands in South America. They are similar to ostriches in behavior and appearance, although they have three toes on their feet, as do most of the other ratites. They are brownish in color and can be five feet tall. They are polygamous, but only the male incubates the eggs.

Emus live on plains in the Australian outback, and flock nomadically according to rainfall patterns and the resulting food supply. The emu is the second largest flightless bird, nearly six feet tall and eighty-five pounds. It has brown feathers and a loose, moplike tail. Emus are monogamous.

Cassowaries live in the rain forests of New Zealand and northeastern Australia. They are solitary and territorial, pairing only to mate. They feed primarily on fruit fallen from trees. Cassowaries have black, loosely hanging feathers, and the wings are composed only of quills. They have bright blue heads and colorful wattles. A distinctive bony crown on the head called a casque helps them push through the dense forest, and is also used to turn over litter in search of food.

Kiwis are elusive, nocturnal birds that live in the forests of New Zealand. They are the smallest ratites, about the size of a chicken. They have round, brown-feathered bodies, short legs, four toes, and run by placing one foot directly in front of the other. Their long, slender beaks have nostrils at the very tip, and are used to probe the ground to locate worms, beetles, spiders and larvae by smell. Males have a shrill, whistling mating call. Females lay only one or two eggs that are enormous in proportion to their body size.

—Barbara C. Beattie

See also: Birds; Fauna: Africa; Fauna: Australia; Fauna: South America.

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Ostriches are one of the few species of flightless birds, but they can run very fast on their long legs. (Corbis)

OTTERS

Types of animal science: Behavior, classification, ecology
Fields of study: Ecology, wildlife ecology, zoology

Otters are found in many parts of the world where there is clean, flowing water. Otters are large members of the weasel family, the Mustelidae, which includes mink, skunks, and badgers.

Principal Terms

CARNIVORE: an animal that feeds on other animals for its diet

DELAYED IMPLANTATION: a process of delaying the implantation in the uterine wall of the fertilized egg

DORSAL: the back portion of an animal

NOTOCHORD: a dorsal, flexible, rodlike structure extending the length of a vertebrate's body; serves as an axis for muscle attachment

PELAGE: a mammal's fur coat

PREDATOR: an animal that preys on other animals for its food

Playful and proud, river otters are born to have fun. At least, it appears that river otters are having fun, because of their playful antics with each other, as well as their facial and body expressions. By any measure, otters are extremely curious and intelligent mammals.

River Otters

Adult river otters reach a length of about 127 centimeters, including their tails, which are nearly one third of that length. Adults weigh between five and fourteen kilograms. Females are slightly smaller than males.

River otters have a dense, short fur with great water resistance. Air is trapped beneath their dense furry coats and acts as insulation against the cold water, where these mostly aquatic mammals feed. Otters roll and rub themselves on sand, rocks, old logs, and even snow in their coat grooming activities. These carnivorous mammals mostly feed on fish. Crayfish also serve as diet items when abundant. Researchers have found that river otters feed directly on fish proportion-

Otters are playful, intelligent, and very curious. They spend much of their lives in and near water. (Corbis) ally to their availability and inversely to the fish's swimming ability.

Shelters that have been abandoned by other animals are frequently used by river otters, such as old beaver dens or riverbank excavations. On occasion, river otters use rock piles and log jams as dens. Some investigators have discovered nests along river and stream banks which river otters had constructed of aquatic vegetation.

Mating activity usually occurs in the water, although there are reports of mating on land. The breeding season is usually late winter to spring. Litter size is between one and six cubs. The newborn otters have full pelage, but their eyes are not open and they have no erupted teeth. Females wean their young at about three months of age.

Several predators, including bobcats, foxes, and alligators, have been observed dining on river otters. Humans also have made their impact on otter populations in at least three ways: habitat destruction, water pollution, and overtrapping.

Otter Facts

Classification:
Kingdom: Animalia
Phylum: Chordata
Class: Mammalia
Order: Carnivora
Family: Mustelidae
Subfamily: Lutrinae
Genus and species: Lutra canadensis (North American river otter), *L. lutra* (European river otter), *L. felina* (marine otter), *L. provocax* (southern river otter), *L. longicaudis* (neotropical river otter), *L. umatrana* (hairy nosed otter); *Hydrictis maculicollis* (spot-necked otter); *Lutrogale perspicillata* (Indian smoothed-coated otter); *Aonyx cinera* (oriental short-clawed otter), *A. capensis* (Cape clawless otter); *Pteronura brasiliensis* (giant otter); *Enhyda lutris* (sea otter)

Geographical location: Until the eighteenth century, North American river otters were found in all major water courses in the United States and Canada; presently, river otters are scattered in several river systems across the United States and Canada, and many river otters have been reintroduced into river systems where they once flourished

Habitat: Exclusively aquatic, adaptable to many nonpolluted aquatic environments

Gestational period: 288 to 375 days, with delayed implantation

Life span: Ten years, with a maximum of twenty-three years

Special anatomy: Webbed feet

Sea Otters

Another interesting otter is the sea otter. These seafaring mammals are confined to the northern Pacific Ocean. Being the largest in the family Mustelidae, sea otters weigh between twenty-seven and thirty-eight kilograms and attain a length of about 148 centimeters. Unlike seals and whales, which have a fat layer (blubber) for insulation, sea otters rely on air trapped beneath their densely packed pelage. Some researchers have estimated the number of hairs in a sea otter's coat to be 800 million.

Sea otters, just as their freshwater cousins, have delayed embryo implantation. Females usually produce one pup in a litter. The pup is unable to swim or dive until it is two to three weeks old.

Food preferences of sea otters include abalones, sea urchins, clams, and crabs. It is a common practice of sea otters to eat while floating on their backs. Furthermore, sea otters use rocks to open the shells of their diet items, making them a member of a small group of animal tool users.

Unlike other members of the Mustelidae, sea otters lack functioning anal scent glands. Also, unlike most carnivores, sea otter teeth are adapted to crushing their prey, rather than tearing.

—*Sylvester Allred*

See also: Fur and hair; Lakes and rivers; Marine animals; Skunks; Tool use; Weasels and related mammals.

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OWLS

Type of animal science: Classification
Fields of study: Anatomy, ornithology, physiology, zoology

Any of the Strigiformes, a group of birds with highly specialized characteristics for nocturnal activity, including soft feathers and enhanced hearing and eyesight.

Principal Terms

ASYMMETRICAL EARS: in some species of owls, the ears are of unequal size and located unequally on the sides of the head

ASYNCHRONOUS: an uneven event; in hawks and owls, the staggered hatching of eggs that results in a nest of different-aged young

FACIAL DISK: the distinctive concentric circles of feathers that encircle the eyes of owls, helping direct sound toward the ears

OWL PELLETS: compacted packets of undigested prey that is regurgitated. Owl pellets may be used to determine food habits

OWLS: any of the strigiformes, a group of birds with highly specialized characteristics for nocturnal activity, including soft feathers and enhanced hearing and eyesight

NEST BOX PROGRAMS: construction and placement of nest boxes in suitable habitat to provide nesting platforms for specific birds of prey

PAIR BOND: close relationship between a male and female for breeding purposes

With their rounded facial disk encircling their large, forward-looking eyes, owls are the most recognizable of birds. Their unique traits also include superb auditory abilities and soft feathers for silent flight. Sharp talons for catching and killing prey and powerful bills for tearing flesh complete their basic characteristics. Most owls are colored in drab shades of brown, buff, and gray, either spotted or streaked, which helps conceal them during daylight hours. Woodland owls tend to be darker, while those of open country are lighter and paler. Thus, the eastern North American race of great horned owl (*Bubo virginianus virginianus*) is much darker than the pale northern race (*B. v. lagophonus*) of interior Alaska and the Yukon. A few smaller owls have rounded, eyelike disks on the back of their head to deter predators. Although once thought to be the nocturnal kin of hawks and eagles, owls are actually most closely related to the frogmouths and nightjars. The similarities between hawks and owls result from the evolutionary convergence of morphological features that facilitate their roles as avian hunters of live animals.

The 205 species of owls are a widespread and successful group that occupies virtually all habitats on all continents, from tundra to tropics, and are even found on most oceanic islands. They range in size from the forty-gram sparrow-sized elf owl (*Micrathene whitneyi*) of the Southwest desert to the formidable eagle owl (*Bubo bubo*) of Eurasia, which may reach 0.6 meter in length and weigh forty kilograms.

All the owls are placed in a single order, the Strigiformes, in which two owl families are recognized. The family Tytonidae includes sixteen species of barn (*Tyto* sp.), grass, and bay owls (*Phodilus* sp.), defined by small, dark eyes set in a narrow skull with a heart-shaped facial disk. The other 189 species are loosely grouped in the family

Strigidae, all of which have rounded skulls and large, wide-set eyes in a concentric facial disk. Owls of both families are named for their plumage colors or patterns (the tawny owl, *Strix aluco*, the black-and-white owl, *Strix nigrolineata*, the spectacled owl, *Pulsatrix perspicillata*, and the spotted owl, *Strix occidentalis*), habitats (the barn owl, *Tyto alba*, and jungle owllet, *Glaucidium radiatum*), size (great gray owl, *Strix nebulosa*, and little owl, *Athene noctua*), power and strength (eagle owls, *Bubo* sp.), presence of ear tufts (great horned, long-eared, *Asio otus*, and short-eared owls, *Asio flammeus*), or for their distinctive songs (screech owls, *Otus* spp., saw-whet owls, *Aegolius* sp., and barking owl, *Ninox connivens*).

Throughout history, owls have been alternately revered and feared. To the ancient Greeks, the solemn owl was the bird of wisdom and a companion of their warrior goddess, Athena. The Romans attached more ominous signs and portents to the ghostly cries of owls in the night. During the Middle Ages, owls were thought to be the companions of witches and the harbingers of evil and death. Many Native American tribes placed owls on a higher footing. The Arikara Plains Indians had secret owl societies, in which initiates were adorned with facial masks of owl feathers, while the Pimi Indians believed spirits of departed warriors assumed the shape of owls. Thanks to enlightened conservation efforts, owls are at long last recognized as important, interesting, and beneficial birds and all are protected by law.

Hunting and Food

All owls are predators, hunting a variety of animals commensurate with their size and strength. Woodland owls mostly hunt by the perch-and-pounce method, but hawk owls (*Surnia ulula*), short-eared owls, and other open country species may forage, harrier-like, over fields and meadows in search of prey. Burrowing owls (*Speotyto cunicularia*) are more terrestrial than most, spending a good deal of time running across the ground pursuing insects and small mammals. Most owls have broad wings—shorter in woodland species that maneuver in vertically complex habitats, longer and more hawklike in species that hunt open

The owl's soft, fluffy feathers allow it to fly in complete silence through the night. (Corbis) country or are migratory. Bird-chasing owls, such as pygmy owls (*Glaucidium* sp.) and brown owls (*Ninox* sp.) have longer wings and tails for agile flight.

Owls use their combination of large eyes, superb hearing, and silent flight to hunt and catch prey. Their relatively large wings and small bodies give owls a low wing loading which, combined with soft, fluffy feathers, enables the quiet flight that makes owls such efficient nocturnal hunters. The large eyes of owls are densely packed with light-gathering rods for seeing in very low light, while the overlapping fields of their binocular vision enable precise parallax judgment of distance to prey. Head bobbing movements seen in many owls also help estimate distance and angle to prey.

If light is absent or nearly so, owls can continue to hunt, substituting ears for eyes. Studies by ornithologist Roger Payne have shown that barn owls, for example, can locate prey in total darkness entirely by sound. When an owl hears rustlings of prey, it turns its head toward the sound, using the facial disk of flattened feathers to direct and amplify faint sounds toward the ears set on either side of the wide, flat face to pinpoint the location of the source. The asymmetrical ears of some species—the right ear is larger and higher on the skull than the left—permits determination of vertical and horizontal direction to the sound. If the sound reaches the higher right ear first, then the source is from above; if it reaches both ears at the same time, the source lies straight ahead. By turning its head, the owl can determine the precise distance and angle of the flight path to the prey to within 1.5 degrees. When flying toward prey, the head is forward of the body to detect prey movements and make minor adjustments. Once within striking range, the owl extends its legs and spreads the talons in a wide oval to snare prey. Most prey are killed by the powerful, slashing talons, but larger animals may be dispatched by a bite to the back of the neck.

Owls tend to be opportunistic in their food habits, hunting a wide variety of mammals, birds, and other vertebrates. Rabbits, rats, and mice are staples of many of the large and medium-sized owls, but birds, lizards, snakes, insects, fish, and occasionally carrion are also consumed when available. The smallest owls, such as the elf owl, tropical screech owls, and boobook owls (*Ninox boobook*) are mostly insectivorous, while the larger and more powerful owls take hares, rabbits, and other medium-sized mammals and birds. The Eurasian eagle owl is a champion hunter, fully capable of killing chamois and foxes. With their long, bare shanks, the fishing owls (*Ketupa* sp.) of Africa and Southeast Asia spear fish from woodland streams or wade in the shallows to search for frogs, crabs, and crayfish.

Although some owls have a reputation for taking chickens and other poultry, most owls help keep injurious rodent populations in check. This awareness has led to the establishment of barn owl nest box programs in some inner cities to pro-

Owl Facts

Classification:
Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Class: Aves
Order: Strigiformes
Families: Tytonidae (barn owls); Strigidae (owls), with subfamilies Buboninae (true owls, eighteen genera, eighty-three species), Striginae (long-eared and dish-eyed owls, six genera, twenty-six species)

Geographical location: All continents except Antarctica

Habitat: Virtually all habitats

Gestational period: Around thirty days, depending on species

Life span: Depending on species, three to ten years

Special anatomy: Rounded facial disk that directs sounds toward the ears; soft feathers for soundless flight; sharp talons and beak; large eyes with densely packed rods to enhance night vision; ability to turn the head up to 270 degrees; some species have asymmetrically spaced ears to assist in locating prey by sound vide nest sites for an urban owl population to control rodents.

Small prey is swallowed whole but larger prey is broken into pieces. Prey is digested to a semiliquid consistency and then passed on to the intestinal tract. The undigested remains, mostly fur, feathers, bones, teeth, and other indigestible substances, are compacted into a small ball which is regurgitated in a reflexive, choking motion that casts the pellet out. The process takes several hours, so that today's pellet contents represent yesterday's meal. Owl biologists collect and analyze the pellets to determine food habits and impact of owl hunting on different species.

Owl Seasons

Tropical owls may breed at any time of year, but temperate owls commence breeding activity in late winter or early spring. Males claim a territory with territorial and courtship songs and postures. Songs of almost all owls consist of a series of hoots or wailing cries that echo ghostly through the night skies. Many owl species pair for life. Courtship may involve alternate duetting, billing and cooing, and mutual preening. Males of many species present food offerings, both as a courtship gift and to display their hunting ability.

Following courtship the female selects a suitable nest site. Although snowy owls (*Nyctea scandiaca*) of the Arctic select a spot beneath a clump of tundra sedge, most owls choose secluded tree hollows, cavities in cliffs, rock outcrops, or caves. Some species may also appropriate hawk or squirrel nests. Nest improvement usually consists of scraping a shallow hole or lining the nest with a few breast feathers. The oval or nearly oval eggs are usually laid at two-day intervals, but incubation begins with the first egg, resulting in a nest of different-aged young. The female incubates the eggs and the male brings food to the female or to a delivery site near the nest. The male may replace the female on the nest for short periods while she hunts, but his role in incubation is unclear.

Recently hatched young are typically fed pieces of food by the female. Later the adults simply deposit food at the nest and allow the young to pick and tear at it. Nest defense is weak or nonexistent during the early stages of nesting, but intensifies when young are in the nest. Defense varies from alarm calls and vigorous bill clacking in smaller species to aggressive and determined attacks by great horned owls and other large species. The female is usually most active in nest defense.

The fledged young typically remain in company of the adults for a few weeks before dispersing in search of new territories, usually in late summer or early fall. This is the most dangerous period of their lives, as they must perfect their hunting skills while avoiding enemies.

Longevity varies greatly; great horned owls and other large species may live ten or more years but the life span of smaller owls is usually only a few years. Other than humans, owls have few enemies. Larger owls prey on smaller owls while ravens and crows steal an occasional egg. Humans continue to be the main threat to owl populations. About thirty-five species are currently listed as threatened or endangered. Pollutants, disturbance, and collisions with vehicles and structures all take their toll of owls, but habitat loss factors most heavily. Several island races have disappeared following habitat alteration or introduction of exotics, and island populations continue to be at risk.

—*Dwight G. Smith*

See also: Beaks and bills; Birds; Claws, nails, and hooves; Domestication; Feathers; Flight; Hearing; Molting and shedding; Nesting; Predation; Respiration in birds; Vision; Wildlife management; Wings.

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PACKS

Types of animal science: Behavior, ecology
Fields of study: Ecology, ethology, population biology, wildlife ecology, zoology

Packs are social groups of carnivores, consisting of one or more families. They are generally highly cooperative for the purposes of rearing young and capturing food, particularly prey that is larger than any one member of the pack. These social packs are often called prides, clans, troops, schools, or packs.

Principal Terms

ANTIPREDATOR BENEFITS: benefits that come from actions that protect individuals from being killed
CARNIVORES: animals that eat the flesh of other animals
DOMINANCE HIERARCHIES: ranks of individuals within a group

Packs occur whenever animals group together in highly organized social systems for traveling, hunting, feeding, and sleeping, usually with bonds of attachment between all members. These social units tend to be fairly stable in composition, in comparison to most herds. This stability results in a social hierarchy, commonly called a dominance hierarchy, in which individuals are ranked in order of the number of other animals below them. Dominance hierarchies are maintained by dominant animals threatening subordinates, but fights are rare. Generally, subordinates engage in appeasement behaviors or avoid the dominant individual(s) altogether.

Dominance characteristics can be linked to body size, age, or weaponry. However, in some packs, dominance is inherited. This is common in baboon and macaque monkey troops, and in hyena clans, and is dependent upon the mother's rank. Females can move up in status every time a younger sister is born; however, several subordinates can form a coalition to challenge an individual above them in status.

Advantages to dominant animals are many. Greater access to food is one common benefit, and in some packs only the dominant pair breeds while the subordinates help to rear their young. Costs to dominants are that they are frequently challenged and run a greater risk of being killed or injured.

Packs and Predation

Predatory methods differ among species that form packs. Lions, who do not display endurance running, rely on stalking their prey and then rushing. During the rushing phase, lions will target any individual that appears to be slower or weaker than others in the prey herd. This tactic, also used by wolves, requires the predator to approach the prey very closely prior to rushing. In contrast, African wild dogs are known as coursers, chasing their prey for many miles until they can either drive it into other pack members or exhaust it. Hunting success in these dogs is very high. Hyenas vary their hunting tactics based on prey species. For attacks on wildebeest, they rush the herd, run for a while, stop to choose a target, and then resume the chase. As the chase continues, more and more hyenas join, and they generally take down their prey when it turns or runs into a lake or stream. They rely upon sheer numbers to overwhelm their target.

Theoretically, the formation of packs allows individuals within the group to exploit more food resources than they would be able to do on their own. In some pack species, this is the case: Cooperative hunts of lions are more successful than those by solitary lions, and there is some evidence to suggest the same for African wild dogs and hyenas. However, the cooperation does not necessarily increase the amount of food available for each member of the pack; in some cases, the nutritional intake per individual decreases with an increase in the size of the pack. Nonetheless, packs may be more able to protect their kills from predators and thus may be more capable of consuming prey completely than could one individual. Packs may also be more successful at driving other packs off from a kill; lions are known for relying on the kills of hyenas for up to half of their food. Hyenas form clans of up to sixty individuals, but these clans break up when food is scarce. Similarly, lions may form larger prides when food is common, but may split into pairs or threesomes as food becomes scarce.

Packs and Rearing of Young

If food per individual is not increased with increasing pack size, then other reasons must be present for the establishment and continuation of a pack. Suggested benefits include better defense of cubs against infanticide by outside coalitions of males that take over the pack (common in lion prides), higher reproductive success because all pack members share in feeding the offspring, and providing food for young while they grow to maturity, thereby ensuring that offspring will survive.

Rearing young in a group can benefit the young because of opportunities to learn from more than

Wolf Packs

Wolves are one of the best-known examples of animals that form packs for cooperative hunting and rearing of cubs. Most packs consist of fewer than eight members, although two or more packs can temporarily come together. When this happens, a pack may accept one member of another pack, while rejecting and chasing other members away. The packs always include a breeding pair of adults, some pups, subadults, and other adults, some of which may be allowed to breed in addition to the dominant pair. Packs can produce up to six cubs per year, and more than one female can reproduce, but often the dominant female will interfere with the care of the subdominant female's cubs.

Wolves prey on deer, moose, buffalo, sheep, caribou, and elk. The stimulus for beginning a hunt is apparently the completion of consumption of a previous kill. Wolves typically pursue prey by direct tracking, although they can occasionally come upon prey by chance encounter. Once they have located their prey, which usually occur in herds (except moose), they begin stalking until they get within feet of their targets. They then rush the target and chase it. Chases can last for less than a mile or for long distances over several days. They focus on the weakest targets: young, old, and sick prey. The wolves can injure a prey animal and then leave it alone for several days, resuming harassment until the prey can no longer rise and run. The pack then attacks from all sides to kill.

Wolves have been described as hunting in an extremely cooperative manner. However, what is more generally observed is that wolves in a pack attack the rear quarters of their prey, and the weight of many wolves biting and slashing on this area helps to bring the prey down. Wolves apparently have a low hunting success rate, which means that they must hunt frequently and test many individuals within a herd before finding one that displays some characteristic likely to be disadvantageous. While many have postulated that wolves form packs to facilitate food capture and that an increase in the pack size will help to increase the amount of food captured per individual, there is, in fact, a negative relationship between pack size and food available per wolf. Packing behavior may instead be more dependent on cooperation between kin where adults can more efficiently share their food with offspring, and young can obtain more food by remaining with their parents than they could by hunting on their own.

Baboon Troops

Hamadryas baboons form groups consisting of a dominant male, one to four females and their offspring, and some accessory males. A number of groups can come together to form bands of forty to fifty individuals. At night, these bands can coalesce to form troops of one hundred to over seven hundred individuals. Groups seem to form for mating purposes and care of the young. Bands are distinct feeding units and troops seem to avoid protection against nocturnal predators. A troop may range over an area comprising three to six square miles, and baboons move in troops to cover this vast area, gathering food, and congregating at water holes. While on the move, the subordinate males take the lead, followed by older juveniles and nonreproductive females. Females with infants and the most dominant males take up the middle positions, and other subdominant males bring up the rear. If a predator approaches the troops from any direction, it must encounter males. Many observers have reported that leopards, cheetahs, lions, and dogs can be run off by the males. Antipredator benefits seem to be one of the major benefits of this species' sociality, but adoption of infants and protection of juveniles from harassment also are known. In contrast to hamadryas baboons, gelada baboons have a social organization that is more similar to that of herding ungulates in that it varies with food availability and consists of distinct types of herds: harem herds, bachelor herds, and juvenile herds. Antipredator benefits dominate.

In both hamadryas and gelada baboons, play behavior by infants and juveniles serves to teach them all the important skills that must be learned and practiced. Thus, in addition to providing protection against predators, grouping in baboons serves to facilitate learning in offspring. Finally, grouping provides advantages because these species' food sources are clumped, and safe sleeping areas are limited.

one adult. It can also provide the young with practice in certain tasks that later prove important when the offspring are on their own. Cooperative hunting can provide young with the opportunity to learn hunting skills from their elders. Generally, this benefit occurs in longer lived species that produce only a few young per year per female.

The formation of packs tends to occur in groups where kin form the nucleus of the association. Dominance hierarchies are common in such packs and serve to stabilize the relationships among group members. Benefits are then realized in terms of hunting larger prey, spreading food resources between the older and younger generation, help in rearing young from all or most members of the pack, and dissemination of skill learning from adults. In a few packs, associations can serve an antipredatory function or can allow the defense of resources that would otherwise be taken by some other species or group.

—Kari L. Lavalli

See also: Communities; Competition; Demographics; Groups; Herds; Hierarchies; Learning; Mammalian social systems; Offspring care; Predation; Reproductive strategies; Territoriality and aggression.

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PAIR-BONDING

Type of animal science: Behavior
Fields of study: Anthropology, ethology, ornithology, zoology

Pair-bonding is the formation of attachments or relationships of various durations for purposes of reproduction and care of the young, relationships that may appear analogous to marriage and family in humans.

Principal Terms

BOND, BONDING: the tie or relationship between opposite-sex partners in a pair bond

BONDING BEHAVIORS: behavior patterns that establish, maintain, or strengthen the pair bond

CONSORT PAIR, CONSORTSHIP: a temporarily bonded pair within a polygamous group

LONG-TERM PAIR BOND: pair bonding that continues beyond a single reproductive period

MONOGAMY: exclusive pair-bonding between one male and one female

PAIR, PAIRING: may refer to mating, sexual coupling (or copulation) or to formation of a pair bond, depending upon the context

POLYGAMY: a mating system in which one male mates with several females (polygyny) or one female mates with several males (polyandry)

PROMISCUITY: a mating system in which sexual partners do not form lasting pair bonds, where their relationship does not persist beyond the time needed for copulation and its preliminaries

In the animal world, there is a great variety of ways in which males and females pair or associate for reproductive purposes (called mating systems). While some animals pair with more than one member of the opposite sex (polygamy), others pair exclusively with only one mate (monogamy). While some animals associate only long enough to copulate (promiscuity), other animals form pair bonds that last for varying lengths of time, from one reproductive period (until young leave the nest) to a lifetime. While some pair-bonding has been observed in all vertebrate classes, and even in some invertebrates (some crabs and insects), it is particularly common in birds, while infrequent in fish and mammals.

Pair-Bonding in Birds

Most bird species are monogamous, although some are polygamous, and a few may be promiscuous. In some birds, such as prairie chickens, male and female pair only for copulation, after which the female is on her own to nest and parent. However, most birds pair bond, remain with their mates, and cooperate in some way until their young can leave the nest and survive independently. Some birds, such as song birds, pair bond for only a single breeding season, while others, such as swans, geese, penguins, and albatrosses, exhibit pair-bonding for more than one season, sometimes for life.

The American robin, for example, is mostly monogamous while it pair-bonds and shares parenting for one breeding season. Typically, in the spring, male robins are the first to migrate north. When the females arrive about a week later, the males have already selected territories and call or carol as though advertising for a mate. Courtship, involving three types of songs (only the males sing) and feeding, leads to mating and pair-bonding. The female builds a nest and lays her clutch of usually three or four eggs. While the female incubates the eggs, the male stands guard nearby, though he may help with the incubation as well. After the eggs hatch, both parents forage and feed the young. When the young leave the nest, they still need approximately two weeks of feeding and parental care before they are mature enough to survive independently. While the father provides this care, the mother repairs the nest and lays another clutch of eggs. American robins typically have two or three broods per year. In this case, the pair bond usually endures for the breeding season, but not through migration south for the winter and the nonbreeding season.

Birds are the most likely of all animals to pair-bond for life. (Adobe)

Pair-Bonding in Fish

Most fish do not form lasting pair bonds. An interesting exception, however, is the seahorse. At the beginning of the seahorse breeding season, males and females court for several days. The female produces eggs, and when they reach maturity, she deposits them into an egg pouch on the male seahorse's trunk. Then she swims away. Male seahorses typically remain in a habitat of approximately one square meter, while females range over an area that may be a hundred times as large. During the male's pregnancy, the female returns every day for a short, five- to ten-minute morning visit. During this visit, the seahorse pair exhibit social interaction and bonding behaviors reminiscent of courtship. Afterward, the female swims away until the next day, when she returns for another visit. After two to three weeks of pregnancy, the male gives birth to a few dozen or more baby seahorses during the night. When his mate returns in the morning for their daily visit, the male is ready for courtship, and the mating and reproductive cycle starts over again. Females have been observed to refuse to mate with other males during their mate's pregnancy, and so appear to be monogamous for the breeding season. In laboratory experiments, where mates were separated during pregnancy and the female interacted with another male, the original pair bond was broken. Thus, the social interaction and bonding behaviors that occur during the seahorse couple's short daily visits appear to be important factors in maintenance and longevity of pair-bonding.

Pair-Bonding in Mammals

Polygamy is the most common mating system among mammals. Within polygamous (or promiscuous) groups, such as baboons and chimpanzees, a male and female may pair temporarily and separate themselves somewhat from the group, while engaging in social grooming and sexual activity. Temporary pairings that do not endure to the end of a reproductive cycle are referred to as consort pairs or consortships in the primate literature. When pair-bonds in a polygamous system are more lasting, the social structure is sometimes called a harem.

Only a small minority (3 to 5 percent) of mammals exhibit monogamous pair-bonding. Gibbons, the smallest of the apes, are particularly interesting because they are the exceptional case, and exhibit not only long-term monogamous pair-bonding but a social organization somewhat analogous to the human nuclear family. Gibbons pair at eight to ten years of age, and have five to six offspring, spaced about three years apart, over their ten- to twenty-year reproductive lifetime. Gibbon offspring remain with their family groups until they approach or reach sexual maturity, when they may leave voluntarily or be evicted by the same-sex parent. Gibbons are territorial, and family members cooperate as needed to defend both territory and mate or family. Just prior to sunrise every morning, mated males sing solo songs that can be heard up to a kilometer away, seemingly identifying their territory as occupied. Later in the morning mated females sing their own songs, and join their mates in singing duets, which appear to publicize both territory and pair-bonding.

Pair-Bond Formation and Maintenance

Formation of a pair-bond usually involves the behavior patterns of courtship and mating. Usually, the male initiates pair formation, while the female decides whether a bond is formed or not. How long a pair-bond endures depends upon various factors. Many animal pairs maintain and strengthen their relationship by continuing the bonding behaviors that were initially used in courtship. Some animals maintain close physical proximity, groom each other, communicate with movement (display) or with vocalizations (call or song), or share food, nests, and territory. Reproductive success and dependency of young also appear to maintain pair-bonding.

—John W. Engel

See also: Birth; Breeding programs; Communication; Copulation; Courtship; Estrus; Grooming; Mating; Pregnancy and prenatal development; Reproduction; Reproductive strategies; Reproductive system of female mammals; Reproductive system of male mammals; Sexual development; Vocalizations.

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PALEOECOLOGY

Type of animal science: Ecology
Fields of study: Evolutionary science, paleontology, zoology

Paleoecology is the study of ancient organisms and their relationships to one another and to their environments. The characteristics of ancient environments may be determined by examining rock and fossil features.

Principal Terms

CATASTROPHISM: a belief that the earth and its features are the result of sudden, violent upheavals that occurred in the relatively recent past

DENDROCLIMATOLOGY: the study of tree-ring growth as an indicator of past climates

FOSSIL: any trace of the presence of an ancient organism, whether track, imprint, or preserved remains

PALYNOLOGY: the study of pollen and spores; also called paleopalynology

RADIOCHRONOMETRY: the determination of the age of an object using radioactive isotope decay rates

TAPHONOMY: the series of events between the death of an organism and its preservation as a potential fossil; also, the study of such events

THANATOCOENOSIS: an assemblage of fossil species from a particular environment; a fossilized community; compare to biocoenosis, an assemblage of living species

UNIFORMITARIANISM: the belief that the earth and its features are the result of gradual biological and geological processes similar to the processes that exist today

Paleoecology is the study of ancient environments. As a field of science, it is most closely related to paleontology, the study of fossils. It is also related to paleoclimatology, paleogeography, and a number of other areas of study dealing with the distant past. All these disciplines have a handicap in common: Because they deal with the past, scientists are unable to apply the usual scientific criteria of direct observation and measurement of phenomena. When ecologists study present environments, direct measurements of environmental variables such as temperature, wind speed, current, soil moisture, and biological interactions can be taken. The organisms may be observed in their habitats—nesting, competing, eating, and being eaten. In order to make any conclusions about the past, scientists must assume at least one statement to be true without direct observation: The processes that exist in the modern universe and on the modern earth existed in the past.

Although one cannot observe any ancient falling objects, one assumes that the law of gravity existed in the past and that objects fell down; since rainfall occurs today, it must have occurred in the past. Similarly, paleontologists must assume that ancient plants and animals had tolerances to temperature, moisture, and other environmental parameters similar to those of modern organisms. This belief that “the present is the key to the past” is called uniformitarianism. It has been a key concept of the biological and earth sciences for almost two hundred years. Uniformitarianism does not include the belief that the ancient earth was like the modern earth in its life-forms or geography. During the early part of the nineteenth century, another worldview dominated: catastrophism, the belief that the earth is relatively young and was formed by violent upheavals, floods, and other catastrophes at an intensity unlike those of modern earth. Many catastrophists explained the presence of fossils at high elevations by the biblical Flood of Noah. The uniformitarian viewpoint prevailed and, although admitting that local catastrophes may be important, their long-term, earthwide importance was denied. It is interesting to note that catastrophism was revived in the 1980's to explain certain important events. The rapid extinction of the large dinosaurs at the close of the Mesozoic era has been attributed to the climatic changes associated with an alleged encounter between the earth and a comet—certainly a catastrophic event.

Types of Evidence About the Past

One of the most intensively investigated paleoecological problems has been the changing environments associated with the ice ages of the past million years. Analysis of pollen from bogs in many parts of the world indicates that there have been at least four advances and retreats of glaciers during that period. Evidence for this is the changing proportions of pollen from tree species found at the various depths of bogs. In North America, for example, spruces (indicators of cool climate) formerly lived much farther south than they do now. They were largely replaced almost eight thousand years ago by other tree species, such as oaks, which are indicative of warmer climates. This warming trend was a result of the latest glacial retreat.

Tree ring analysis not only enables paleoecologists to date past events such as forest fires and droughts, but also allows them to study longer-term cycles of weather and climate, especially those of precipitation and temperature. In addition, trees serve as accumulators of past mineral levels in the atmosphere and soil. Lead levels in tree wood showed a sharp increase as the automobile became common in the first half of the twentieth century because of lead additives in gasoline. Tree rings formed since the 1970's have shown a decrease in lead because of the decline in use of leaded fuels. Tree-ring analysis has also been a valuable tool for archaeologists' study of climatic changes responsible for shifting patterns of population and agriculture among native Americans of the southwestern United States.

Fossil evidence is the chief source of paleoecological information. A fossil bed of intact clam shells with both valves (halves) present in most individuals usually indicates that the clams were preserved in the site in which they lived (autochthonous deposition). Had they been transported by currents or tides to another site of deposition (allochthonous deposition), the valves would have been separated, broken, and worn. Similarly, many coal beds have yielded plant fossils that indicate that their ancient environments were low-lying swamp forests with sluggish drainage periodically flooded by water carrying a heavy load of sand. The resulting fossils may include buried tree stumps and trunks with roots still embedded in their original substrate and numerous fragments of twigs, leaves, and bark within the sediment.

Certain dome- or mushroom-shaped structures called stromatolites are found in some of the most ancient of earth's sedimentary rocks. These structures may be several meters in diameter and consist of layers of material trapped by blue-green algae (cyanobacteria). Such structures are currently being formed in shallow, warm waters. Uniformitarian interpretation of the three-billion-year-old stromatolites is that they were formed under similar conditions. Their frequent association with mud cracks and other shallow- and above-water features leads to the interpretation that they were formed in shallow inshore environments subject to frequent exposure to the air.

Relative oceanic temperature can be estimated by observing the direction in which the shells of certain planktonic organisms coil. The shell of *Globigerina pachyderma* coils to the left in cool water and to the right in warmer water. *Globigerina menardii* shells coil in an opposite fashion—to the right in cool water and to the left in warmer water. Uniformitarian theory leads one to believe that ancient *Globigerina* populations responded to water temperature in a similar manner. Sea-bottom core samples showing fossils with left- or right-coiling shells may be used to determine the relative water temperature at certain periods. Eighteen-thousand-year-old sediments taken from the Atlantic Ocean show a high frequency of left-handed *pachyderma* and right-handed *menardii* shells. Such observations indicate that colder water was much farther south about eighteen thousand years ago, a date that corresponds to the maximum development of the last Ice Age.

Fossil Shape and Content

Fossil arrangement and position can be a clue to the environments in which the organisms lived or in which they were preserved. Sea-floor currents can align objects such as small fish and shells. Not only can the existence of the current be inferred, but also its direction and velocity. Currents and tides can create other features in sediments which are sometimes indicators of environment. If a mixture of gravel, sand, silt, and clay is transported by a moving body of water such as a stream, tide, or current, the sediments are often sorted by the current and deposited as conglomerates—sandstones, siltstones, and shales. Such graded bedding can be used to determine the direction and velocity of currents. Larger particles, such as gravel, would tend to be deposited nearer the sediment source than smaller particles such as clay. Similarly, preserved ripple marks indicate current direction. Mud cracks in a rock layer indicate that the original muddy sediment was exposed to the atmosphere at least for a time after its deposition.

Certain minerals within fossil beds or within the fossil remains themselves can sometimes be used to interpret the paleoenvironment. The presence of pyrite in a sediment almost always indicates that the sedimentary environment was deficient in oxygen, and this, in turn, often indicates deep, still water. Such conditions exist today in the Black Sea and even in some deep lakes, with great accumulations of dead organic matter.

The method of preservation of the remains of the fossilized organism can be an indication of the environment in which the creature lived (or died). Amber, a fossilized resin, frequently contains the embedded bodies of ancient insects trapped in the resin like flies on flypaper. This ancient environment probably contained resin-bearing plants (mostly conifers), and broken limbs and stumps that oozed resin to trap these insects. Mummified remains in desert areas and frozen carcasses in the northern tundra indicate the environments in which the remains were preserved thousands of years ago.

Marks made on fossil parts by other organisms offer indirect evidence of the presence and activity of other species that might not have left fossil remains. Predators and scavengers can leave such marks on bones and shells by boring, scratching, and gnawing. One of the most controversial taphonomic problems in paleoecology is distinguishing between tooth marks left by animal scavengers and predators on bones and those marks left by the stone and bone tools of early human ancestors.

Studying Paleoecology

Fossils, especially fossil assemblages (thanatocoenoses), are the most commonly used indicators of ancient environments. The use of any fossil in interpreting the past must be subject to several qualifications. The fossil record is sparse for most groups of organisms because fossilization itself is a relatively rare event. Rapid burial of the remains and the presence of hard body parts (wood, shells, bones, and teeth) are only two of several fossilization prerequisites that must usually be met. This means that terrestrial organisms and soft-bodied organisms are seldom fossilized. Events leading to fossilization after the death of an organism (taphonomy) usually destroy the soft tissues through decay and scavenging and often disrupt and distort the remaining hard parts through transportation and weathering. An additional taphonomic problem is encountered when clumps or clusters of fossil remains are located. Without careful study, it is difficult to determine whether these assemblages are truly representative of the groupings of the organisms in life or if they are simply coincidental aggregations of such items as shells and limbs that were swept together by currents or wind and thus not indicative of the living situation and environment. Because of limitations on the interpretation of ancient environments by the use of fossilized body parts, trace fossils are often more reliable indicators of environmental conditions. Trace fossils are preserved tracks, burrows, trails, and other indirect indications of the presence of an organism. The presence of marine worm burrows, for example, can indicate environmental factors such as salinity and depth. Such traces are not transported from one site to another because transportation results in their destruction. Whenever these imprints are found, therefore, paleoecologists are able to make some inferences about the environment in which they were formed.

One of the most important methods to be mastered by paleoecologists is stratigraphy—the science of correlating and determining the age of rock layers with those of the fossils contained within these layers or formations. Rock layers or strata are not usually connected over large regions. While they might have been deposited as sediments at the same time and under the same conditions, subsequent erosion has usually made the layers discontinuous. Stratigraphers attempt to correlate discontinuous rock strata by measuring and describing them and by noting the presence of unique fossils called index fossils. If two strata are correlated, then they were probably deposited during approximately the same period, although there may be a gradation of conditions. For example, there may be a layer of sediment deposited at the same time, but under nearshore conditions at one spot and under offshore conditions at another. Relative ages are determined by using the law of superposition: Older rocks lie beneath younger rocks. One can say that a certain stratum is older than, the same age as, or younger than another layer, depending upon their relative positions. Absolute ages (estimated age in years before the present) are determined by measuring the amounts of certain radioactive elements within igneous rocks. Such radiometric age determinations are of less value for sedimentary rocks since they give the age of the minerals of the rock, not the age of the rock itself.

Uses of Paleoecological Research

Paleoecological data are applicable to other, related paleo-fields of the earth and life sciences. The study of fossils, paleontology, is enhanced by the inclusion of information about the fossil organisms' environments and relationships with other organisms. Paleontologists should attempt to reconstruct ancient environments because organisms did not exist alone or in vacuums: They lived in dynamic biological communities. Paleogeography relies heavily on paleoecological information to discern the locations, directions, and time intervals of glaciation, deposition of sediments, temperature, and other environmental variables. This information has been used to determine the past positions of continents and has been a valuable contribution to scientists' knowledge of continental drift.

Paleoclimatologists, who study ancient regional and planetwide conditions, must make use of local bits of paleoecological information to see the big picture of climate. One of the major concerns of paleoclimatology is the recognition of planetary climatic cycles and associated environmental and biological cycles. If there is a repeated recurrence of global environmental change, then predictions about future climatic change become more accurate and probable.

—P. E. Bostick

See also: Apes to humans; Communities; Demographics; Dinosaurs; Ecology; Ecosystems; Evolution: Animal life; Evolution: Historical perspective; Extinction; Fossils; Habitats and biomes; Human evolution analysis; Paleontology; Plant and animal interactions; Predation.

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PALEONTOLOGY

Types of science: Anatomy, classification, ecology, evolution
Fields of study: Anatomy, anthropology, evolutionary science, human origins

Paleontology is the branch of geology that deals with prehistoric forms of life through the study of fossil animals, plants, and microorganisms. Many bursts of evolution and many extinction events have been uncovered by this field.

Principal Terms

- EVOLUTION: the science that studies the changes in astronomical bodies, the earth, and living organisms and creates explanations of how changes occur and how things are related.
- FOSSILS: the hardened, petrified (rocklike) impressions of animal, plant, and microbial remains
- GEOLOGICAL PERIODS: the twelve divisions in successive layers of sedimentary and volcanic rocks, which are differentiated by the distinctive fossils present within each division
- MASS EXTINCTIONS: five events in the history of life that resulted in the disappearance of more than 75 percent of all species
- PALEONTOLOGY: the branch of geology that deals with prehistoric forms of life through the study of fossil animals, plants, and microorganisms
- PLATE TECTONICS: the branch of geology that studies the fragmentation of the earth's crust into plates (crust fragments), the movement of plates, and the subduction or uplifting of plates
- RADIOISOTOPES: unstable elements that decay into stable forms at a constant rate, which are used to determine how long ago volcanic rocks solidified

When organisms die, their soft parts usually decompose into their constituent elements, leaving no trace. The harder parts, such as wood, exoskeletons, bones, teeth, and shells, may survive many years, but eventually even they decompose. Sometimes, however, organisms are buried in an avalanche, are covered by volcanic ash, or sink into mud. If the burial inhibits decomposing microorganisms and prevents the rapid replacement of the buried tissue with inorganic material, a fossil is likely to form.

There are a number of different ways in which fossils form. Most fossils form through a process of mineralization. In this type of fossilization, buried material is slowly replaced by minerals such as calcium carbonate ($CaCO_3$), silicate (SiO_2), pyrite (FeS_2), sulfate ($Ca [SO_4] - H_2O$), and iron-phosphate ($Fe_3[PO_4] - H_2O$). These mineralized remains can be separated from the surrounding sediment and may superficially appear to be the actual remains. Sometimes fossils can form when the remains completely decompose. Organisms encased in a highly compacted sediment or covered by volcanic ash that quickly hardens, imprint into the covering a replica of their surfaces. When the organisms degrade, the space fills with minerals that harden. This is how surface replicas of organisms form. Mineralization and replication are responsible for most fossils. In some cases, organisms crawling through or stepping in sediment leave imprints of their passing, called trace fossils. Imprinted sediment explains some fossils.

Microorganisms, plants, and animals often get caught in tree sap (resin) that ages over millions of years, first into copal and then into amber. Amber

Continued on page 1206

The Leakey Family

Louis Leakey
Born: August 7, 1903; Kabete, Kenya
Died: October 1, 1972; London, England
Fields of study: Anthropology, evolutionary science, human origins, paleontology
Contribution: African paleontologist-anthropologist whose most notable works were the characterization of a nearly complete 1.8-million-year-old skull of *Australopithecus boisei* and the piecing together of a 1.8-million-year-old skull of *Homo habilis*.

Mary Leakey
Born: February 6, 1913; London, England
Died: December 9, 1996; Nairobi, Kenya
Fields of study: Anthropology, evolutionary science, human origins, paleontology
Contribution: African paleontologist-anthropologist whose most notable works include the discovery of 3.6-million-year-old humanlike foot prints made by *Australopithecus afarensis*, the piecing together of the 1.8-million-year-old skull of *Australopithecus boisei*, and the characterization of the nearly complete 1.5-million-year-old *Homo erectus* fossil known as Turkana boy.

Richard Leakey
Born: December 19, 1944; Nairobi, Kenya
Fields of study: Anthropology, evolutionary science, human origins, paleontology
Contribution: African paleontologist-anthropologist, son of Louis and Mary, whose most notable works include the piecing together of a 1.9-million-year-old skull of *Homo habilis*, the reconstruction of a 1.8-million-year-old skull of *Homo rudolfensis*, and the unearthing and characterization of Turkana boy.

Maeve Leakey
Born: 1948
Fields of study: Anthropology, evolutionary science, human origins, paleontology, zoology
Contribution: African zoologist-paleontologist, wife of Richard, whose most notable works include her reconstruction of 1.8-million-year-old *Homo rudolfensis* and her characterization of 4.1-million-year-old *Australopithecus anamensis*. In early 2001, her announcement of the discovery of a new 3.5-million-year-old fossil hominid, *Kenyanthropus platyops*, threw the previous understanding of human evolution into confusion.

Louis Seymour Bazett Leakey was born in Kenya to English missionary parents. He trained as an anthropologist at the University of Cambridge, where he developed the dream of looking for evidence of ancient humans in Africa. Mary Douglas Leakey was born in England and studied archaeology, specializing in stone tools. After their marriage in 1936, Mary and Louis left England for Africa, establishing their home in Kenya.

In 1959, Mary discovered the first traces of a very ancient apelike animal at a site in Olduvai Gorge in northern Tanzania. Louis and Mary pieced together the fossilized fragments, recreating the nearly complete skull of a 1.8-million-year-old bipedal apelike creature now known as *Australopithecus boisei*. This animal had a brain capacity of approximately 500 cubic centimeters. At the time, Louis thought this apelike creature was the "missing link" between apelike creatures and humans because of the nearby discovery of very primitive paleoliths (stone tools) dated between 1 and 2.5 million years ago.Then in 1971, the skull of 1.8-million-year-old *Homo habilis* was pieced together by Mary and Louis. It was discovered in the same strata as *A. boisei*. *Homo habilis* had a brain capacity of approximately 600 cubic centimeters and appeared to be more closely related to modern humans than *A. boisei*. Richard Leakey characterized two very important *Homo* skulls: one of a 1.9-million-year-old *Homo habilis*, with a brain capacity of only 510 cubic centimeters, and a second of 1.8-million-year-old *Homo rudolfensis*, with a brain capacity of 775 cubic centimeters. These and other discoveries suggest that the paleoliths were produced by one of the *Homo* populations and not by any of the *Australopithecus* populations. Turkana boy's fossil remains, characterized by Richard and Maeve, suggest that this 1.5-million-year-old *Homo erectus* was about 4.5 feet tall and would have grown to about 5.5 feet. He had a brain capacity of about 880 cubic centimeters.

In 1975, Mary Leakey discovered the traces of humanlike footprints in hardened volcanic ash at Laetoli, near Tanzania's Olduvai Gorge. These footprints have been dated at 3.6 million years by the potassium-argon method. Since no *H. habilis* fossils this old have been discovered, the footprints must be of an *Australopithecus*, possibly related to *Australopithecus afarensis*, whose fossil remains have been discovered in the area and in much of East Africa. Although these animals lived between 3.8 and 2.7 million years ago, they were fully erect, and their footprints appear very human. Maeve Leakey discovered the fossil remains of 4.1-million-year-old *Australopithecus anamensis*. Her discovery of this very apelike creature has increased the span of time in which bipedal apelike creatures evolved.

The discoveries made by the Leakey family helped to establish the fact that a number of different biped species of *Australopithecus* and different species of *Homo* were living together in Africa 1.8 million years before the present. Locomotion on two legs was the first human trait to develop, at least 3.6 million years ago, but it developed first in a number of nonhuman animals, various species of *Australopithecus*. The crude stone tool culture first characterized by Louis and Mary, as well as the proximity of *Homo habilis* fossils suggests that *H. habilis* or closely related species such as *H. rudolfensis* were the first animals to be both bipeds and toolmakers. The Leakey discoveries indicate that some early human population closely related to *H. habilis* or *H. rudolfensis* was the ancestor of *H. erectus*, although Maeve Leakey's discovery of a new genus, *Kenyanthropus platyops*, announced in early 2001, suggests that the lineage of human ancestry in the middle Pliocene is more complex than previously thought. The Leakeys' discoveries also established that Africa, over a period of four million years, was the birthplace of numerous species of both *Australopithecus* and *Homo*.

—Jaime Stanley Colomé

The Leakey family (left to right, Richard, Mary, and Louis) have been a major force in the discovery of hominid ancestors in Africa. (Win Parks, National Geographic Society)

Periods and Extinctions

Era	*Period*	*Date (millions of years ago)*	*Newly dominant fossils*	*Extinctions*	*Most Likely Causes*
Cenozoic	Quaternary	2-present	Recent mammals	One lesser extinction at the T-Q boundary.	
	Tertiary	65-2	Diversified small and large mammals	Two lesser extinctions: one each at around 30 million years and around 10 million years before the present. Mass extinction that eliminated around 75 percent of all species. All dinosaurs except for birds, many land reptiles, all marine reptiles (plesiosaurs and ichthyosaurs), and all flying reptiles (terosaurs) went extinct.	Separation of North and South American land masses from European and African land masses. This altered oceanic currents and atmospheric streams, which produced glaciers. Glacier formation caused the sea level to drop around 200 feet. Volcanic activity may also have contributed to glacier formation. Deep water may have been anoxic because of poor circulation. A huge meteor impact may have contributed to the mass extinction.
Mesozoic	Cretaceous	145-65	Diversified dinosaurs, flowering plants	Three lesser extinctions: one at the J-K boundary and one each at around 110 million years and around 90 million years before the present.	

	Jurassic	205-145	Diversified early dinosaurs, first birds, small early mammals	Lesser extinction at around 138 million years before the present. Seed-ferns all went extinct. Mass extinction that eliminated about 80 percent of all species.	Breakup of Pangaea initiated. Newly forming continents in the northern hemisphere, equatorial continent, and South Pole continent. This altered oceanic currents and atmospheric streams. The temperature was increasing during the T-J transition, yet sea levels fell slightly (around 50 feet), suggesting some glacier formation. Volcanic activity may have contributed to glacier formation. Deep water may have been anoxic because of poor circulation.
	Triassic	250-205	Early dinosaurs, diversified reptiles: mammal-like reptiles, marine reptiles; cycads, diversified ginkgoes	Mass extinction that eliminated around 95 percent of all species. All trilobites, all armored fishes, and all reptilelike amphibians went extinct.	Formation of Pangaea completed. A massive continent from the Northern hemisphere to the South Pole. Water level dropped around 300 feet suggesting huge glacier formation at the poles. Extensive volcanism lowered the temperature, as did altered water currents and atmospheric streams. Volcanism produced huge amounts of toxic sulfur dioxide and acid rain as well as carbon dioxide. Deep water may have been anoxic because of poor circulation.
Paleozoic	Permian	290-250	Diversified reptiles, decline of reptilelike amphibians	One lesser extinction occurred at the C-P boundary.	

Continued

Periods and Extinctions—continued

Era	*Period*	*Date (millions of years ago)*	*Newly dominant fossils*	*Extinctions*	*Most Likely Causes*
	Carboniferous	360-290	Diversified sharks, bony fishes; early reptiles, reptilelike amphibians; seedless ferns, seed ferns, ginkgoes, pine forests	At least one lesser extinction occurred. Mass extinction that eliminated around 80 percent of all species. Most armored fishes and most jawless fishes went extinct.	Movement of northern continents toward Gondwana at the South Pole. Glaciers formed, and sea level dropped around 100 feet due to altered oceanic currents and atmospheric streams. Volcanic activity may have contributed to glacier formation. Deep water may have been anoxic because of poor circulation.
	Devonian	400-360	Diversified armored jawless and bony fishes; amphibians; insects; seedless, spore-forming tree ferns	At least two lesser extinctions and six minor extinctions occurred.	
	Silurian	440-400	Armored jawless fishes, first bony fishes, first fishes with jaws (placoderms and sharklike fishes); simple land plants	At least one lesser extinction occurred. Mass extinction that eliminated around 85 percent of all species. Most Burgess shale organisms went extinct. Trilobites survived, but just barely.	Fusion of some northern continents with each other at the equator. Movement of Gondwana toward the South Pole. Massive glaciers formed and sea level dropped 150 feet. Glaciers were caused by altered oceanic currents and atmospheric streams. Volcanic activity may have contributed to glacier formation. Deep water may have been anoxic because of poor circulation.

	Ordovician	500-440	Diversified arthropods, first jawless fishes, primitive chordates, filter feeders, mollusks	At least two lesser extinctions occurred.	
	Cambrian	540-500	Burgess shale fossils: early arthropods, animals with mineralized shells like the brachiopods, animals with notochords	At least five lesser extinctions occurred in which different groups were affected to different degrees.	Unknown causes.
Proterozoic	Precambrian	600-540	Ediacaran fossils: sponges, jellyfish, segmented wormlike animals, colonial filter feeders	Lesser extinction that eliminated up to 50 percent of all species near the end of the Precambrian.	Unknown causes.
Archaeozoic		1000-600 3800-1000	Microscopic animals, algae Bacteria		

and the organisms encased in it are often referred to as fossils. Ethanol or isopropyl alcohol dropped on copal makes its surface sticky but has no effect on amber. Copal is usually less than 2 million years old, whereas the oldest ambers are about 150 million years old.

The hard parts (skin, cellulose walls, wood, and exoskeletons) of organisms are generally preserved in copal and amber, although some tissues are replaced by minerals such as pyrite (FeS_2). The pyrite turns portions or all of the fossil black. Completely blackened fossils retain little of the original organism. The fossils in copal and amber have given paleontologists a picture of life during different ancient (Jurassic and Cretaceous) and recent (Tertiary and Quaternary) periods.

Radioisotopes Used to Date Fossils

The radioisotope often used to date very old fossils is potassium-40 (^{40}K), which decays into argon-40 (^{40}Ar) by the conversion of a proton into a neutron. It takes 1,300 million years for one half of a ^{40}K sample to decay into ^{40}Ar. By using the half-life for $^{40}K(T_{1/2}$ = 1300 million years) and measurements of ^{40}K and ^{40}Ar in volcanic rock, the volcanic rock can be dated. If, for example, a sample of volcanic rock contains equal amounts of ^{40}K and ^{40}Ar, then the volcanic rock would be 1,300 million years old. Fossils are dated by determining the age of volcanic rock below and above the fossils. The age of the fossils would be between the ages determined for the volcanic rock.

Carbon-14 (^{14}C) and carbon-12 (^{12}C) measurements are used to date fossils less than thirty thousand years old. ^{14}C decays into ^{12}C by losing two neutrons. The half-life for this decay is 5,700 years. Generally, in living organisms the ratio of radioactive ^{14}C to nonradioactive ^{12}C remains constant because fresh ^{14}C replaces the lost ^{14}C. When an organism dies, however, ^{14}C no longer replaces the ^{14}C lost, and so the ratio of ^{14}C to ^{12}C decreases in the surviving tissue. The smaller the ratio of ^{14}C to ^{12}C, the older the sample is. A fossil may be dated by directly measuring the age of the fossil, by determining the age of organic material closely associated with the fossil, or by determining the age of organic material both below and above the fossil. The errors become quite large for dates greater than forty thousand years.

Mass Extinctions

The five mass extinctions during the last five hundred million years have been very important in the evolution of life because they eliminated nearly all of the most highly adapted species that existed before each extinction. This allowed many of the surviving, more generalized species to evolve into highly specialized species that filled vacated and new environments. The species that arose after each mass extinction were very different from those they replaced.

In most cases, mass extinctions were caused by the plate tectonics that fused and fragmented continents. Colliding continents created shallow seas and mountains. Fragmenting continents initially created shallow seas. In some cases, these shallow seas developed into deep oceans. The fusion and the fragmentation of continents drastically changed oceanic currents and weather patterns, which often lowered temperatures both in the ocean and on land. The movement of plates to and from the equator and poles also affected the world's environments. Extensive volcanic activity occurred both when small continents collided and fused with each other and when massive continents fragmented and the volcanic debris blown into the upper atmosphere absorbed and reflected light, resulting in a cooling of the earth. Large decreases in temperature, changes in rainfall, and environmental loss were deleterious for highly adapted species.

Huge comets, asteroids, or meteoroids colliding with the earth may have played a minor role in any of the mass extinctions. The mass extinction that marked the end of the Cretaceous period about sixty-five million years before the present, which eliminated more than 75 percent of all species and all of the dinosaurs except the birds, may have been helped along by a meteoroid about ten miles across. Although this impact spewed millions of tons of earth into the atmosphere, it is not known whether the debris was sufficiently fine to remain in the atmosphere long enough to drastically alter the temperature and weather. Many biologists favor the idea that plate tectonics, not a meteoroid, ended the Cretaceous period. During the late Cretaceous period, the supercontinent Pangaea was fragmenting into northern and southern continents. In addition, these continents themselves were fragmenting from north to south, and an ocean was forming between them, slowly becoming the Atlantic Ocean.

At least nineteen lesser extinctions and five minor extinctions (Devonian and Devonian-Carboniferous transition) occurred during the last 600 million years. In some cases, the lesser extinctions eliminated up to 50 percent of all species. This allowed new species to evolve into the environments vacated.

Geological Periods and Dominant Fossils

The preceding table, titled Periods and Extinctions, characterizes each of the geological periods by listing some of the newly dominant fossils (organisms) that appeared during each period. The timing of the five major and nineteen lesser extinctions is indicated, along with the most likely cause of the extinctions.

Dating the different layers in sedimentary rock, some many hundreds of feet thick, establishes the great age of the fossils in the layers. The fossils in the different layers of sediment clearly illustrate the gradual and in many cases the rapid disappearance of most early forms of life as well as the repeated appearance of totally new forms of life. Numerous extinctions induced by the evolving earth eliminated countless species and allowed countless other species to evolve. Geology (plate tectonics, dating of strata, and paleontology) and evolution have produced a complex picture of the evolving earth and life.

—Jaime Stanley Colomé

See also: Apes to humans; Communities; Demographics; Dinosaurs; Ecology; Ecosystems; Evolution: Animal life; Evolution: Historical perspective; Extinction; Fossils; Habitats and biomes; Human evolution analysis; Paleontology; Plant and animal interactions; Predation.

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PANDAS

Type of animal science: Classification
Fields of study: Anatomy, conservation biology, physiology, reproduction science, wildlife ecology

The giant panda, with its distinctive black and white coat, is one of the most easily recognized animals in the world. It is extremely specialized for a bamboo diet. Despite efforts by many conservationists, the panda is highly endangered.

Principal Terms

CARNIVORE: animal dependent on an animal diet
DELAYED IMPLANTATION: an extended period after fertilization when an embryo stops developing, and before it attaches to the uterine wall and resumes embryonic development
HERBIVORE: animal dependent on a plant diet
RADIAL SESAMOID: forefoot wrist bone

Giant pandas are members of the bear family, and resemble other bears in size and shape. In contrast, the red panda, which lives in the same habitat as the giant panda, is closely related to and resembles the raccoon. The black-and-white giant panda coat is recognizable to people all over the world. Its legs, ears, eye patches, and a band across the shoulders are black, while the rest of the coat is white. Pandas have large jaws and broad teeth, with an increased number of cusps that help them chew tough bamboo stalks. The wide jaw contributes to the large, round shape of the panda's head. The black eye patches create an illusion of very large eyes. These features, along with short legs, give the panda a cute, infantlike appearance to humans, which contributes to their enormous popularity. Another remarkable feature is the "thumb." Pandas have the same five digits of other bears, plus a sixth digit, an opposable thumb, which is actually a modified wrist bone (sesamoid). The thumb allows them to grasp bamboo with considerable dexterity.

Diet and Reproduction

Giant pandas are the most nearly herbivorous of the bears. Ninety-nine percent of their diet consists of bamboo. They also eat other plants and meat that they can scavenge, and will eat a variety of foods in captivity. However, pandas live in areas once covered by vast bamboo forests, and their jaws, teeth, paws, and behavior are all adapted to eating bamboo. Nonetheless, they have a short, simple digestive tract similar to those of other bears, a sign of their carnivorous ancestry, which is not well-adapted to digesting the leaves and fiber of bamboo. Accordingly, pandas can only digest 21 percent of the bamboo that they consume, whereas ruminants such as cows digest up to 60 percent of the plant material that they eat. Because of this inefficiency, pandas consume 12 to 15 percent of their body weight in bamboo each day, and must spend twelve to fourteen hours each day eating.

Pandas mate in the spring between March and May, with cubs born in late summer. The total gestational period varies from 87 to 165 days. Cubs are born very small, between three and five ounces. Combined with hormonal data, these characteristics suggest that pandas have a delayed implantation. That is, after fertilization, the embryo remains free-floating in the uterus for several months before attaching to the uterine wall. After attachment, pregnancy is only about forty days, resulting in small newborns. Delayed implantation also occurs in some other bear species. Pandas have between one and three cubs at a time. However, they usually raise only one cub, which the mother nurtures intensively for several months.

The panda's distinctive black-and-white coloration makes it one of the most recognized wild animals. (Corbis)

Status and Distribution

The giant panda is an endangered species, with fewer than 1,500 individuals remaining. Panda habitat once covered an area of roughly 450,000 square miles in southeastern China, ranging from central China, to Hong Kong, into Burma and Vietnam. Today, they are found within only a 5,400-square-mile area. Even within this area, they are separated into many subpopulations, which prevents interbreeding. Within their range, pandas live at elevations above human settlements (four to eight thousand feet) to the upper edges of bamboo forest (ten to eleven thousand feet). The continuing expansion of human farms and villages has forced them from the lower elevations, which further contributes to the fragmentation of their populations. Small subpopulations are at a high risk for inbreeding, which reduces the genetic variability and individual fitness, placing panda survival in doubt.

Because of the giant panda's endangered status and charismatic traits, extensive efforts are being made to prevent its extinction. It is considered a national treasure in China, and killing one is punishable by death. Western conservationists, including the World Wildlife Fund, which uses the panda as its symbol, are also aiding the preservation efforts. Captive panda breeding, mostly in China, has been a focus of these efforts. Unfortunately, breeding programs have never produced enough cubs to introduce into the wild, or even to sustain the captive populations. Still, many scientists and conservationists around the world are working to ensure a future for the giant panda.

—*Laura A. Clamon*

See also: Bears; Breeding programs; Endangered species; Fauna: Asia; Grizzly bears; Polar bears; Raccoons and related mammals; Zoos.

Panda Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Carnivora
Family: Ursidae (bears)
Genus and species: Ailuropoda melanoleuca (giant panda)
Geographical location: China
Habitat: Bamboo forests
Gestational period: Probably a three-month embryonic diapause, followed by a forty-day gestation
Life span: Twenty to twenty-five years; known record, thirty years
Special anatomy: Coloration is white with black splotches; opposable "thumb"

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PARROTS

Types of animal science: Anatomy, classification, reproduction
Fields of study: Anatomy, ornithology, zoology

Parrot species include macaws, cockatoos, true parrots, parakeets, and lories. They are kept as pets for their beautiful coloring and ability to learn to talk.

Principal Terms

PLUMAGE: the feathers of birds

ZYGODACTYL: having two toes pointing backward and two toes pointing forward

The hundreds of parrot species are vivid-colored members of the bird family Psittacidae. They belong to five classes: macaws, cockatoos, true parrots, parakeets, and lories. In parrot plumage, reds and greens often predominate, but blue, purple, yellow, and black also appear.

Parrots inhabit warm South and Central America, southern North America, Africa, Madagascar, Indonesia, and southern and Southeast Asia. They live in lowland tropical or subtropical and mountain forests. Parrot sizes range from three-inch New Guinea pigmy parrots to South American macaws, over three feet long.

Macaws, the largest parrots, have long, pointy tails. Cockatoos of Australia and Indonesia are white, with colored crests and other touches of yellow, red, or pink. True parrots are smaller, square-tailed, and have many green feathers. Parakeets, smaller than most true parrots, have long, pointy tails. Lories have red or orange bills, in-

Parrots and their relatives are distinguished by their curving beaks, which they use to help them climb. (Adobe) stead of gray bills like true parrots. In most species, males and females look similar, but males are more brightly colored.

Physical Characteristics of Parrots

The most noticeable features of parrots, beyond color, are their down-curved, hooked bills, thick, muscular tongues, and short legs. The bills have strong grasping ability that helps parrots to climb well. Parrot feet are zygodactyl, meaning that the two outer toes of the foot point backward and grip in the opposite direction to the two forward-pointing inner toes. Because of this, parrots walk awkwardly. However, zygodactyly makes them excellent climbers.

Parrots eat seeds, fruits, and nuts. Australian lories also eat pollen and nectar. The thick, muscular tongues of most parrots manipulate nuts and seeds, breaking them open as needed. Longer lorie tongues have brushlike tips for eating pollen and nectar. Most parrots find their food in trees, using feet and bills to navigate search areas.

The Lives of Parrots

Parrots are social birds that often live in flocks. Their loud voices are harsh and used in constant communication. Parrot breeding seasons depend on the geographic location of their habitat and the food they eat. Species living outside the tropics, where food supply changes seasonally, have yearly mating seasons. Those in tropical regions breed at irregular intervals when food is available.

Most parrots pair for life. Males attract mates by hopping, bowing, wagging tails, and flapping wings. After mating, females lay two to eight small white eggs. A mated pair does not part after breeding. They eat together and groom each other year round. Most parrots nest in holes in trees, termite mounds, and rock or ground tunnels. Others lay eggs in large grass or twig nests. Females incubate eggs for eighteen to thirty-five days, while males supply mates with food. Parrots are born blind and dependent on their parents. Young leave the nest after 1 month in smaller species and after 3.5 months in larger species. Some parrots live for sixty to eighty years.

Parrot Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata (have backbone)
Class: Aves
Order: Psittaciformes
Family: Psittacidae, with subfamilies Nestorinae (keas, one genus, 5 species); Psittrichasinae (vulturine parrots); Kakatoeinae (cockatoos, five genera, 14 species); Micropsittinae (pygmy parrots, one genus, 4 species); Trichoglossinae (lories, two tribes, fourteen genera, 21 species); Strigopinae (owl parrots); Psittacinae (true parrots, five tribes, fifty-four genera, 126 species)

Geographical location: South and Central America, southern North America, Africa, Madagascar, Indonesia, and southern and Southeast Asia

Habitat: Lowland tropical or subtropical and mountain forests

Gestational period: Eggs hatch in seventeen to thirty-five days

Life span: Forty to eighty years, in captivity

Special anatomy: Down-curved bills, muscular tongues, zygodactyly

Some Representative Parrot Species

African gray parrots (*Psittacus erithracus*) of Central and Western Africa grow to one-foot lengths and one-pound weights. They have gray bodies, black wingtips, and red tail feathers. They eat fruit, seeds, nuts, and berries, nesting in holes in trees. Females lay about four eggs and incubate them for a month, while males feed them. Chicks are fed by both parents. They fly in 2.5 months and parents feed them for 5 more months. These birds form flocks of up to thirty-six individuals. In captivity they live for up to eighty years.

Princess parrots (*Polytelis alexandrae*) live in the scrub land of central and western Australia. They nest in eucalyptus tree holes and eat acacia buds, seeds, berries, and fruit. They are high-altitude fliers, who travel widely seeking food. Their flocks contain up to twenty-four birds. Full-grown, they are fifteen inches long including the tail, and weigh around four ounces. Back, belly, and wing plumage is olive green and yellow; tail feathers are violet; throats are pink; bills are red-orange; and heads are light blue. Breeding occurs between September and December. Females lay four to six eggs and incubate them for three weeks. Young can fly at three months old. An endangered species, they are protected by law.

Indonesian salmon-crested cockatoos (*Cacatua moluccensis*) have plentiful, pink-tinted white plumage. Atop their heads are crests of salmon-red feathers, raised to show desire to mate. They eat berries, seeds, nuts, fruits, and insects. Breeding season is in November, and after mating they pair for life. Nests are in tree hollows. Females lay four to seven white eggs. Both birds incubate them for a month. After hatching, young remain in the nest for three months, and then live on their own. Salmon-crested cockatoos live for sixty years in captivity.

Wild parrots are pests. For example, farmers see cockatoos as nuisances because they eat crops. An interesting side note is that parrots are very ingenious. This is due to their great intelligence, estimated to equal that of porpoises and primates.

Parrots are liked as pets, due to their attractive coloring and ability to learn to talk. The popularity of pet parrots has brought some species close to extinction. In most countries, laws regulate their capture, export, and import. However, the laws are difficult to enforce.

—Sanford S. Singer

See also: Beaks and bills; Birds; Domestication; Feathers; Flight; Molting and shedding; Nesting; Respiration in birds; Wildlife management; Wings.

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PARTHENOGENESIS

Type of animal science: Reproduction
Fields of study: Embryology, reproductive science

Parthenogenesis is a process of asexual reproduction found mostly in lower animals. The egg divides and develops normally in the absence of fertilization.

Principal Terms

ARTHROPOD: a highly diverse phylum of animals that contains the crustaceans, insects, and spiders

DIPLOID: a cell containing two sets of chromosomes, usually one derived from the father and one derived from the mother; the normal condition of all cells except reproductive ones

HAPLOID: a cell (egg or sperm normally) containing one set of chromosomes, half the number found in nonreproductive cells

MEIOSIS: a special process of cell division consisting of two nuclear divisions in rapid succession, resulting in four haploid cells

OVUM: the female sex cell, or egg; usually undergoes meiosis following fertilization by a sperm

The term parthenogenesis comes from the Greek, meaning "to create from a virgin." Hence, it is sometimes popularly referred to as virgin birth. Parthenogenesis is a form of reproduction in which an ovum develops into a new individual without having been fertilized by a sperm. It is akin to other forms of asexual reproduction in that the offspring inherits all genetic information and traits from a single parent. The offspring is, therefore, genetically identical to the mother, and may be considered to be (in the broader sense of the word) a clone. The offspring may or may not look identical to the mother, since environment plays a large role in outward appearance. In fact, offspring may be male as well as female in those species where gender is determined by factors other than genetics alone, or by genetic factors different from those that occur in humans.

Natural Parthenogenesis

Parthenogenesis as a mode of reproduction is common in the animal kingdom up through the arthropods. In some, such as the aphid, parthenogenesis is the primary method of reproduction. Aphid eggs laid in the fall survive the winter and hatch as wingless females. These aphids mature in two weeks and reproduce parthenogenetically, giving live birth to daughters only, who in turn give live birth to the next generation of daughters. This cycle of parthenogenesis repeats itself through the spring and summer months until finally, in the fall, the next to last generation gives live birth to both females and males. These mate with each other and, rather than giving live birth, produce eggs that will hatch the following spring to start the cycle of parthenogenesis once again.

Other insects, such as honeybees and most species of ants, use both parthenogenesis and sexual reproduction side by side. In these species, unfertilized eggs give rise to haploid male drones, whereas fertilized eggs lead to diploid female workers and queens. The only insect known to be completely female (no males have ever been reported) is the white-fringed weevil. Since no males exist for fertilization, all reproduction is by parthenogenesis alone.

Ernest Everett Just

Born: August 14, 1883; Charleston, South Carolina
Died: October 27, 1941; Washington, D.C.
Fields of study: Cell biology, developmental biology, embryology, invertebrate biology, marine biology, reproduction science
Contribution: A pioneer in the fields of marine biology, cell biology, and fertilization, Ernest E. Just challenged many of the leading biological theories of his day. He significantly increased our understanding of the process of artificial parthenogenesis and the physiology of cell development.

Following graduation from Dartmouth College (1907) with a degree in zoology and special honors in botany and history, Ernest Just was offered a teaching position at Howard University. An excellent teacher with clear leadership skills, he was appointed head of the new Zoology Department in 1912. At Howard he also served as a professor in the Department of Physiology at the Medical School. He was awarded the first National Association for the Advancement of Colored People (NAACP) Spingarn Medal for exceptional contributions, in 1915, and received his doctorate in experimental embryology from the University of Chicago in 1916.

In 1909, Just was invited by Dr. Frank Lillie to spend his summer doing research at the Marine Biological Laboratory at Woods Hole, Massachusetts. His research there over the next twenty years, and the fifty papers which he published, led to international acclaim in several scientific fields. His work included the subjects of fertilization, experimental parthenogenesis, hydration and dehydration in cells, cell division, and the effects of magnetic fields and ultraviolet rays on chromosome number in animals and in altering the organization of the egg with respect to polarity. He successfully challenged Jacques Loeb's theory of artificial parthenogenesis, pushing the understanding of the process well ahead. Much of his early work is reported in his book, *Basic Methods for Experiments on Eggs of Marine Organisms* (1939), and in *General Cytology* (1924), which he coauthored with several of the other prominent biologists of the day, including Frank R. Lillie, T. H. Morgan, M. H. Jacobs, and E. G. Conklin.

A gifted, versatile, and productive researcher, Dr. Just was often referred to as a scientist's scientist. Even so, he experienced much of the racism of this period in history, and found the walls of prejudice and discrimination in America too high to climb. It was for that reason that he chose to move his research to Europe, and spent most of his time after 1933 working in Germany, France, and Italy.

Ernest Everett Just was a leading researcher, prior to World War II, in the fields of cell biology and parthenogenesis. (Associated Publishers, Inc.)

While he was living in France, his masterpiece, *The Biology of the Cell Surface* (1939), was published in Philadelphia. This important book summarized his life's work on small marine animals, and provided new knowledge for people interested in biological research. Unfortunately, Germany invaded France in 1940, and Dr. Just was imprisoned by the Germans. His health had begun to fail before his imprisonment, and it worsened during this time. After he was released, he returned to the United States, but was too ill to continue his research. He died of cancer a year after his return.

Dr. Ernest Everett Just was recognized in 1997 by a U.S. Postal Service commemorative stamp (Black Heritage Stamp Series) for his contributions to biology.

—*Kerry L. Cheesman*

Parthenogenesis has also been reported in aquatic organisms, such as rotifers, marine nematodes, and some mollusks. It rarely occurs in higher orders of animals, except in certain birds. A good example of avian parthenogenesis is the turkey, where it appears to be fairly common. The work of M. W. Olsen and others in the 1960's and 1970's established the fact that parthenogenesis is fairly common in most fowl, including chickens, and usually occurs in eggs that are incubated for a few days in the absence of fertilization. Thus, there may be economic implications associated with parthenogenesis in these birds.

Two processes collectively referred to as abortive parthenogenesis are known to occur in the animal kingdom. In gynogenesis, a sperm enters the egg in the normal way, but the egg begins to develop without including the nucleus (genes) of the sperm. In androgenesis, the nucleus of the egg fails to begin development following fertilization, and the genes of the sperm take over the role of directing early development. Neither of these is considered a normal reproductive process.

Most naturally occurring parthenogenesis is associated with a modification of the meiotic process that restores the diploid condition to the egg. Little evidence exists concerning the stimuli needed or the process required to produce haploid individuals from haploid eggs (as in bees and ants).

Artificial Parthenogenesis

The phenomenon of natural parthenogenesis was discovered in the eighteenth century by Charles Bonnet. In 1900, Jacques Loeb (and T. H. Morgan, in a separate study) accomplished the first clear case of artificial parthenogenesis when he pricked unfertilized sea urchin eggs with a needle and found that normal embryonic development ensued. Through further studies he claimed that both butyric acid and hypertonic seawater (water with an excess of salt in it) were necessary to stimulate parthenogenesis.

Several years later, E. E. Just demonstrated that Loeb's understanding of what he had done was in error, and showed that hypertonic seawater alone could stimulate parthenogenesis. He also demonstrated that the larvae produced looked no different than those produced from eggs that had been normally fertilized by sperm in the ocean. Through this and other experiments on sea urchins, Just advanced the knowledge of the cellular events of parthenogenesis tremendously.

Since then other investigators have been able to stimulate parthenogenetic development in silk moths, starfishes, marine worms, and various amphibians by pricking them, shaking them, changing the temperature, or washing them in acids, alkalis, salt solutions, or other fluids. In turkeys and chickens, factors such as temperature, viruses, additives in feed, and even the age of the hen have all been shown to increase the incidence of artificial parthenogenesis.

In mammals, there is no good evidence that complete development can occur by stimulated parthenogenesis, although a few reports have appeared over the years. For instance, in 1936, Gregory Pincus induced parthenogenesis in rabbit eggs through temperature change and chemical agents, but development was not complete. Abortive or incomplete parthenogenesis does appear to be a normal, or at least common, occurrence in some species of mammals, although the reason for such developmental quirks remains unclear. No reliable reports of human parthenogenesis experiments have been published.

—*Kerry L. Cheesman*

See also: Asexual reproduction; Birth; Breeding programs; Cleavage, gastrulation, and neurulation; Cloning of extinct or endangered species; Copulation; Courtship; Determination and differentiation; Development: Evolutionary perspective; Estrus; Fertilization; Gametogenesis; Hermaphrodites; Hydrostatic skeletons; Mating; Pregnancy and prenatal development; Reproduction; Reproductive strategies; Reproductive system of female mammals; Reproductive system of male mammals; Sexual development.

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PELICANS

Type of animal science: Classification
Fields of study: Anatomy, ornithology, physiology, population biology, wildlife ecology

Pelicans, unmistakable due to their large size, long bills, and enormous throat pouches, have existed for forty million years.

Principal Terms

BROOD: to cover the young with the wings
CREST: tuft of feathers on the head
MANDIBLE: the upper or lower portion of the bird's bill
THERMALS: rising currents of warm air
TOTIPALMATE: having all four toes fully webbed

Pelicans are large water birds that live on seacoasts or in warm inland water habitats. There are seven generally recognized species. The coastal brown pelican lives from North Carolina to the Gulf of Mexico and the Caribbean, and from British Columbia to Chile, as well as the Galápagos Islands. The American white pelican inhabits inland habitats in the western, central, and southeastern United States, Mexico, and Canada. The remaining species live in Australia, Europe, Asia, and Africa.

Physical Characteristics of Pelicans

Pelicans rank among the largest of living birds, ranging in size from four to six feet in length, and weighing from four to sixteen pounds. The brown pelican is smallest, and the large eastern great white pelican has a wingspan of up to ten feet. They have short legs and broad, fully webbed feet, which act as powerful paddles in the water, and cause them to walk with an awkward waddle on land.

The pelican is famous for its huge, featherless throat pouch that is attached to the lower mandible. The pouch stretches as it fills with water when the bird is fishing, and can hold nearly three gallons. The pouch also functions as an evaporative cooling mechanism. The pelican opens it mouth and flutters its pouch, which keeps air flowing over the moist surface.

Plumage color varies among species and according to age. Pelicans can be predominantly white, black, brown, or gray, with markings on the head, wingtips, underfeathers, or tail. The legs and feet are orange, brown, or black, and the bill and pouch are reddish, orange, or black. During the breeding season, these body parts change color, and many pelicans develop a yellow patch on the chest, a distinctive crest, and a bright ring around the eyes. The American white pelican also grows a noticeable horny knob on its beak.

Feeding and Other Behaviors

Pelicans feed on many species of saltwater and freshwater fish, from tiny anchovies to fish weighing over a pound. Small crayfish, salamanders, frogs, and snakes are also consumed. The pelican thrusts its head and neck underwater and uses its pouch as a dip net to scoop up its prey. It drains out the water, then tilts its head back and swallows the fish whole. Many pelicans are social fishers, swimming in a circle to close in on the school, then all thrusting and dipping at once. Brown pelicans are solitary feeders, utilizing a spectacular plunge dive from about twenty feet above the water, with neck outstretched and bill pointed down. They hit the water hard, stunning the fish and trapping them in the pouch. Air sacs beneath

Pelicans have large, featherless pouches under their beaks that are used for scooping fish out of the water and for evaporative cooling. (PhotoDisc)

ship, the male uses various behaviors such as bowing, stretching, and pouch displaying to attract a female. Both engage in nesting, the male often gathering sticks and bringing them to the female to incorporate into the nest. Nests are built on the ground or in trees. One to three eggs are laid, and take thirty days to hatch. The chicks are born featherless, and the parents brood them, protecting them from the elements until their feathers come in. Unless the food supply is abundant, only the strongest chick survives. Young chicks eat the parent's regurgitated food. Older chicks feed by sticking their

the pelican's skin cushion its dive and help it to surface quickly.

Pelicans are graceful fliers. They take off against the wind, beating their wings and pumping their feet simultaneously, hopping until they are airborne. They fly at a relatively slow speed, with their necks retracted and their heavy bills tucked in and resting on the breast, and often glide on thermals to conserve energy. Pelicans regularly fly in flocks in a V-formation, flapping their wings in unison. They often travel a great distance in search of food.

Pelicans sleep standing or sitting on their bellies, with the head twisted back and the beak tucked into its feathers. Self-care activities include muscle exercises such as body shaking, wing flapping, tail wagging, leg stretching, bill throwing, and yawning. Pelicans groom themselves by splash bathing, preening with their beaks, and by rubbing their heads over the body to distribute waterproofing oil to their feathers.

Reproduction

Pelicans are warm weather birds, migrating in large flocks to nest in huge colonies. During court-

Pelican Facts

Classification:
Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Class: Aves
Order: Pelicaniformes
Suborder: Pelecani
Family: Pelecanidae
Genus and species: Pelecanus onocrotalus (eastern great white pelican), *P. erythrorynchos* (American white pelican), *P. occidentalis* (brown pelican), *P. rufescens* (pink-backed pelican), *P. philippensis* (spot-billed pelican), *P. crispus* (Dalmatian pelican), *P. conspicillatus* (Australian pelican)
Geographical location: North and South America, eastern Europe, Asia, Africa, Australia
Habitat: Coastal areas or inland lakes and rivers
Gestational period: Incubation lasts thirty days
Life span: Eight to twenty years
Special anatomy: Webbed feet; long, pointed bill with retractable throat pouch; air sacs under the skin; large wingspan

heads in the parent's pouch and throat. By twelve weeks of age, the chicks can fly and begin to hunt for themselves. By one year they have their full plumage. They begin reproduction at three to four years of age.

Endangerment

Pesticides, oil spills, habitat destruction, entanglement in fishing lines, and human disturbance have affected pelican populations in various parts of the world. In 1970, the U.S. Fish and Wildlife Service listed the brown pelican as an endangered species due to the heavy usage of dichloro-diphenyl-trichloroethane (DDT) and endrin. When pelicans ate DDT-contaminated fish, they produced thin-shelled eggs that crushed during incubation. Endrin was toxic. Populations improved after the pesticides were banned, but the birds are still endangered. The spot-billed pelican of Asia and the Dalmatian pelican of Europe and China also face difficulties.

—*Barbara C. Beattie*

See also: Beaks and bills; Birds; Domestication; Feathers; Flight; Molting and shedding; Nesting; Pollution effects; Respiration in birds; Wildlife management; Wings.

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PENGUINS

Type of animal science: Classification
Fields of study: Anatomy, ornithology, physiology, population biology

Penguins, highly specialized for their flightless aquatic existence, have origins dating back sixty million years. Their unique lifestyle and behavior have long fascinated observers.

Principal Terms

CRÈCHE: penguin chicks grouped together for warmth and safety
KRILL: small, shrimplike sea creatures
MOLT: to lose feathers and grow new ones
ROOKERY: a nesting penguin colony

Penguins are flightless marine birds that dwell only in the southern hemisphere. They do not inhabit the Arctic, where polar bears live. There are seventeen generally recognized species of penguins. Six species, the Adelie, gentoo, chinstrap, rockhopper, king, and emperor penguins, live in the cold environments of the Antarctic region. The rest live in subantarctic and temperate regions. The macaroni, fiordland, Snares, erect-crested, yellow-eyed, fairy, and royal penguins live off the coasts of New Zealand and Australia and nearby islands. The Magellanic and Humboldt penguins live off the coast of South America. The African penguin lives off the southern coast of Africa, and the Galápagos penguin is native to the Galápagos Islands. Penguins spend much of their lives in the ocean, coming to shore mainly to breed.

Physical Characteristics

All penguins are black with white undersides, and are commonly described as wearing tuxedos. This color pattern acts as camouflage when the penguin is swimming, protecting it from predators. From underneath, the white belly blends with the bright water surface, and from above, the black back is indistinguishable from the dark water. Penguin species can be grouped according to common characteristics. Banded penguins have black and white stripe patterns on their chests and heads. The crested penguins all have bright yellow or orange plumes on their heads. Brushtail penguins have long stiff tail feathers. The king and emperor penguins have bright yellow and orange chest and head patches, and the yellow-eyed penguin has a yellow crown. The fairy penguin's feathers are bluish.

The emperor penguin is the largest, at nearly four feet tall and seventy-five pounds. The small fairy penguin is sixteen inches tall and about three pounds. All have solid, heavy bones that help them dive deeply into the water. They have streamlined bodies that move smoothly through the water as they pump their strong, flipperlike wings and steer using their webbed feet and tails as rudders. Penguins can hold their breath for many minutes at a time, and they frequently leap out of the water, porpoiselike, to take in more air.

On land, penguins walk with an awkward sideways waddle. Because their short legs are set back on their bodies, they stand erect and must hold out their flippers for balance. Penguins often toboggan themselves by flopping on their bellies and pushing with their flippers and feet.

Penguin feathers are tiny and stiff, overlapping to form a waterproof coat. An underneath layer of down helps to trap warm air and protect the penguin from the cold water and wind. Penguins of the Antarctic region have an insulating layer of blubber. Those in temperate climates often have to cool themselves down by ruffling their feathers and holding out their flippers. They can control the flow of blood to their unfeathered areas, such as the feet and under their flippers, which helps regulate their body temperature. Penguins preen their feathers regularly, to spread waterproofing oil from a gland near the tail.

Feeding Behavior and Enemies

Penguins are carnivores. They eat many types of small sea creatures, such as fish, squid, and krill. After locating a school they snatch quickly with their sharp beaks. The tongue and upper palate are covered with stiff spines that grip the slippery food and assist in moving it toward the throat. Penguins make several catches per dive, swallowing the prey whole along with some seawater. Their specialized salt glands above each eye help them drain the extra salt they ingest.

Penguins usually enter and exit the water in large groups, to protect themselves from predators who often lurk near the shore. Their main enemies are sea lions, leopard seals, and killer whales. On land, adult penguins are safe. Petrels, skuas, gulls, and sheathbills hunt babies and eggs.

Reproduction

Most penguins follow an annual breeding cycle that begins in the spring, but timing varies according to species and climatic conditions. The Galápagos penguin will breed any month that the water temperature is right, and sometimes twice a year. Emperors begin their cycle in autumn, so there is a good food supply when their chicks hatch in spring. King penguins only reproduce twice every three years, because they follow a fifteen-month cycle.

Some penguins nest on the shore and others travel many miles inland to reach their rookeries, and they return to the same ones each year. Penguins are social, and one rookery may have thousands of penguins in closely spaced nests. They often squabble over nesting materials, mates, and territory. Nests are built of grass or stones on the ground, in rock crevices, or in burrows. The male engages in an ecstatic display to attract a female, pointing his beak, flapping his flippers, and squawking. Penguins usually mate for life, and in subsequent years the pair will greet each other affectionately. Two eggs are laid, and the parents take turns incubating for a few weeks at a time while the other leaves to feed. The incubating parent does not eat, and often loses a great deal of weight. Each penguin has a brood patch, an area of bare skin on its

Penguin Facts

Classification:
Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Class: Aves
Order: Sphenisciformes (penguins)
Family: Spheniscidae
Genus and species: Six genera and twenty-five species, including *Eudyptes chrysocome* (rockhopper penguin), *E. pachyrhychus* (fiordland penguin), *E. robustus* (Snares penguin), *E. sclateri* (erect-crested penguin), *E. chrysolophus* (macaroni penguin), *E. schlegeli* (royal penguin); *Spheniscus magellanicus* (Magellanic penguin), *S. humboldti* (Humboldt penguin), *S. mendiculus* (Galápagos penguin), *S. demersus* (African penguin); *Pygoscelis adeliae* (Adelie penguin), *P. antarctica* (chinstrap penguin), *P. papua* (gentoo penguin); *Aptenodytes patagonicus* (king penguin), *A. forsteri* (emperor penguin); *Megadyptes antipodes* (yellow-eyed penguin); *Eudyptula minor* (fairy penguin)

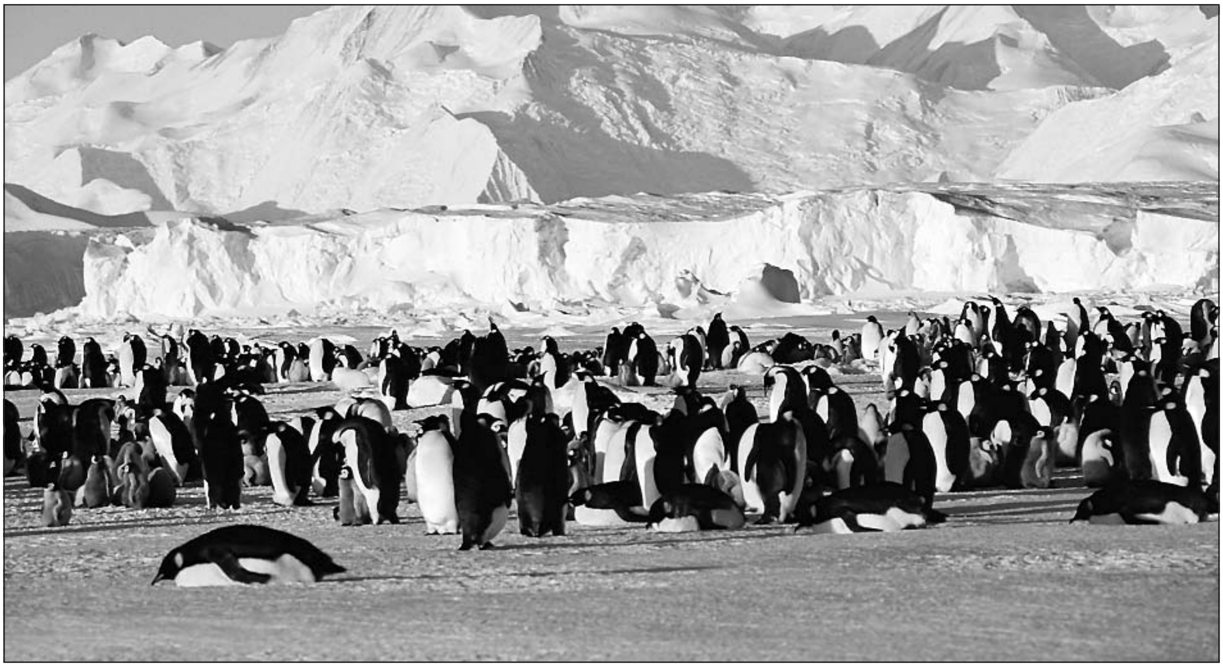
Geographical location: Along the coasts of Antarctica, Australia, New Zealand, South Africa, Chile, Peru, Argentina, and the Galápagos Islands

Habitat: Oceans and coasts in both cold and temperate latitudes

Gestational period: Incubation varies by species from thirty-three to sixty-four days

Life span: Twenty to thirty years

Special anatomy: Aerodynamic body shape; flippers; webbed feet; short, stiff, overlapped feathers; spiked tongue



The penguin's black-and-white coloration serves as camouflage, with the white underbelly making the swimming penguin difficult to locate from underneath while its black back blends into the water when seen from the top. (Digital Stock)

lower belly, that allows for better heat transfer to the eggs. Incubation varies from five weeks for the small fairy penguin to nine weeks for the emperor.

The king and emperor penguins are exceptions to the nesting rule. They lay only one egg, which they cradle on their feet instead of building a nest. They cover it with a flap of skin to keep it warm. Kings take turns incubating, while with emperors, only the male incubates.

Chicks are born down-covered, except for emperor chicks, which are naked. The parents brood them while they are young and feed them regurgitated food. When the chicks get too large for brooding, they huddle in crèches while the parents leave to hunt for food. When the chicks are grown and go off on their own, the parents molt. They cannot go into the water without their full coats of feathers, so they fast during this two- to four-week period.

—Barbara C. Beattie

See also: Beaks and bills; Birds; Domestication; Fauna: Africa; Fauna: Antarctica; Fauna: South America; Feathers; Flight; Molting and shedding; Nesting; Respiration in birds; Wildlife management; Wings.

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pH MAINTENANCE

Type of animal science: Physiology
Field of study: Biochemistry

The maintenance of pH, which means "potential of hydrogen," is the regulation of acidity in the body fluids of animals; pH is the measure of acidity. Conditions that are too acidic or are not acidic enough will alter proteins such as enzymes and render them less effective. It is, therefore, vital that living organisms maintain proper acidity in body fluids.

Principal Terms

ACIDOSIS: a body fluid pH of less than 7.4 at 37 degrees Celsius

ALKALOSIS: a body fluid pH greater than 7.4 at 37 degrees Celsius, the opposite of acidosis

ANAEROBIC METABOLISM: metabolism in the absence of oxygen that leads to the production of lactic acid, a strong acid

PARTIAL PRESSURE: the pressure exerted by a specific gas in a mixture of gases such as the atmosphere; it is analogous to concentration

PH: the negative logarithm of the hydrogen ion concentration, with higher hydrogen ion concentrations indicating lower pH; the pH scale goes from 0 to 14, with a pH of 7 being neutral, values below 7 indicating acidity, and values above 7 indicating alkalinity

STRONG ACID: an acid that dissociates almost completely into its component ions; hydrochloric acid, for example, dissociates almost completely into hydrogen ions and chloride ions

WEAK ACID: an acid that does not dissociate to a great extent; carbonic acid, for example, dissociates to produce some ions, but most of the molecules remain in their original forms

The maintenance of pH is a collection of processes that regulate the hydrogen ion concentration of body fluids. The total body fluids account for about 60 percent of body mass. The body fluids are divided into several compartments. The largest volume of body fluid is in the intracellular compartment, and this consists of about 40 percent of body mass. The extracellular fluid consists of interstitial fluid (about 15 percent of body mass) and several specialized compartments. The largest of the specialized compartments is the vascular space, or blood volume. About half of the blood volume is in blood cells that belong to the intracellular volume. The other half is plasma, which makes up about 5 percent of the body mass. There are several other small extracellular spaces, such as the cerebrospinal fluid and the aqueous and vitreous humors of the eyes, that comprise smaller percentages of the extracellular volume. Each of these compartments is regulated in order to maintain normal pH. The pH levels of the different compartments can be very different. In mammals, the extracellular pH as measured in the plasma is generally 7.4. The specialized fluids within the extracellular compartment can differ. For example, the cerebrospinal fluid has a pH of 7.32. Intracellular pH can vary from cell type to cell type but tends to be lower than extracellular pH. For example, skeletal muscle has an intracellular pH of 6.89, while red blood cells have a pH of 7.20.

pH Maintenance

The first line of defense in the maintenance of pH is through the use of chemical buffers. Buffers are chemicals that resist pH change by absorbing hydrogen ions from acidic solutions or contributing hydrogen ions to alkaline solutions. They are made by producing a mixture of a weak acid and the salt of a weak acid. An example of a buffer is given by the bicarbonate buffer system. The components are H_2CO_3 (weak acid) and $NaHCO_3$ (salt of the weak acid). When a strong acid such as HCl is added to a solution containing this buffer pair, the H^+ released from the highly dissociated HCl combines with HCO_3^-; that is completely dissociated from the $NaHCO_3$ to form weakly dissociated H_2CO_3. This prevents the large pH drop that would otherwise occur because the H_2CO_3 is a weak acid. This buffer system is primarily extracellular. The body fluids also contain intracellular buffer systems which can resist pH changes when acids are introduced.

Acids can be introduced in several ways. Exercise and oxygen deprivation cause a buildup of lactic acid as a result of anaerobic metabolism. Metabolism of sulfur-containing amino acids causes the production of sulfuric acid, another strong acid. Both aerobic and anaerobic metabolism cause the buildup of carbon dioxide, which combines with water to form carbonic acid; even though this is a weak acid, the large accumulation of carbon dioxide can lower pH.

Acids produced by any of these means are buffered by one of the buffer systems in the body. In addition to the bicarbonate ($NaHCO_3$) buffer system described above, there are two intracellular buffers that participate in pH maintenance. In the phosphate buffer system, monosodium phosphate (H_2NaPO_4), a weak acid, dissociates to produce H^+ and $HNaPO_4^-$. The H^+ is exchanged for Na^+ by the kidneys or buffered on protein, leaving the salt disodium phosphate (HNa_2PO_4). This salt dissociates into Na^+ and $HNaPO_4^-$. The $HNaPO_4^-$ can then absorb H^+ ions which have dissociated from strong acids to form H_2NaPO_4, which is weakly dissociated. The phosphate buffer system is the least important of the buffer systems because there is so little phosphate in the body. The most important buffer system in the body is protein. Some of the individual amino acids in proteins can act as weak acids and accept H^+ ions; the amino acid histidine is the most significant of these under the temperature and pH conditions of the body. Protein buffering is primarily an intracellular phenomenon, as the protein concentration in extracellular fluid is relatively low. The intracellular protein buffer makes up about three quarters of the total body buffering capacity.

Acid-Base Disturbances

The most important extracellular buffer is the bicarbonate buffer system discussed above. This system is aided directly by a second line of defense against pH disturbances. This is called physiological buffering. Physiological buffering refers to the fact that the supply of the most important components of the bicarbonate buffer system, carbon dioxide and bicarbonate, can be controlled. The organs responsible for this control are the lungs (carbon dioxide) and kidneys (bicarbonate). For example, during exercise, the buildup of lactic acid consumes bicarbonate (HCO_3^-) and lowers pH. This is called a metabolic acidosis. The low pH stimulates the rate of breathing, which in turn results in increased elimination of carbon dioxide by the lungs. This lowers the partial pressure (concentration) of carbon dioxide in the blood, reducing the amount of carbonic acid (H_2CO_3) that can dissociate to form H^+. The reduction of carbon dioxide is called a respiratory alkalosis. This respiratory alkalosis compensates for the metabolic acidosis caused by the depletion of bicarbonate. The kidneys provide the final correction for the initial metabolic acidosis. These organs accomplish this in two ways: reabsorption of bicarbonate, and secretion of H^+ into the urine in exchange for Na^+. When bicarbonate concentration in the extracellular fluid is reduced by a metabolic acidosis, the hormone aldosterone, produced by the adrenal glands, stimulates the secretion of H^+ and reabsorption of bicarbonate. This raises both the pH and bicarbonate concentration back to normal. The increased pH relaxes stimulation of breathing, allowing breathing rate to slow and the partial pressure of carbon dioxide to return to normal.

The above is an example of one of the four basic types of acid-base disturbance: metabolic acidosis (bicarbonate concentration reduced), metabolic alkalosis (bicarbonate concentration increased), respiratory acidosis (an increase in the partial pressure of carbon dioxide), and respiratory alkalosis (a decrease in the partial pressure of carbon dioxide). As before, metabolic acidosis is compensated for by respiratory alkalosis. This is part of a general pattern in which one condition is compensated for by the opposite condition. Another example would be a respiratory acidosis, lowering the pH and stimulating bicarbonate retention and H^+ excretion in the kidneys to produce a compensatory metabolic alkalosis.

Body Temperature and Ion Exchange

Temperature also affects pH. This is usually of no consequence to warm-blooded animals such as mammals and birds, which have a constant body temperature. It is, however, of great consequence to cold-blooded animals such as fish, amphibians, and reptiles, in which body temperatures vary with the environmental temperature. There is a decrease in pH by about 0.015 for each degree increase in temperature. This means that the pH at 5 degrees Celsius is 7.88, or 0.48 pH units higher than at mammalian body temperature (pH 7.40 at 37 degrees Celsius). This does not mean that cold-blooded animals do not regulate pH. While the regulation differs from that of warm-blooded animals in that pH varies, it is still regulated in the sense that it varies in a very predictable manner. By controlling partial pressures of carbon dioxide and bicarbonate ion concentrations in much the same way that mammals do, cold-blooded vertebrates maintain their body fluid pH at a constant 0.6 to 0.8 pH units higher than the pH of pure water at the same temperature. It is, thus, the relative alkalinity that is regulated, rather than the pH.

While the kidneys of mammals are intimately involved in pH maintenance, the situation in lower vertebrates can be much different. Most fish use ion exchange transport systems in their gills to regulate pH. Specialized cells in the exterior lining of the gill surfaces transport sodium ions (Na^+) from the water bathing the animals into the blood in exchange for H^+. Similarly, chloride ions (Cl^-) are transported into the animal in exchange for HCO_3^-. When fish become acidotic, they increase Na^+/H^+ exchange and decrease Cl^-/HCO_3^- exchange. This results in a net elimination of H^+ and a net conservation of HCO_3^- to elevate the pH of the body fluids. While the kidneys of fish do participate in pH maintenance, they seem to play only a minor role, usually about 5 percent of the total regulatory effort. The kidneys of amphibians also appear to play a minor role in pH maintenance. The major regulatory organs in these animals are the skin and urinary bladder. Aquatic salamander larvae increase Na^+/H^+ exchange and decrease Cl^-/HCO_3^- exchange across their skin to regulate internal pH. Toads, which are primarily terrestrial and thus seldom in contact with water, appear to use their urinary bladders for pH regulatory ion exchanges. Relatively little is known about the role of the reptilian kidney in pH maintenance. The alligator kidney plays a major role in acid elimination. The urinary bladder of turtles also participates in pH regulation in much the same manner as the urinary bladder of the toad. The bird kidney plays a major role in pH maintenance, and its urine pH values are similar to the pH values of mammalian urine.

Studying pH Maintenance

The regulation of pH is usually studied by measuring the pH and the partial pressure of carbon dioxide of the blood. This measurement of the regulation of extracellular pH is a reflection of the overall acid-base status of the individual being studied. The first requirement is to be able to sample blood from an undisturbed, resting subject. This usually means an indwelling arterial cannula, through which blood from an artery can be sampled. The blood is then injected into a chamber in a blood-gas analyzer containing a glass pH electrode that measures the pH of the plasma. Additional blood is injected into another chamber that contains oxygen and carbon dioxide electrodes that measure the partial pressures of these two gases. Bicarbonate concentration can be calculated from the mathematical relationship among pH, the partial pressure of carbon dioxide, and the bicarbonate concentration when the former two are known. When making these kinds of measurements, it is important to measure the pH and partial pressure of the blood at the same temperature as the animal. Thermostated electrodes are used for this. The calculation used to estimate bicarbonate concentration requires the use of two constants which are also temperature-dependent. It is important to use the constants that are appropriate to the temperature of the animal and the measurement conditions.

Alternatively, bicarbonate concentration can be approximated by measuring the total amount of carbon dioxide (the sum of the carbon dioxide, carbonic acid, bicarbonate, and carbonate concentrations). Under physiological conditions, more than 99 percent of the carbon dioxide is in the form of HCO_3^-. When strong concentrated acid (HCl) is added to a measured volume of blood or plasma, all the carbonic acid, bicarbonate, and carbonate are released as carbon dioxide. This carbon dioxide can then be measured with a carbon dioxide electrode. The resulting total carbon dioxide, minus the concentration of carbon dioxide measured before adding the HCl, is very close to being equal to the concentration of bicarbonate.

While there are a number of indirect methods for measuring intracellular pH, the best results are achieved directly with micro pH electrodes which can be used to impale single cells. These techniques must be done on isolated tissues or anesthetized, restrained animals, whose acid-base status does not, in the least, resemble that of resting, undisturbed animals. The techniques are useful for studying pH maintenance at the cellular level and useful extrapolations can be made to the whole animal.

The usual approach to the study of pH maintenance is to induce a disturbance in the pH of an experimental animal and then to follow changes in the pH, partial pressure of CO_2, and the concentration of HCO_3^- in the blood. Breathing rates and volumes of air exchanged by the lungs can be measured to determine the contribution of the lungs to pH maintenance. For example, increasing the rate of breathing will increase the rate of elimination of carbon dioxide and lower the partial pressure of this gas in the blood. Urine collection can be done to assess the contribution of the kidneys to pH maintenance, and in aquatic animals that do not rely heavily on their kidneys for pH maintenance, changes in the composition of the water in which the animals are situated can be used to assess the contribution of the gills (fish) or skin (amphibians) to pH maintenance.

Examples of experimental manipulations that can produce pH disturbances in animals include infusion of acids and bases into the blood to produce metabolic acidosis and alkalosis respectively. Alternatively, animals can be exercised to elevate lactic acid in their blood to produce a metabolic acidosis. Respiratory acidosis and alkalosis can be induced by artificially altering breathing rates. Alternatively, elevation of the partial pressure of carbon dioxide in the air or water of an experimental animal will produce a respiratory acidosis.

pH Maintenance and Homeostasis

Maintenance of pH is part of the overall phenomenon of homeostasis or constancy of the internal environment in a changing external environment. The primary reason for maintaining consistent acid-base balance is the need to keep constant the conformation (shape) of proteins. Proteins are very sensitive to changes in pH, and the usual consequence of such changes is a change in the shapes of proteins. Protein conformation is critically important to proper protein function.

All enzymes (proteins that cause necessary biochemical reactions to occur) have very specific shapes that must be maintained in order for them to function properly. Changes in pH cause alterations in those shapes and compromise the effectiveness of the enzymes. Many other proteins require certain conformational states. Cell membranes contain proteins that determine which chemicals can enter and leave the cell's interior. These proteins are called carriers if they actively transport specific substances into or out of the cell interior. Alternatively, membrane proteins can act as specific channels that allow passive movement of only specific molecules or ions across the membrane. Both carriers and channels are sensitive to pH-induced conformational changes. There are other membrane-bound proteins called receptors that respond best to hormones and other chemical messengers when the pH is maintained at the norm. Proteins in the immune system, such as antibodies, also require proper pH in order to function optimally.

Cold-blooded animals do not regulate their pH to a specific point, but instead regulate the difference between their pH and the pH of pure water at the same temperature. This relative alkalinity ensures constant protein conformation in the same way that constant pH at constant temperature ensures constant protein conformation in warm-blooded animals, because the weak acid nature of proteins causes them to be partially dissociated from H^+ in the pH and temperature range experienced by animals. The conformation of protein is determined, to a large extent, by the net electrical charge (distribution of + and – charges over the protein). The net charge is influenced by the degree of dissociation of the protein and H^+. As discussed above, the dissociation in protein that is important to pH maintenance is the dissociation of H^+ from histidine. As long as the dissociated fraction of histidine remains constant, the protein conformation will remain constant. As long as the relative alkalinity is maintained, the fractional dissociation of histidine remains constant and thus protein conformation does not change. In reality, the regulation of mammalian pH at 7.4 (at 37 degrees Celsius) is one specific example of this general rule. The relative alkalinity of mammalian blood at 37 degrees is the same as the relative alkalinity of fish blood at 5 degrees or of reptile blood at 42 degrees.

—Daniel F. Stiffler

See also: Cell types; Gas exchange; Osmoregulation; Respiration; Water balance in mammals.

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PHEROMONES

Type of animal science: Physiology
Fields of study: Ecology, ethology, evolutionary science, invertebrate biology

Pheromones are chemicals or mixtures of chemicals that are used as messages between members of a species. They are integral parts of the social communication within most species. They may prove to be of great value in pest control and in enhancing agricultural production.

Principal Terms

ALLELOCHEMIC: a general term for a chemical used as a messenger between members of different species; allomones and kairomones are allelochemics, but hormones and pheromones are not

ALLOMONE: a chemical messenger that passes information between members of different species, resulting in an advantage to the sender

KAIROMONE: a chemical messenger that passes information between members of different species, resulting in an advantage to the receiver

PRIMER PHEROMONE: a chemical that generates an often subtle physiological response in another member of the same species; a behavioral response may follow

SEMIOCHEMICAL: a chemical messenger that carries information between individual organisms of the same species or of different species; pheromones and allelochemics are semiochemicals, but hormones are not

VOLATILES: chemical compounds that are vapor or gas at environmental temperatures or that readily release many of their molecules to the vapor phase

Pheromones are chemical signals. Originally defined to include only signals between individuals of the same animal species, the term has been generalized to designate any chemical or chemical mixture that, when released by one member of any species, affects the physiology and/or behavior of another member of the same species. "Pheromone" is one of a set of terms developed to express the chemical interactions in ecological communities, and it can best be understood in the context of that set of terms.

In this context, pheromones are semiochemicals that carry information between members of a single species. To do so, the pheromone must be released into the atmosphere or placed on some structure in the organism's environment. It is thus made available to other members of the species for interpretation and response. It is also available to members of other species, however, so it is a potential allelochemic.

For example, klipspringer antelope mark vegetation in their environment with a chemical secreted from a special gland. Other klipspringer investigate the marks to gather information on the marking individual. Ticks that parasitize the klipspringer, however, are also attracted to the chemical marks and thus increase their chance of attaching to a host when the mark is renewed or when another klipspringer investigates it. The tick is using the pheromone as a kairomone. Pheromones can act as allomones as well, though the interaction is sometimes less direct. Bolas spiders produce the sex-attractant pheromone of a female moth and use it to lure male moths to a trap. The spider uses the moth pheromone as an allomone.

To appreciate fully the complexity of the interactions under consideration, it is important to remember that a pheromone may also be acting as a kairomone, allomone, or hormone. There are two general types of pheromone: those that elicit an immediate and predictable behavioral response, called releaser or signal pheromones, and those that bring about a less obvious physiological response, called primer pheromones (because they prime the system for a possible behavioral response). Pheromones are also categorized according to the messages they carry. There are trail, marker, aggregation, attractant, repellant, arrestant (deterrent), stimulant, alarm, and other pheromones. Their functions are suggested by the terms used to name them.

Pheromone Composition and Function

The chemical compounds that act as pheromones are numerous and diverse. Most are lipids or chemical relatives of the lipids, including many steroids. Even a single pheromonal message may require a number of different compounds, each present in the proper proportion, so that the active pheromone is actually a mixture of chemical compounds.

Different physical and chemical characteristics are required for pheromones with different functions. Attractant pheromones must generally be volatile to permit atmospheric dispersal to their targets. Many female insects emit sex-attractant pheromones to advertise their readiness to mate. The more widely these can be dispersed, the more males the advertisement will reach. On the other hand, many marking pheromones need not be especially volatile because they are placed at stations which are checked periodically by the target individuals. The klipspringer marking pheromone is an example. Some pheromones are exchanged by direct contact, and these need not have any appreciable volatile component. Many mammals rub, lick, and otherwise contact one another in social contexts and exchange pheromones at these times.

Specificity also varies for pheromones with different functions. Sex attractants usually need to be very specific, directed only to members of the opposite sex and the same species. Alarm pheromones, on the other hand, need not be so specific. These pheromones simply alert other members of the same species to a disturbance. It is usually harmless, and sometimes even helpful, to alert members of other species as well. In keeping with this argument, related groups of ant species produce species-specific sex-attractant pheromones: Each female attracts only males of its own species. In contrast, alarm pheromones of any species in the group will stimulate defensive reactions in individuals in many of the species.

Pheromonal systems are not organized in any standard way in different species. Many mites and ticks also have nonspecific alarm pheromones. Surprisingly, some groups also have nonspecific sex-attractant pheromones. In these cases, the specificity necessary for reproductive efficiency is generated by species-specific mating stimulant pheromones. These pheromones are produced by a female after males have been attracted to her. They stimulate mating behavior, but only in males of the same species. Thus the required specificity is achieved by a different mechanism. This is only one of many examples of the diversity of pheromonal schemes among organisms.

Pheromone Sources and Receptors

The sources of pheromones are also diverse. Some pheromones are produced by specialized glands; many insect species have glands specialized for the production of pheromones. One example is the harvester ant's alarm pheromone, which is produced in the mandibular gland at the base of the jaws. Other pheromones seem to be byproducts of other bodily functions. The lipids of mammalian skin are probably primarily important in waterproofing and in maintaining the outer layer of the skin, but many also function as pheromones.

The reproductive tract is an important source of pheromones in many species. These usually act as sex-attractant or sex-stimulant pheromones or as signal pheromones that give information on the sexual state of the emitter. The urine and feces of many species also contain pheromones which are used to mark territory boundaries and to transmit other information about the marking individual. Many pheromones seem to be produced not by the sending organism alone but by microorganisms living on the skin or in the glands or cavities of the sender's body. These microbes convert products of their host into the actual signal molecules, or pheromones, used by the host.

The receptors for pheromones are also of many different types, and the chemical receptors for taste and smell are often involved. In vertebrates, the vomeronasal organ (Jacobson's organ) seems to be an important receptor for many pheromones. It is a pouch off the mouth or nasal passages, and it contains receptors similar to those for smell. It is nonfunctional in humans, but it functions in more primitive mammals and seems to be of great importance to snakes and other reptiles. Insects and other invertebrates have many specialized structures for receiving pheromonal messages. Perhaps the best-known example is the feathery antennae of many male moths, which are receptors for the female moth's sex-attractant pheromone. Some pheromones seem to be absorbed through the skin or internal body linings and to bring about their effects by attaching to some unknown internal receptor.

Pheromones are widespread in nature, occurring in most, if not all, species. Most are poorly understood. The best-known are those found in insects, partly because of their potential use in the control of pest populations and partly because the relative simplicity of insect behavior allowed for rapid progress in the identification of pheromones and their actions. Despite these advantages, much remains to be learned even about insect pheromones. Mammalian pheromones are not as well known, although they may also be of economic importance. The more complex behavior of mammals makes the study of their responses to pheromones much more difficult.

Behavioral and Chemical Research

Both behavioral and chemical techniques are required in order to study pheromones and other semiochemicals. The observation of behavior, either in nature or in captivity, often suggests pheromonal functions. These hypothesized functions are then tested by presenting the pheromone to a potentially responsive organism and observing the response. Situations may be arranged which demand the subject's response to a particular pheromone under otherwise natural conditions. Alternatively, the organisms may be observed in enclosures to help control the experimental context. The presentation of the hypothetical pheromone may be in the form of another organism of the same species or some structure to which the presumed pheromone has been applied. The observed response (or lack of response) gives information on the status of the presented chemical as a pheromone in that behavioral context.

While the pheromonal function of secretions from a gland or other source can be determined from these behavioral tests, the tests can give information on specific chemical compounds only if the compounds can be isolated and identified. The isolation and identification of pheromonal compounds are challenging because of the great complexity of the secretions in which they are found and the exceptionally small amounts that are required to elicit a response. Many separation and identification techniques are used. One of the most powerful is a combination of gas chromatography and mass spectrometry.

Gas chromatography is used to separate and sometimes to identify chemicals that are volatile or can be made volatile. The unknown chemical is mixed with an inert gas, called the mobile phase of the gas chromatography system. This mixture is passed through a tube containing a solid, called the stationary phase. The inert gas does not interact with the solid; however, many of the compounds mixed with it do, each to an extent determined by the characteristics of the compound and the characteristics of the stationary phase. Some members of the mixture will interact very strongly with the solid and so move slowly through the tube, whereas others may not interact with the solid at all and so pass through rapidly. Other members of the mixture interact at intermediate strengths and so spend intermediate amounts of

Image Not Available

time in the tube. The different compounds are recorded and collected separately as they exit from the tube.

For identification, the compounds are often passed on to a mass spectrometer. In mass spectrometry the compound is broken up into electrically charged particles. The particles are then separated according to their mass-to-charge ratio, and the relative number of particles of each mass-to-charge ratio is recorded and plotted. The original compound can usually be identified by the pattern produced under the specific conditions used. After separation and identification, the individual chemicals may be subjected to behavioral studies.

Uses for Pheromones

Pheromones and other semiochemicals are of interest simply from the standpoint of understanding communication between living things. In addition, they have the potential to provide effective, safe agents for pest control. The possibilities include sex-attractant pheromones to draw pest insects of a particular species to a trap (or to confuse the males and keep them from finding females) and repellant pheromones to drive a species of insect away from a valuable crop species. One reason for the enthusiasm generated by pheromones in this role is their specificity. Whereas insecticides generally kill valuable insects as well as pests, pheromones will often be specific for one or a few species.

These chemicals were presented as a panacea for insect and other pest problems in the 1970's, but most actual attempts to control pest populations failed. Many people in the field have suggested that lack of understanding of a particular pest and its ecological context was the most common cause of failure. They maintain that pest-control applications must be made with extensive knowledge and careful consideration of pest characteristics and the ecological system. In this context, pheromones have become a part of integrated pest management (IPM) strategies, in which they are used along with the pest's parasites and predators, resistant crop varieties, insecticides, and other weapons to control pests. In this role, pheromones have shown great promise.

Some consideration has been given to the control of mammalian pests with pheromones, though this field is not as well developed as that of insect control. Pheromonal control of mammalian reproduction has received considerable attention for other reasons: Domestic mammals are of great economic importance, and many wild mammalian species are endangered to the point that captive breeding has been attempted. The manipulation of reproductive pheromones may be used to enhance reproductive potentials in both cases. The complexity of mammalian behavioral and reproductive systems, however, and the subtle changes brought about by mammalian pheromones present a particular challenge. As with insect pest control, the key to progress is a complete understanding of the entire system being manipulated.

Pheromones and other semiochemicals are of great potential economic importance as substitutes for or adjuncts to toxic pesticides in pest management. Mammalian reproductive pheromones are being explored as tools to enhance reproductive efficiency in domestic and endangered mammals. A complete understanding of the complex roles of pheromones in each of the systems being managed is necessary for success in all these endeavors.

—Carl W. Hoagstrom

See also: Communication; Courtship; Ecology; Endocrine systems of invertebrates; Endocrine systems of vertebrates; Ethology; Hormones and behavior; Insect societies; Insects; Mammalian social systems; Mating; Sexual development; Territoriality and aggression.

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PHYLOGENY

Type of animal science: Evolution
Fields of study: Anthropology, archaeology, evolutionary science, population biology, systematics (taxonomy), zoology

Phylogeny is the study of the evolutionary history of an animal or of groups of animals. It is the methodology that traces the lines of descent among living things and tries to classify them in some systematic order based on ancestry.

Principal Terms

DEOXYRIBONUCLEIC ACID (DNA): the genetic material of most living organisms
EVOLUTION: the process by which the variety of plant and animal life has developed over time from the most primitive to the most complex life-forms
KINGDOM: the highest category into which organisms are classified; there are now believed to be five kingdoms
MOLECULE: the smallest part of a chemical compound
PHYLUM: a group that consists of several closely related classes
SPECIES: a group of organisms that can produce offspring with each other

Phylogeny traces the history of life on earth through the study of how animals and plants have developed over time and how they are related to one another. It is similar to taxonomy, the science of classifying organisms based on their structure and functions. Taxonomists create family trees of living and extinct species in order to discover the origins and lines of descent of various forms of life. Very few family trees are complete to their fossil origins, however, because of gaps in the fossil record. The first system of classification was devised by the eighteenth century Swedish scientist Carolus Linnaeus. Linnaeus classified life-forms based on their appearance; the more they resembled each other in size, shape, and form, he believed, the more closely they were related.

The theory of evolution developed by nineteenth century naturalist Charles Darwin was based on accumulated changes over time through natural selection and led to a new way of looking at the history of life and to the development of phylogeny as a method of classification. The new system classified the living world by similarities in ancestry rather than appearance. Life histories of species were derived from the study of comparative anatomy (the search for common features in different species), embryology (the study of the development of life from the egg to birth), and biochemistry (the study of invisible chemical characteristics of cells that link species that can look very dissimilar). Modern technology allows scientists to measure differences in deoxyribonucleic acid (DNA) molecules among species. DNA carries the genetic material of an organism and plays a central role in heredity. The degree of difference between two species helps scientists determine how much modern species have changed from their ancestors and to estimate when important events in evolution occurred. If a sufficient fossil record exists, biochemists can determine the timing of a major change that led to the development of a new characteristic such as a longer neck in giraffes or a different size eyeball in a bat.

Classifying Earth's Species

Studies of evolutionary change suggest that anywhere from three million to twenty million species now exist, with millions more having become extinct. The earth began about 5 billion years ago, and it has been occupied by living organisms for about 3.5 billion years. For about 2.5 billion years, the planet was populated only by single-celled bacteria. The earliest forms of life evolved by chance during a long period of chemical reactions. Random encounters between chemicals in the seas and the atmosphere produced amino acids and proteins. Small drops of proteins, made up of carbon, hydrogen, oxygen, nitrogen, and sulfur, somehow bound together and became organisms; that is, they began to reproduce themselves, which is the quality that makes them life-forms.

Every living thing is given a two-part Latin name under a system of binomial nomenclature. This name is usually based on an evolutionary, phylogenetic relationship. The first part of the name indicates the organism's genus; the second part identifies the specific species. For example, *Acer saccharum, Acer nigrum*, and *Acer rubrum* are all kinds of maple trees. They share the genus *Acer*, and their species names mean sugar, black, and red, respectively. No rules govern species names, though frequently they refer to a prominent feature such as color or characteristic, such as in the case of *Homo sapiens*, the Latin name for human beings, which literally means "the thinking one."

Of the five kingdoms of life-forms, one (containing the bacteria) is made up of prokaryotes; the other four are eukaryotes. Prokaryotes do not have cell nuclei; eukaryotes do. In prokaryotes, cells are smaller and simpler in structure, and the DNA is not organized into chromosomes. Chromosomes, the threadlike structures found in the cell nucleus of all eukaryotes, determine the characteristics of individual organisms, with offspring receiving an equal number of chromosomes from each parent. In bacteria, however, reproduction takes place by a simple division of the parent into two masses that eventually separate. Bacteria do not share chromosomes with other members of the species; in other words, reproduction is asexual.

The Nonanimal Kingdoms

All bacteria belong to the kingdom Prokaryotae. They are in terms of total numbers the most successful form of life in the universe. Some bacteria, which are germs, can cause disease, while some bacteria, such as antibiotics, can be used to cure disease. Bacterium-like fossils that were found in rocks from an Australian gold mine are about 3.5 billion years old. Bacteria are found in every climate and habitat, and are the first to invade and populate new habitats. Seventeen phyla of bacteria are known to exist, and none can be seen without a microscope.

The four other kingdoms of living things and the common names given to their most important phyla are Protoctista (algae, protozoa, slime molds), Fungi (mushrooms, molds, lichens), Animalia (sponges, jellyfish, flatworms, ribbon worms, rotifers, spiny-headed worms, parasitic nematodes, horsehair worms, mollusks, priapulid worms, spoon worms, earthworms, tongue worms, velvet worms, insects, beard worms, starfish, arrowworms, and chordates), and Plantae (mosses, ferns, and pine-bearing and flowering plants). Phyla are based on similarities in evolutionary development. Life-forms are divided into ninety-two phyla: There are seventeen phyla in the kingdom Prokaryotae; twenty-seven in Protoctista; five in Fungi; thirty-three in Animalia, and ten in Plantae. Each phylum is divided into classes, then orders, families, genera (the singular form is genus), and finally, species. The last two divisions are based on the most recent evolutionary differences. Some phyla have only a few genera and species, while others, such as those in Animalia, have millions. A species consists of a group of similar individual organisms that can breed and reproduce offspring. A genus contains similar species, but members of a genus cannot reproduce; only members of a species can.

Protoctista (also called Protista) means the "very first to establish." It is the kingdom made up of living forms that are neither animals, plants, nor fungi. It includes red, green, and brown algae, seaweeds, water and slime molds, and most protozoa (single-celled life-forms including amoebas). The twenty-seven phyla in this kingdom are found mostly in water habitats such as rivers, freshwater lakes, and oceans.

The kingdom Fungi (from a Greek word meaning "sponge") may have descended from the kingdom Protoctista. The oldest fossil Fungi are about 300 million years old. There are more than one hundred thousand identified species, including bread molds, yeasts, and mushrooms. Thousands more species are believed to exist but have yet to be identified.

The Animal Kingdom

All plants, from mosses to giant redwoods, belong to the kingdom Plantae (from a Latin word for "plant"), and most animals belong to the kingdom Animalia. This kingdom contains all multicellular, heterotrophic, diploid organisms that develop from an egg and sperm. A heterotrophic animal takes food into the body and digests it, or breaks it down, into energy for use. A diploid organism has two sets of chromosomes, one derived from the female parent and the other from the male. The characteristic that defines all Animalia, however, is that they develop from a blastula, a hollow ball of cells found in animal embryos (the earliest stage of development, when the egg just begins to divide) but not in plants. The blastula forms a layer around a central open space or cavity in the embryo.

Animalia (from a Latin word meaning "soul" or "breath") is the kingdom with the largest number of life-forms, from Placozoa, a phylum with a single species usually found growing on aquarium walls, to the phylum Arthropoda (from a Greek word meaning "jointed foot") that contains more than a half million identified species, including spiders, scorpions, beetles, shrimp, lobsters, crayfish, crabs, flies, centipedes, millipedes, butterflies, moths, and all other species of insects. Seventeen of the thirty-three phyla in Animalia are various kinds of worms found in the shallow and deep water of lakes, rivers, and oceans and in the ground. One worm phyla, Pentastoma, consists of more than seventy species that live exclusively in the tongues, lungs, nostrils, and nasal sinuses of dogs, foxes, goats, horses, snakes, lizards, and crocodiles. Another phyla, Platyhelminthes, consists of worms that live in bat dung and other equally unusual environments. Only two of the phyla, Arthropoda and Chordata (animals with nerve cords), live entirely on land. Among the phyla, Arthropoda has the largest number of identified species, more than a million, and possibly millions more not yet identified. Most of the species of Animalia that have ever lived are now extinct. Thirty-two of the thirty-three phyla are invertebrates, which means they lack backbones.

The History of Life-Forms

The phylogenetic method of classifying life, using animals as an example, begins with the earliest fossil records available. The earliest members of the Animalia kingdom evolved from members of the Protoctista kingdom about 565 million years ago. Exactly when and which members were the first is subject to debate; however, the first large, multicellular fossils date to this time. About 530 million years ago, there was a gigantic explosion of life-forms, including all kinds of clams, snails, arthropods, crabs, and trilobites. After a few tens of millions more years came echinoderms (starfish and sea urchins) and eventually chordates, out of which emerged fish and mammals.

The periods of explosive growth and massive extinction of life-forms are believed to have been caused by some major environmental changes, the exact nature and cause of which have not been determined. Scientists believe an explosion of new life could have been caused by an increase in atmospheric oxygen, which would allow life-forms to live out of water, and a mass extinction could have been the result of gigantic dust clouds, large enough to darken the sun's light for millions of years, stirred up by huge meteors crashing into earth. Such a critical darkening of the earth is believed to have taken place about sixty-five million years ago, plunging temperatures to near freezing and killing off thousands of species including all the dinosaurs.

The Phylum Chordata

Despite the tremendous losses resulting from the extinction of as much as 95 percent of the existing species, life-forms continued to survive and evolve. The most successful of the new forms emerged from the ancestors of the phylum Chordata (from a Latin word for "cord"). This phylum includes all mammals, birds, amphibians, reptiles, and species with backbones (vertebrates). More than forty-five thousand species of chordates exist. Three key features are used to classify members of the phylum. A member must have a single nerve cord along its back. In mammals, this cord has developed into the spinal cord and brain. It must also have a notochord, a bony rod located between the nerve cord and the digestive tract, which supports the body and the muscles and is found in the embryo and the adult. The last requirement is that members have gill slits in the throat at some stage of development, whether in the embryo stage as is true with land animals or throughout their entire life as in fish. Gill slits show that land animals developed from sea creatures.

The phylum Chordata includes two superclasses, Pisces (fish) and Tetrapoda (four-limbed forms). There are two classes of living Pisces, Chondrichthyes (boneless creatures), which includes sharks, skates, and rays, and Osteichthyes (bony fish), a class that contains about twenty-five thousand species. The earliest fish fossils are about 500 million years old. There are four classes in Tetrapoda: Amphibia, Reptilia, Aves, and Mammalia.

The class Amphibia contains about two thousand species of frogs, toads, and salamanders. Members of this class evolved about 370 million years ago and were the first vertebrates to live on land. Amphibia must lay their eggs in water and must live close to water, or their soft skin will dry out and cause their deaths.

The class Reptilia has more than five thousand species. It includes turtles, lizards, snakes, and crocodiles. Reptiles develop from an egg, live on land, and have dry, scaly skin. The largest reptiles, the dinosaurs, died out more than sixty million years ago. Reptiles are cold-blooded, which means they cannot control the temperature of their blood, they breathe air through lungs, and they are not required to lay their eggs in water. They probably evolved out of an amphibian species between 300 million and 320 million years ago.

The class Aves contains nine thousand species of living birds, with thousands more extinct. Aves evolved from dinosaur species perhaps 200 million years ago. Unlike reptiles, Aves class members have the ability to regulate their internal temperature. They have feathers rather than scales, but they lack teeth.

The fourth class is Mammalia, which has more than forty-five hundred living species, including human beings. Mammals are classed into Metatheria (marsupials) and Eutheria (placentals). Metatheria, such as kangaroos, have external pouches in which their young are born live. Eutheria have vaginas through which the fully developed young pass during birth. Most mammals are members of Eutheria. This includes the orders of Insectivora (hedgehogs, shrews, and moles), Primates (lemurs, monkeys, apes, and human beings), Carnivora (dogs, cats, and bears), and Pinnipedea (seals and sea lions.)

The Benefits of Classification

Life on earth includes millions of different types of organisms. Phylogeny is one method of making sense out of so many different life-forms. It provides a system that links organisms together on the basis of their evolutionary history of development. By grouping vast numbers of forms into related groups, phylogenetics helps bring some order to what seems like chaos. Attempts to classify life-forms have always been controversial, and there still is much disagreement in the scientific community over various types of classification. However, phylogeny is the most widely agreed upon system.

Developments in techniques used to analyze molecules and DNA in the 1980's have shed light on the evolutionary development of species and have demonstrated new links among living plants and animals. The information gleaned using these techniques can also be used to trace the ancestry of modern species back to the earliest fossil evidence available from 575 million years ago. Molecular comparisons have shown that the development of species from spores and eggs into embryos and adult stages is very similar across a wide range of phyla.

These techniques produce data that consist of long sequences of the four nucleic acids that make up the information contained in DNA. The patterns formed by the acids are very similar among related organisms. The more closely related the sequence of nucleic acids, the more closely the species are related. Closely related species differ only very slightly in the way their DNA is structured. The more species differ in their DNA structure, the more distant they are in evolutionary terms. By measuring and comparing the differences in a gene that controls basically the same function in various species, scientists can construct an evolutionary tree. Species can be placed on the tree at the points where they begin to diverge from other genus members. In this way, examinations of the phylogenetic development of organisms can be used to create a tree of life showing the close relationships among all organisms. The tree also shows that all forms of life are related because they originally came from the same source in some ancient pool where the right chemicals just happened to bump into one another, mix, and begin to produce offspring.

—Leslie V. Tischauser

See also: Amphibians; Evolution: Historical perspective; Extinction; Fish; Genetics; Human evolution analysis; Insects; Mammals; Multicellularity; Primates; Reptiles; Sex differences: Evolutionary origin; Systematics.

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PHYSIOLOGY

Types of animal science: Anatomy, fields of study, physiology
Fields of study: Anatomy, developmental biology, embryology, evolutionary science, physiology, zoology

Physiology is a fundamental branch of biology, predating all disciplines except perhaps anatomy. Physiologists study the functions of living organisms. These functions are studied at many levels of organization: the molecular level, the cellular level, the tissue-organ level, and even the organismic (whole animal) level. The goal is to explain living functions in quantifiable terms that obey the laws of chemistry and physics.

Principal Terms

ARTERY: a blood vessel that carries blood from the heart to the body tissues

CAPILLARY: a small vessel that connects arteries to veins; this is where respiratory gases, nutrients, and wastes are exchanged between blood and tissues

GLOMERULUS: a specialized capillary in the kidneys that filters blood

NEPHRON: a tubular structure in the kidneys that extracts filtrate, and reabsorbs nutrients and other valuable substances and secretes wastes

NEURON: an individual nerve cell; nerves are made up of many neurons bundled together

VEIN: a blood vessel that returns blood to the heart

How animal bodies work is the subject of physiology. Early Greek philosophers such as Aristotle used deductive reasoning (the use of observations, logic, and intuition) to explain function. William Harvey (1578-1657) is generally considered the father of modern physiology, as he was among the first and most successful in employing inductive reasoning (experimentation) to explain body function. Inductive reasoning uses the scientific method to study unsolved problems. This approach starts with a hypothesis. Experiments are designed to test the hypothesis. Data are collected using quantified measurements; physiologists never simply say heart rate increased in response to the experimental treatment. The result is always expressed in quantified terms; for example, one might say that heart rate increased from thirty to forty-five beats per minute. Once the data are collected, they are analyzed and interpreted in terms of the original hypothesis. The interpretation usually leads to new hypotheses which are then tested with new experiments.

The Study of Systems

Classically, physiology has been divided into several organ systems. These include the neuromuscular system, the cardiovascular system, the pulmonary system (lungs), the renal system (kidneys), the digestive system, and the endocrine system. This nomenclature is based on mammalian systems and has had to be modified to include such alternative systems as gills (branchial system) in aquatic animals.

Physiology has been characterized as a synthetic science because it involves a synthesis of biology, chemistry, mathematics, and physics to describe body functions. The objective is to explain a given physiological function in terms which obey the laws of chemistry and physics. This often involves model building. A physiological model is a construct of hypotheses, which can be qualitative or quantitative. Harvey proposed a model in which the blood circulates from the heart to arteries, and then to capillaries which connect to veins to return the blood to the heart. He then did experiments to prove this. Quantitative or mathematical models are used to describe many functions using mathematical constructs and equations.

Physiology is studied at the molecular, cellular, tissue, organ, system, and organismic levels. There are several branches of physiology. Mammalian, fish, and insect physiologists restrict their studies to a certain group. General physiology seeks to describe functions that are common to all life forms, such as cell membrane function. Comparative physiology seeks to examine how different groups of animals accomplish similar goals while living in completely different circumstances, for example, in aquatic environments exchanging oxygen and carbon dioxide with water versus living on land and exchanging these respiratory gases with air.

Comparative studies are important for several reasons. First, the acquisition of each new piece of specific knowledge raises questions about its broader applicability. Once it is known that land animals need oxygen in air to breathe, the question arises: If a fish spends its entire life under water, why does it not drown? The answer is that it uses gills to extract oxygen efficiently from water (with a notoriously scarce oxygen supply) and to excrete carbon dioxide. Comparative physiology also helps to better understand evolution. The evolution of the vertebrate cardiovascular system from fish with two-chambered hearts, to amphibians and most reptiles with three-chambered hearts, to birds and mammals with four-chambered hearts, has attracted much interest in how the circulation of oxygen-rich blood is kept separate from oxygen-poor blood. Finally, comparative physiology can be used to study simple physiological systems in primitive animals such as invertebrates to help explain more complex systems in more advanced animals such as mammals.

Gaining Knowledge Through Experimentation

Our knowledge of how information is carried by neurons (the individual fibers of nerves) began with studies of squid neurons. Squid have giant neurons; they are so large that physiologists were able to insert electrodes inside them to discover the electrical events that produce nervous impulses and thus information transfer. Beyond this, the neurons are so large that it is possible to remove their contents and substitute artificial solutions to see how this alters neural impulse production. This is how it was discovered that the ions sodium and potassium are responsible for neural impulses. This research started in the 1920's, and developing technology has shown that mammalian neural function operates essentially the same way as squid neural function. Another example of such use of comparative physiology has led to the understanding of kidney function. In the early twentieth century, it was observed that kidney tubules in amphibians such as frogs and salamanders are large enough to allow samples of nephric tubular fluid to be removed and analyzed. Such studies led to the discovery that the initial event in urine formation is filtration of blood plasma in glomerular capillaries and that the final urine composition results from selective reabsorption and filtration of water and solutes in nephrons.

Physiology is a very interesting field that can prepare one for careers in teaching at all levels, basic research, or commercial research and development.

—*Daniel F. Stiffler*

See also: Adaptations and their mechanisms; Anatomy; Antennae; Beaks and bills; Biology; Bone and cartilage; Brain; Cell types; Circulatory systems of invertebrates; Circulatory systems of vertebrates; Convergent and divergent evolution; Digestive tract; Ears; Embryology; Endoskeletons; Exoskeletons; Eyes; Feathers; Fossils; Genetics; Heart; Horns and antlers; Hydrostatic skeletons; Kidneys and other excretory structures; Lungs, gills, and tracheas; Muscles in invertebrates; Muscles in vertebrates; Nervous systems of vertebrates; Noses; Reproductive system of female mammals; Reproductive system of male mammals; Respiratory system; Scales; Sense organs; Shells; Tails; Teeth, fangs, and tusks; Tentacles; Wings.

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PIGS AND HOGS

Type of animal science: Classification
Fields of study: Anatomy, zoology

Pigs are social animals of the genus Sus, *living in family groups led by an older female and her offspring. The male likes to be alone except during the breeding season. The female will have between six and twelve babies at a time.*

Principal Terms

BARROW: a castrated male pig that has not produced any secondary sexual characteristics
BOAR: male pig
GILT: a young female pig that has not produced a litter
HOG: the general name applied to a pig over three months old
PORK: the meat of the pig used for food
SHOAT: an immature pig of either sex that weighs between 35 and 160 pounds
SOW: female pig that has produced a litter of babies
SWINE: the general name applied to the domesticated pig

Pigs are estimated to have evolved about 38 million years ago in central Europe, and about 25 million years ago to have become established in Africa and Asia. Pigs became domesticated in China about 5000 B.C.E. The reason for the delay in agricultural domestication is believed to be that pigs were unwilling to adapt to a nomadic lifestyle, as dogs, sheep, and goats did. The domesticated pig is thought to have descended from two different lines of wild hogs. It is believed that the East Indian pig (*Sus vittatus*) has had major influence on the swine of China and the surrounding region. The European wild boar has probably had major influence on the rest of the various breeds of pigs in the world.

The domestic pig is a compact, solid-looking animal with a large head, short, fast-moving legs, a rough coat, and a small tail. The color of a pig can vary greatly, from white or black to brownish-red, and any combination thereof, including spotted, solid colored, and banded. Some may reach a height of only twelve inches at the shoulder, others may reach all the way to four feet. The weight

Pig Facts

Classification:
Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Subclass: Theria
Order: Artiodactyla
Family: Suidae
Subfamily: Suinae
Genus: Sus
Geographical location: There are no true wild pigs in the Western Hemisphere, but there are feral hogs, except in Antarctica; the javelina, native to North and South America, is not a true pig; wild pigs are found in Southeast Asia and Eurasia
Habitat: Wide range, from swamps and rain forests to dry lands and mountains
Gestational period: A little less than four months (111-115 days)
Life span: Domestic pigs generally have a life span of from six to ten years, with an occasional occurrence of over twenty years
Special anatomy: Pigs have an excellent sense of smell and exceptional hearing, but their eyesight is weak

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of a pig also can vary, with some weighing only about 60 pounds, where others can go over 900. The average meat pig falls in the range from 225 to 300 pounds.

Humans use pigs in many different ways. From the point of view of the percentage of the carcass used, the pig is the most utilized of all domesticated animals. The hair is used for brushes because it is very strong, yet flexible. The hide is used for numerous products, from shoes to purses; in general it is lightweight and durable. The blood and offal are used for fertilizers, soaps, and medical supplies. Domestic pigs have been used by mankind for centuries as a main supplier of dietary protein.

Types of Pigs

Pigs are cloven-hoofed ungulates, and are closely related to the hippopotamus. As mentioned, the domestic pig (*Sus scrofa*) is now found worldwide. They are omnivorous, eating almost anything. However, pigs generally prefer to eat soft tissue plants, especially roots and tubers, which they dig up with their noses. They will also eat leaves, seeds, bugs, and anything that is found on the ground, including bird eggs, baby birds, snakes, and carrion.

There are hundreds of different breeds of pigs in the world. Most of the breeds that the various departments of agriculture recognize as major contributors to current swine production come from the United States or Europe. The pigs can be identified as being either meat, lard, or bacon types. Lard types have lost a great deal in numbers over the past fifty years, and have been bred into a style more like meat. The pig population in the world is large, and is approaching almost one billion in number, with China having the largest number, 250 million. Russia and the United States are tied in second place with about 60 million each. Brazil would be fourth with 35 million.

The largest consumer of pork per capita is Denmark (105 pounds annually), followed by Hungary, Germany, Austria, Luxembourg-Belgium, and the United States. In the United States, the state of

Iowa leads in production of hogs, followed by Illinois, Missouri, Indiana, and Minnesota.

Pigs are very smart domesticated animals. Their abilities are thought of as being greater than those of the domestic dog. Indeed, pigs make fine pets, as is evidenced by the pot-bellied pig of Southeast Asia.

—*Earl R. Andresen*

See also: Domestication; Claws, nails, and hooves; Omnivores; Ungulates.

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PLACENTAL MAMMALS

Types of animal science: Development, reproduction
Fields of study: Anatomy, biochemistry, cell biology, embryology, physiology, reproductive science

Placental reproduction is the most common form of mammalian reproduction. All mammals except the marsupials (such as the kangaroo and opossum) and the monotremes (platypus and echidna) form placentas.

Principal Terms

CHORION: the outer cellular layer of the embryo sac of reptiles, birds, and mammals; the term was coined by Aristotle

EMBRYO: a young animal that is developing from a fertilized or activated ovum and that is contained within egg membranes or within the maternal body

ENDOMETRIUM: an inner, thin layer of cells overlying the muscle layer of the uterus

FETUS: a mammalian embryo from the stage of its development where its main adult features can be recognized, until birth

MATERNAL: referring to the female parent

OVUM: an unfertilized egg cell

UTERUS: in female mammals, the organ in which the embryo develops

VIVIPAROUS: producing young that are active upon birth (often referred to as live birth); the embryo is nurtured within the uterus

Monotremes are oviparous, or egg-laying mammals. Marsupials are ovoviviparous, meaning that the egg is large and has a yolk adequate to nourish the embryo during its early development, but it remains unattached to the wall of the uterus. Gestation in marsupials is necessarily short, therefore, and the young are born in an immature, fetal stage. They make their way to the mother's pouch and continue to grow, nourished by the mother's milk. All other mammals, termed placental, are viviparous. The small egg, lacking food substance, becomes attached to the uterine wall, and the developing embryo is nourished by the mother's blood passing through a placenta. This process allows longer gestation, and as a result the young are born in a more advanced (precocial) state of development.

The placental mammals form a diverse and successful group that includes the insectivores (such as shrews, hedgehogs, and moles), bats, sloths, anteaters, armadillos, primates (to which humans belong), rodents, rabbits, whales, dolphins and porpoises, carnivores (such as cats, dogs, and bears), seals, aardvarks, elephants, hyraxes, manatees, uneven-toed mammals (such as tapirs, horses, and rhinoceroses), and even-toed (cloven-hoofed) mammals such as pigs, camels, deer, sheep, cattle, and goats.

Placenta Structure

The term "placenta" comes from the Latin meaning "flat cake," and is used to describe the flat structure (in most animals) which attaches the developing embryo and fetus to the wall of the uterus. The term was first used in 1559 C.E., although knowledge of the placenta, at least in humans, goes far back into antiquity. Reference to it may be found in many ancient texts and drawings, including the Old Testament books of the Bible. Early Egyptians considered the placenta to be the seat of the external soul.

The placenta is the organ responsible for the transmission of materials between mother and fetus prior to birth—the only bridge between them. In many species, it has important endocrine functions, producing hormones necessary for development of the fetus or for maintenance of the pregnant state. It is essentially a product of both the developing ovum and the mother. The placenta is commonly referred to as the afterbirth, extruded from the mother's uterus at the end of the birth process.

When the ovum is released by the ovary and fertilized by sperm, it eventually comes to rest in the hollow cavity of the uterine horn (one of two chambers) or the uterus (single chamber). While it moves toward that area it begins to divide, forming a ball of cells known as a morula. As development continues, the ball becomes hollow, and it is then referred to as a blastocyst. Within this hollow blastocyst a few cells protrude into the cavity, forming a knob. These are the only cells that will eventually develop into the embryo and fetus. The rest of the cells are responsible for forming the supportive structures, including the chorion, the placenta, and the umbilical cord (which attaches the embryo to the placenta).

Among the eutherian (placental) mammals, a variety of placental configurations occurs. In many species the entire chorionic sac becomes connected to the uterine wall, and transfer of materials between the maternal and fetal compartments occurs over the whole surface. In other species, a much more specialized system develops. Here parts of the chorion (a membrane equivalent to the one that lines the shell of reptile and bird eggs) become highly specialized, establishing an intimate relationship with the uterine tissues. Thus, transfer of materials occurs only in one select region of the chorion, referred to as the placenta. It is these tissues, with their flattened, cakelike appearance, from which the name derives.

The most important feature of the placenta is the close contact between the fetal blood vessels in the placenta and the maternal blood vessels in the uterine wall. While it is a common misconception that the fetal and maternal blood mix or flow together, this is not a correct picture. What actually occurs is that the two blood systems come close to each other, at which point materials that can diffuse out of one vessel may diffuse into another. Thus, transfer of materials from mother to fetus, and vice versa, can occur. The closer the two blood pools come to each other, the better it is for transfer. Nutritional, respiratory, and excretory products are transferred.

Placenta Types

In the epithelio-chorial placenta, as found in the hoofed mammals (such as Artiodactyla and Perissodactyla), whales, and lemurs, the wall of the uterus retains its surface epithelium. The minimum separation of bloods is four cells thick (two epithelial cell layers and the endothelium of the blood vessels). Thus, it is vital to have a very large surface area to allow for adequate movement of materials. While this is a large improvement over the marsupial system, it is nonetheless 250 times less efficient at salt transfer than the placenta used by humans.

The separation between mother and fetus is reduced in carnivores and sloths. Here the chorion invades the uterine epithelium and comes in direct contact with the epithelium of the maternal blood vessels, allowing a more uniform transfer of materials. The most advanced form, showing minimal separation, is the hemo-chorial placenta, found in humans, rodents, bats, and most insectivores. Here the maternal blood vessel walls are chemically broken down and the invading chorion is now in direct contact with the maternal blood stream. Because this is so much more efficient for materials exchange, the size of the interacting surfaces can be much reduced.

In addition to the exchange of materials, the placenta plays an important role in immunology, and without the placenta, the mother's body would reject the developing embryo like any other foreign body. It is this tolerance of the embryo that separates the placental mammals from the marsupials, and allows for gestation periods to be extended. Fetuses in placental mammals receive antibodies from their mothers, thus enhancing their early immunity to disease.

The epithelio-chorial placenta, being only in contact with the uterine wall and not being invasive, is readily shed by the uterus when the fetus is born. There is no damage to the maternal tissue. The more invasive types of placenta, including the hemo-chorial type, can only be lost by separation through the uterine tissues. Thus, birth in species with hemo-chorial placentas is of necessity associated with some degree of maternal bleeding. In fact, in many hemo-chorial placentas, the blastocyst actually digests (chemically) the endometrial lining of the uterus and comes to lie completely within it. The endometrium then heals over the blastocyst, which then grows, fully surrounded by endometrium. The true placenta forms on the deep pocket of the endometrium in which the blastocyst lies. When the fetus is expelled from the uterus (that is, at birth), it ruptures the now very thin layer of stretched endometrium that covers the chorion. The placenta separates from the uterus as a result of rupture of the uterine blood vessels and tissues when the uterus contracts down after expulsion of the fetus. Bleeding between uterus and placenta produces a clot which eventually seals off the broken blood vessels and forms the basis for endometrial repair.

Most mammalian placentas, regardless of type, have some type of endocrine (hormonal) function. While the specific hormones may vary from species to species, two in particular are found in most placental mammals. Chorionic gonadotropin is a hormone secreted by the placenta which acts upon the ovary to increase progesterone synthesis. Progesterone, in return, is responsible for maintenance of pregnancy during the early phases. Placental lactogen, another hormone secreted by most placentas, acts on the mother to stimulate mammary gland development. This occurs throughout gestation, so that the mammary glands are ready for suckling by the time the offspring is born.

Gestation Periods

The length of gestation varies tremendously among placental mammals. In elephants the gestation period is as long as twenty-two months. However, size alone is not the determining factor. The giant among all mammals, the blue whale, has a gestation period of only eleven months, not appreciably longer than the human (nine to ten months).

Many bats and other mammals have a delayed implantation, in which the fertilized ovum remains dormant or its development is retarded at first, thus considerably extending the gestation period and delaying birth until the optimal season of warm weather or abundant food is present. Often a placenta is not found during this period of delay, with arrest of development occurring in the blastula stage. Thus, the gestation period of the fisher, a small North American carnivore with delayed implantation, is forty-eight to fifty-one weeks, or about the same as that of the blue whale. Gestation varies from twenty-two to forty-five days in squirrels, twenty to forty days in rats and mice, two to seven months in porcupines, six months in bears, and fourteen to fifteen months in giraffes.

Gestation length is ultimately constrained by the size of skull which will fit through the maternal pelvis. Where agility, speed, or long distances of travel put a premium on the mother's athleticism, gestation length is often shortened, and the birth weight of the offspring will be low.

Animals having long gestation periods, or whose young mature slowly and are suckled for a long period of time, generally do not breed as often as others. Many species of mice breed repeatedly throughout the spring, summer, and fall, having a gestation period of about twenty days, and being mature and ready to breed by twenty-one days of age. Many others, such as bears, coyotes, and weasels, breed only once a year. Environmental conditions, and the adaptability of various species to these conditions, play a large role in breeding cycles. It is clearly advantageous for young to be born during the season of least severe weather and to be weaned when food is most abundant. Many tropical mammals breed and give birth throughout the year, whereas in temperate or cold climates young are usually born in the spring or summer.

Similar factors also influence the number of young born in each litter among different species. Their rate of growth until weaned, mortality rates, adult activity cycles, and other factors no doubt help determine the litter size as well. Many rodents have three to six young per litter; a few species of mice can have as many as eighteen. Seals, whales, and most species of bats and primates bear only a single young at one time.

—Kerry L. Cheesman

See also: Asexual reproduction; Birth; Breeding programs; Cleavage, gastrulation, and neurulation; Cloning of extinct or endangered species; Copulation; Courtship; Determination and differentiation; Development: Evolutionary perspective; Estrus; Fertilization; Gametogenesis; Hermaphrodites; Hydrostatic skeletons; Mating; Parthenogenesis; Pregnancy and prenatal development; Reproduction; Reproductive strategies; Reproductive system of female mammals; Reproductive system of male mammals; Sexual development; Vertebrates.

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PLANT AND ANIMAL INTERACTIONS

Type of animal science: Ecology
Fields of study: Physiology, zoology

Interactions between plants and animals in natural environments often revolve around either food acquisition or pollination and seed dispersal. By studying such processes, scientists have discovered strategies to increase agricultural production and to duplicate naturally produced pesticides.

Principal Terms

CELLULAR RESPIRATION: the release of energy in organisms at the cell level, primarily through the use of oxygen

CHLOROPHYLL: one of several forms of photoactive green pigments in plant cells that is necessary for photosynthesis to occur

COEVOLUTION: a mutualistic relationship between two different organisms in which, as a result of natural selection, the organisms become interdependent

CROSS-POLLINATION: the transfer of pollen grains and their enclosed sperm cells from the male portion of a flower to a female portion of another flower within the same species

FOOD CHAIN: a diagram illustrating the movement of food materials from green plants (producers) through various levels of animals (consumers) within natural environments

NATURAL SELECTION: the survival of variant types of organisms as a result of adaptability to environmental stresses

PISTIL: a female portion of a flower that produces unfertilized egg cells

STAMEN: a male portion of a flower that produces pollen grains and their enclosed sperm cells

Ecology represents the organized body of knowledge that deals with the interrelationships between living organisms and their nonliving environments. Increasingly, the realm of ecology involves a systematic analysis of plant-animal interactions through the considerations of nutrient flow in food chains and food webs, exchange of such important gases as oxygen and carbon dioxide between plants and animals, and strategies of mutual survival between plant and animal species through the processes of pollination and seed dispersal.

Ecologists study both abiotic and biotic features of such plant and animal interactions. The abiotic aspects of any environment consist of nonliving, physical variables, such as temperature and moisture, that determine where species can survive and reproduce. The biotic (living) environment includes all other plants, animals, and microorganisms with which a particular species interacts. Certainly, two examples of plant and animal interactions involve the continual processes of photosynthesis and cellular respiration. Green plants are often classified as ecological producers and have the unique ability to carry out both these important chemical reactions. Animals, for the most part, can act only as consumers, taking the products of photosynthesis and chemically releasing them at the cellular level to produce energy for all life activities.

Plant-Animal Mutualism

One topic that has captured the attention of ecologists involves the phenomenon of mutualism, in which two different species of organisms beneficially reside together in close association, usually revolving around nutritional needs. One such example demonstrating a plant and animal association is a certain species of small aquatic flatworm that absorbs microscopic green plants called algae into its tissues. The benefit to the animal is one of added food supply; the adaptation to this alga has been so complete that the flatworm does not actively feed as an adult. The algae, in turn, receive adequate supplies of nitrogen and carbon dioxide and are literally transported throughout tidal flats in marine habitats as the flatworm migrates, thus exposing the algae favorably to increased sunlight. A similar example of mutualism has been reported by ecologists studying various types of reef-building corals, which are actually marine, colonial animals that grow single-celled green algae called zooxanthellae within their bodies. The coral organisms use the nutrients produced by these algae as additional energy supplies, enabling them to build more easily the massive coral reefs associated with tropical waters. In 1987, William B. Rudman reported a similar situation while researching the formation of such coral reefs in East African coastal waters. He discovered a type of sea slug called a nudibranch that absorbs green algae into its transparent digestive tract, producing an excellent camouflage as it moves about on the coral reefs in search of prey. In turn, the algae growing within both the coral and sea slugs receive important gases from these organisms for their own life necessities.

An example of plant-animal mutualism that has been documented as a classic example of coevolution involves the yucca plant and a species of small, white moth common throughout the southwestern United States. The concept of coevolution builds upon Charles Darwin's theories of natural selection, reported in 1859, and describes situations in which two decidedly different organisms have evolved into a close ecological relationship characterized by compatible structures in both. Thus, coevolution is a mutualistic relationship between two different species that, as a result of natural selection, have become intimately interdependent. The yucca plant and yucca moth reflect such a relationship. The female moth collects pollen grains bearing sperm cells from the stamens of one flower on the plant and transports these pollen loads to the pistil of another flower, thereby ensuring cross-pollination and fertilization. During this process, the moth will lay her own fertilized eggs in the flower's undeveloped seed pods. The developing moth larvae have a secure residence for growth and a steady food supply. These larvae will rarely consume all the developing plant seeds; thus, both species (plant and animal) benefit.

Defensive Mutualism

Although these examples demonstrate the evolution of structures and secretions that reflect mutual associations between plants and animals, other interactions are not so self-supportive. Plant-eating animals, called herbivores, have always been able to consume large quantities of green plants with little fear of reprisal. Yet, some types of carnivorous plants have evolved that capture and digest small insects and crustaceans as nutritional supplements to their normal photosynthetic activities. Many of these plants grow abundantly in marshlike environments, such as bogs and swamps, where many insects congregate to reproduce. Such well-known plants as the Venus's-flytrap, sundews, butterworts, and pitcher plants have modified stems and leaves to capture and consume insects and spiders rich in protein. On a smaller scale, in freshwater ponds and lakes, a submerged green plant commonly known as the bladderwort partially satisfies its protein requirements by snaring and digesting small crustaceans, such as the water flea, within its modified leaves.

A form of ecological interaction commonly classified as mimicry can be found worldwide in diverse environments. In such situations, an animal or plant has evolved structures or behavior patterns that allow it to mimic either its surroundings or another organism as a defensive or offensive strategy. Certain types of insects, such as leafhoppers, walking sticks, praying mantids, and katydids (a type of grasshopper), often duplicate plant structures in environments ranging from the tropical rain forests to the northern coniferous forests of the United States. Such exact mimicry of their plant hosts affords these insects protection from their predators as well as camouflage that enables them to capture their own prey readily. In other examples of mimicry, some insects will absorb unpalatable plant substances in their larval stages and retain these chemicals in their adult forms, making them undesirable to birds as food sources. The monarch butterfly demonstrates this type of interaction with the milkweed plant. The viceroy butterfly has evolved colorations and markings similar to those of the monarch, thereby ensuring its own survival against bird predators. Certain species of ambush bugs and crab spiders have evolved coloration patterns that allow them to hide within flower heads of such common plants as goldenrod, enabling them to grasp more securely the bees and flies that visit these flowers.

Nonsymbiotic Mutualism

Many ecologists have been studying the phenomenon known as nonsymbiotic mutualism: different plants and animals that have coevolved morphological structures and behavior patterns by which they benefit each other without necessarily living together physically. This type of mutualism can be demonstrated in the often unusual and bizarre shapes, patterns, and colorations that more advanced flowering plants have developed to attract various insects, birds, and small mammals for pollination and seed dispersal purposes. Pollination essentially is the transfer of pollen grains (and their enclosed sperm cells) from the male portion of a flower to the egg cells within the female portion of a flower. Pollination can be accomplished by the wind, by heavy dew or rains, or by animals, and it results in the plant's sexual production of seeds that represent the next generation of new embryo plants. Accessory structures, called fruits, often form around seeds and are usually tasty and brightly marked to attract animals for seed dispersal. Although the fruits themselves become biological bribes for animals to consume, often the seeds within these fruits are not easily digested and thus pass through the animals' digestive tracts unharmed, sometimes great distances from the original plant. Other types of seed dispersal mechanisms involve the evolution of hooks, barbs, and sticky substances on seeds that enable them to be easily transported by animals' fur, feet, feathers, or beaks to new regions for possible plant colonization. Such strategies of dispersal reduce competition between the parent plant and its new seedlings for moisture, living space, and nutritional requirements.

The evolution of flowering plants and their resulting use of animals in pollination and seed dispersal probably began in dense, tropical rain forests, where pollination by the wind would be cumbersome. Because insects are the most abundant form of animal life in rain forests, strategies based upon insect transport of pollen probably originated there. Because structural specialization increases the possibility that a flower's pollen will be transferred to a plant of the same species, many plants have evolved a vast array of scents, colors, and nutritional products to attract many insects, some birds, and a few mammals. Not only does pollen include the plant's sperm cells, but it is also rich in food for these animals. Another source of animal nutrition is a substance called nectar, a sugar-rich fluid often produced in specialized structures called nectaries within the flower itself or on adjacent stems and leaves. Assorted waxes and oils are also produced by plants to ensure plant-animal interactions. As species of bees, flies, wasps, butterflies, and hawkmoths are attracted to flower heads for these nutritional rewards, they unwittingly become agents of pollination by transferring pollen from male portions of flowers (stamens) to the appropriate female portions (pistils). Some flowers have evolved distinctive, unpleasant odors reminiscent of rotting flesh or feces, thereby attracting carrion beetles and flesh flies in search of places to reproduce and deposit their own fertilized eggs. As these animals consummate their own relationships, they often become agents of pollination for the plant itself. Some tropical plants such as orchids even mimic a

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female bee, wasp, or beetle, so that its male counterpart will attempt to mate with it, thereby ensuring precise pollination.

Among the bird species, probably the hummingbirds are the best examples of plant pollinators. Various types of flowers with bright, red colors, tubular shapes, and strong, sweet odors have evolved in tropical and temperate regions to take advantage of the hummingbirds' long beaks and tongues as an aid to pollination.

Because most mammals, such as small rodents and bats, do not detect colors as well as bees and butterflies do, flowers that use them as pollinators do not rely upon color cues in their petals but instead focus upon the production of strong, fermenting or fruitlike odors and abundant pollen rich in protein to attract them. In certain environments, bats and mice that are primarily nocturnal have replaced day-flying insects and birds in these important interactions between plants and animals.

Experiments with Plant-Animal Interaction

Contemporary ecologists have gone beyond the purely descriptive observations of plant-animal interactions (initially within the realm of natural history) and have designed controlled experiments that are crucial to the development of such basic concepts as coevolution. For example, the use of radioactive isotopes and the marking of pollen with dye and fluorescent material in field settings have allowed ecologists to demonstrate precise distances and patterns of pollen dispersal. Ecologists and insect physiologists have cooperatively studied how certain insects, such as bees, are sensitive to ultraviolet light. When some flowers are viewed under ultraviolet light, distinct floral patterns become evident to guide these insects to nectar pollen sources. Through basic research, Carolyn Dickerman reported in 1986 that animal color preferences vary throughout the season. Insect pollinators, who must feed every day, will adapt to these changes by shifting their foraging behavior. Research in the field has demonstrated that some species of flowers, such as the scarlet gilia, will produce differently colored flowers to accommodate shifts in pollinator species. Early in the growing season, this plant will produce long, red, tubular-shaped flowers to attract hummingbirds. As the hummingbirds migrate, the flowers will later become lighter in hue and be pollinated primarily by nocturnal hawkmoths.

In the laboratory, ecologists and biochemists have cooperatively analyzed the chemical composition of plant secretions and products. The chemical analysis of nectar indicates great variation in composition, correlating with the type of pollinator. Flowers pollinated by beetles generally have high amino acid content. The nectar associated with hummingbird-pollinated flowers is rich in sugar. Pollen also varies widely in chemical composition within plant species. Oils and waxes are major chemical products in the pollen of plants visited primarily by bees and flies. For bat-pollinated flowers, the protein content is quite high.

Research has also successfully analyzed how certain plants have been able to develop toxins as chemical defenses against animals. These protective devices include such poisons as nicotine and rotenone that help prevent insect and small mammal attacks. A more remarkable group of protective compounds recently isolated from some plants are known as juvocimines. These chemicals actually mimic juvenile insect hormones. Insect larvae feeding on leaves containing juvocimines are prevented from undergoing their normal development into functional, breeding adults. Thus, a specific insect population that could cause extensive plant damage is locally reduced.

Ecological interactions between plants and animals are diverse and varied. These plant-animal interactions can be viewed as absolute necessities for developing food chains and food webs and for maintaining the global balances of such important gases as oxygen and carbon dioxide. The interactions can also be very precise, limited, and crucial for determining species survival or extinction. By analyzing varied plant-animal interactions, from the microscopic level to the global perspective, one can more fully appreciate all the ecological relationships that exist on the earth.

The Ecology of Interaction

The ecological importance of plant-animal interactions cannot be stressed enough. Modern-day agriculture owes its existence to the activities of such insect pollinators as honeybees in regard to the production of domestic fruits, vegetables, and honey. It is becoming increasingly evident to many ecologists and forestry scientists how important certain bird species, such as blue jays and cedar waxwings, are in natural reforestation of burned and blighted areas through their seed dispersal strategies. The plant horticulture and floral industries also are developing an appreciation of specific plant-animal interactions that produce more viable natural strains of flowers and ornamental shrubbery. The study of natural chemical defenses produced by some plants against animal invasions is most promising. The renewed interest in earlier efforts to extract such plant products as nicotine, rotenone, pyrethrum, and caffeine may produce natural compounds that can be effective insecticides without the long-term, environmental hazards associated with such human-made pesticides as malathion, chlordane, and dichlorodiphenyl-trichloroethane (DDT).

Finally, humankind is realizing that it is important to understand and protect certain plant-animal interactions associated with the tropical regions of the earth; otherwise, the global balance of oxygen and carbon dioxide could be seriously disrupted. Also, these tropical areas represent the last natural environments for the continuation of important plant species that produce secretions and products that have favorable medicinal qualities for humans and domestic livestock. By maintaining these populations and understanding how certain animals interact with them, humans can be guaranteed a viable supply of beneficial plant species whose medicinal values can be duplicated within the laboratory.

—*Thomas C. Moon*

See also: Adaptations and their mechanisms; Coevolution; Digestion; Ecological niches; Ecology; Ecosystems; Food chains and food webs; Habitats and biomes; Herbivores; Insect societies; Predation; Rhythms and behavior; Symbiosis.

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PLATYPUSES

Type of animal science: Classification
Fields of study: Conservation biology, embryology, reproduction science, wildlife ecology, zoology

The platypus is one of only three egg-laying mammals and is the only member of its family, Ornithorhynchidae. Its evolution in the relative isolation of Australia has led to such unique characteristics that the first specimen collected was believed to be a hoax.

Principal Terms

DORSAL: at or near the back

ELECTRORECEPTORS: sensors in the bill of the platypus that detect the weak electric field given off by animals; the electroreceptors help the platypus locate prey in murky water

METAZOA: organisms which are multicellular

MONOTREME: an animal that has a single, common, outer body opening for the excretory and reproductive systems; includes platypuses and echidnas

NOTOCHORD: longitudinal, flexible rod located between the gut and nerve cord

When the first platypus pelt arrived at London's Natural History Museum in the late 1790's, it was thought to be a fake made from bits of animals sewn together. This unusual mammal has a leathery bill, webbed feet, and fur, and it is one of only three mammals that lay eggs. Its body length is about eighteen inches, and its broad, flat tail is about seven inches long. The reclusive platypus spends most of its time in streams, rivers, and some lakes, foraging for food in the evening and sleeping during the day in burrows dug into the river banks.

Platypus Life

The unusual anatomical features of the platypus provide perfect adaptations for its life in water. The webbed feet are efficient paddles for swimming through the water. Claws on the feet help the platypus to dig burrows. Dense, waterproof fur covers the entire body except the feet and bill. The eyes and ear holes of the animal lie in folds that close when the animal is submerged, and the nostrils are located toward the end of the beak and also close under water. The bill is highly sensitive to touch, and is equipped with electrosensors that detect weak electrical fields produced by prey. Thus, the platypus can locate and capture prey in murky river bottoms without relying on vision, hearing, or smell.

Bottom-dwelling invertebrates, especially crustaceans, aquatic insects, and insect larvae, compose the majority of the platypus diet. Behind the bill are located two internal cheek pouches containing horny ridges that substitute for teeth, which are lost early in the life of the platypus. The pouches are used to store food while it is being chewed and sorted by the animal.

A male platypus has a spur on each rear ankle that is connected to a venom gland in the thigh. The spur is used against attackers, but also against competing males during the mating season. The venom is not fatal to humans, but can cause a great deal of pain. This feature makes the platypus one of very few mammals that are venomous.

From Egg to Adult

Courtship and mating occur in the water. After initial approaches by the female, the male chases and grasps her by the tail and inseminates her. After mating, a female will lay two to three eggs

Platypus Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebra
Class: Mammalia
Subclass: Prototheria
Order: Monotremata
Family: Ornithorhynchidae
Genus and species: Ornithorhynchus anatinus
Geographical location: Eastern Australia, Tasmania, Kangaroo Island in southern Australia
Habitat: Streams, rivers, and some lakes; must have permanent water and banks suitable for burrows
Gestational period: Seven to fourteen days
Life span: Ten or more years in the wild; seventeen years and longer in captivity
Special anatomy: Rubbery beak equipped with electrosensors used to detect prey; webbed feet; females have slits in abdominal walls from which milk expresses during lactation; males have spurs on rear feet used primarily to inject venom into rivals during mating season; reproductive and excretory tracts have one common opening to the exterior of the body

and incubate them in a special nesting burrow, which may extend one hundred feet away from the water. The female blocks the entry to the nesting burrow with soil plugs to protect the eggs and young from predators and flooding. She removes and replaces the plug each time she leaves to forage for food. When the eggs hatch, in seven to fourteen days, the young are about one inch long and totally dependent on the mother. Platypuses do not have nipples, but milk is produced in the mammary glands and expressed through openings in the abdominal wall. The young suck the milk directly from the fur. At about five months of age, the young emerge from the nesting burrow and begin learning to search for prey themselves. A typical platypus in the wild will live about ten years.

—*Karen E. Kalumuck*

See also: Beaks and bills; Fauna: Australia; Lactation; Monotremes; Poisonous animals.

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POISONOUS ANIMALS

Types of animal science: Classification, ecology, geography, physiology
Fields of study: Anatomy, biochemistry, ecology, invertebrate biology, zoology

Poisons disrupt life processes or kill. Animal poisons are venoms, delivered by biting, stinging, or body contact. Poisonous species occur throughout the animal kingdom, and include snakes, insects, spiders, other arachnids, mammals, lizards, and fish.

Principal Terms

ANAPHYLAXIS: hypersensitivity to a foreign substance, such as a venom, that causes discomfort and can even kill

ARACHNID: an arthropod having eight legs; a spider

ARTHROPOD: an organism with a horny, segmented external covering and jointed limbs

HEMOTOXIN: a substance that causes blood vessel damage and hemorrhage

NEUROTOXIN: a substance that damages the nervous system, most often nerves that control breathing and heart action

VENOM: a poison made by an animal

Substances that cause disease symptoms, injure tissues, or disrupt life processes on entering the body are poisons. When ingested in large quantities, most poisons kill. Poisons may be contacted from minerals, in vegetable foods, or in animal attack. Any poison of animal origin is a venom. Venoms are delivered by biting, stinging, or other body contacts. These animal poisons are used to capture prey or in self-defense. Often, it seems that ability to make venom arose in animals that were too small, too slow, or too weak to otherwise maintain an ecological niche. The mechanism for development of the ability to make venom is not clear.

The most familiar poisonous animals are snakes, insects, spiders, and some other arachnids. Poisonous species, however, occur throughout the animal kingdom, including a few mammals and lizards, and some fish. The severity of venom effects depends on its chemical nature, the nature of the contact mechanisms, the amount of venom delivered, and victim size. For example, all spiders are poisonous. However, their venom is usually dispensed in small amounts that do not affect humans. Hence, few spiders kill humans, though they kill prey and use venom in self-defense very effectively.

Chemically, venoms vary greatly. Snake venoms are mixtures of enzymes and toxins. Study of their effects led to the identification of hemotoxins, which cause blood vessel damage and hemorrhage; neurotoxins, which paralyze nerves controlling heart action and respiration; and clotting agents, which excessively promote or prevent blood clotting. Cobras, coral snakes, and arachnids all have neurotoxic venoms.

Poisonous Lizards, Arachnids, and Insects

The poisonous lizards are useful to explore first, because only two species are known: Gila monsters and beaded lizards (both holoderms). They inhabit the southwestern deserts of the United States and Mexico. They do not strike like snakes; rather, they bite, hold on, and chew to poison. Holoderm bites kill prey, but rarely kill humans. Beaded lizards grow to three feet long and Gila monsters grow to two feet long.

Most poisonous arthropods are spiders and scorpions. Both use venom to subdue and/or kill prey. As stated earlier, few spiders endanger humans because their venom is weak and is not injected in large quantities, but some species have very potent venom and harm or even kill humans. Best known of these are black widow spiders. Though rarely lethal to humans, black widow bites cause cramps and paralysis.

There are approximately six hundred scorpion species, of sizes between one and ten inches. All have tail-end stingers. Large, tropical scorpions can kill humans, while American scorpions are smaller and less dangerous. Scorpions are more dangerous than spiders because they crawl into shoes and other places where their habitat overlaps that of humans.

Many insects, such as caterpillars, bees, wasps, hornets, and ants, use venom in self-defense or to paralyze prey to feed themselves or offspring. Caterpillars use poison spines for protection. Bees, wasps, hornets, and ants use stingers for the same purpose. The venom of insects also kills many organisms that seek to prey on them. Humans, however, are rarely killed by insect bites. Such bites are usually mildly to severely painful for a period from a few minutes to several days. However, severe anaphylaxis occurs in some cases, followed by death.

Bee Stings

Most American honeybees came from Europe. They were brought to North America by early colonists to make honey for human consumption. Due to hive escapees, honeybees are now found wild throughout the country. Familiar worker honeybees are often seen collecting nectar and pollen from flowers.

When alarmed, worker bees sting. This is unfortunate for them, as their barbed stingers stay in the skin of victims, and in pulling away after stinging, essential bee body tissue is ripped away. This causes the bee to die quickly. Workers also defend hives in this way, committing suicide to protect the hive. Bee stings often disable or kill predators who seek to eat the bees or their honey.

Honeybees are so widespread that most people are stung at least once during their lives. Some individuals are severely allergic to bee stings, and occasionally the severe anaphylactic shock kills. Sensitive individuals should carry sting kits. A kit includes epinephrine and antihistamine, a tourniquet, and alcohol swabs. A stinger works its way deep into the skin and can cause infection. Thus, it should scraped off after a sting.

Poisonous Snakes

Poisonous snakes are colubrids, elapids, or vipers, depending on their anatomic characteristics. All have paired, hollow fangs in the front upper jaw. The fangs fold back against the upper palate when not used, and when a snake strikes they swing forward to inject a venom that attacks the victim's blood and tissues. The heads of poisonous snakes are scale-covered and triangular. Such snakes are found worldwide and among them are pit vipers, named for the pits on each side of the head that contain heat receptors. The pits detect warm-blooded prey, mostly rodents, in the dark. Pit vipers include rattlesnakes, moccasins, copperheads, fer-de-lance, and bushmasters.

The population and species of American and European poisonous snakes differ. In North America, twenty such snake types occur: elapid coral snakes and copperheads, sixteen rattler types, and cottonmouths (all vipers). Vipers are found everywhere but Alaska. Rattlers have the widest habitat, as shown by their abundance in the snake-rich Great Plains, Mississippi Valley, and southern Appalachia. In contrast, copperheads and cottonmouths are abundant in Appalachia and the Mississippi valley, respectively. Mexican poisonous snakes are divided into two ranges, the northern from the U.S.-Mexican border to Mexico City, and the southern, south of Mexico City. In the north, snakes are mostly rattlers, as in the contiguous United States. Coral snakes and pit vipers are plentiful in the south. Most perilous are the five- to eight-foot fer-de-lance, whose venom kills many humans. In South America, all vipers but rattlers are tropical. Bushmasters, the largest South American vipers, and elapid coral snakes are nocturnal and rarely endanger humans. Tropical rattlers and lance-headed vipers, somewhat less nocturnal, kill many. Europe has few snakes, due to its cool climates and scarce suitable habitats. Its few vipers range almost to the Arctic Circle. Eastern Mediterranean regions hold most of the European vipers.

There are many poisonous snakes in Africa and Asia. North Africa, mostly desert, has few snakes. Central Africa's diverse poisonous snakes are colubrid, elapid, and viper types. Elapids include dangerous black mambas, twelve to fourteen feet long, and smaller cobras, which also occur in South Africa. Among diverse vipers, the most perilous are Gaboon vipers and puff adders. The Middle East, mostly desert, has few poisonous snakes. Southeast Asia has the most poisonous snakes in the world—elapids, colubrids, and vipers. This is due to snake habitats that range from semiarid areas to rain forests. The huge human population explains why this area has the world's highest incidence of snakebite and related death, due to vipers, cobras, elapids, and sea snakes. Vipers bite most often, but elapids cause a larger portion of deaths. The Far East snake population is complex and its snakebite incidence is also high. Its important poisonous snakes are pit vipers.

Australia and New Guinea have large numbers of poisonous snakes. Australia has 65 percent of the world's snakes, while New Guinea has 25 percent. Also, sea snakes occur offshore and in some rivers and lakes. However, these countries have few snakebite deaths, due to the small size and nocturnal nature of most of indigenous snakes.

Sea Snakes

The name sea snake identifies members of about fifty species of poisonous water snakes, living in tropical oceans from the Persian Gulf to the southwest Pacific. They are very abundant in the Indian Ocean and Australian coastal waters. Sea snakes are five to nine feet long, depending on species. They have strong, flat, paddlelike tails used in swimming. Most species have nostrils atop the head. Sea snakes have lungs, not gills, and must surface for air. However, they remain underwater for several hours and can dive down twenty to thirty feet.

Most species live in warm, shallow waters, especially river mouths, bays, and swamps. Most rarely leave the water, so they lack the enlarged abdominal scales that terrestrial snakes use to move along the ground. A few types have abdominal scales like terrestrial snakes because they spend part of the time crawling in marshes. The eggs of sea snakes hatch internally and young are born alive. Sea snakes eat fish, especially eels, prawns, and fish eggs. They paralyze prey with their venom. They usually bite humans only if stepped on in shallow water or when removed from nets.

Poisonous Fish and Amphibians

Venomous fish are dangerous to those who enter the oceans, especially fisherman who take them from their nets. The geographical distribution of these fish is like that of all other fish. The highest population density is in warm temperate or tropical waters. Numbers and varieties of poisonous fish decrease with proximity to the North and South Poles and they are most abundant in Indo-Pacific and West Indian waters.

A well-known group of poisonous fishes is the stingrays (dasyatids). They inhabit warm, shallow, sandy-to-muddy ocean waters. Dasyatids lurk almost completely buried, awaiting prey that they sting to death with barbed, venomous teeth in their tails. The tail poison is made in glands at the bases of the teeth. Small, freshwater dasyatids are found in South American rivers, such as the Amazon, hundreds of miles from the river mouths. Stingrays near Australia grow to fifteen-foot lengths. Emphasizing wide distribution of stingrays and their danger to humans is their mention in Aristotle's third century B.C.E. writings, and the death of John Smith in 1608, killed by a stingray while exploring Chesapeake Bay.

Also well known are the venomous Scorpaenidae fish family, many members of which cause very painful stings. Zebra fish and stonefish are good examples. Both, like all scorpaenids, have sharp spines supporting dorsal fins. The spines, used in self-defense, have venom glands. The most deadly fish venom is that of the stonefish, which, when stepped on, can kill humans.

Poisonous animals which endanger by contact are exemplified by zebra fish and stonefish, just mentioned, and by poisonous frogs or toads. Most such frogs and toads, such as poison dart frogs, live in Africa and South America. They secrete poisons through the skin. Contact with the poisons causes effects which range from severe irritation to death in humans. The poisons frighten away or kill most predators that attempt eat them. The ecological function of poisonous animals is seen as helping to keep down the population of insects, rodents, arachnids, and small fishes. They thus contribute to maintaining the balance of nature. Poisonous land animals, such as scorpions and many poisonous snakes, are often nocturnal and add another dimension to pest control by nighttime predation.

—*Sanford S. Singer*

See also: Ants; Arthropods; Bees; Defense mechanisms; Fish; Frogs and toads; Insects; Jellyfish; Lizards; Predation; Scorpions; Snakes; Spiders; Wasps and hornets.

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POLAR BEARS

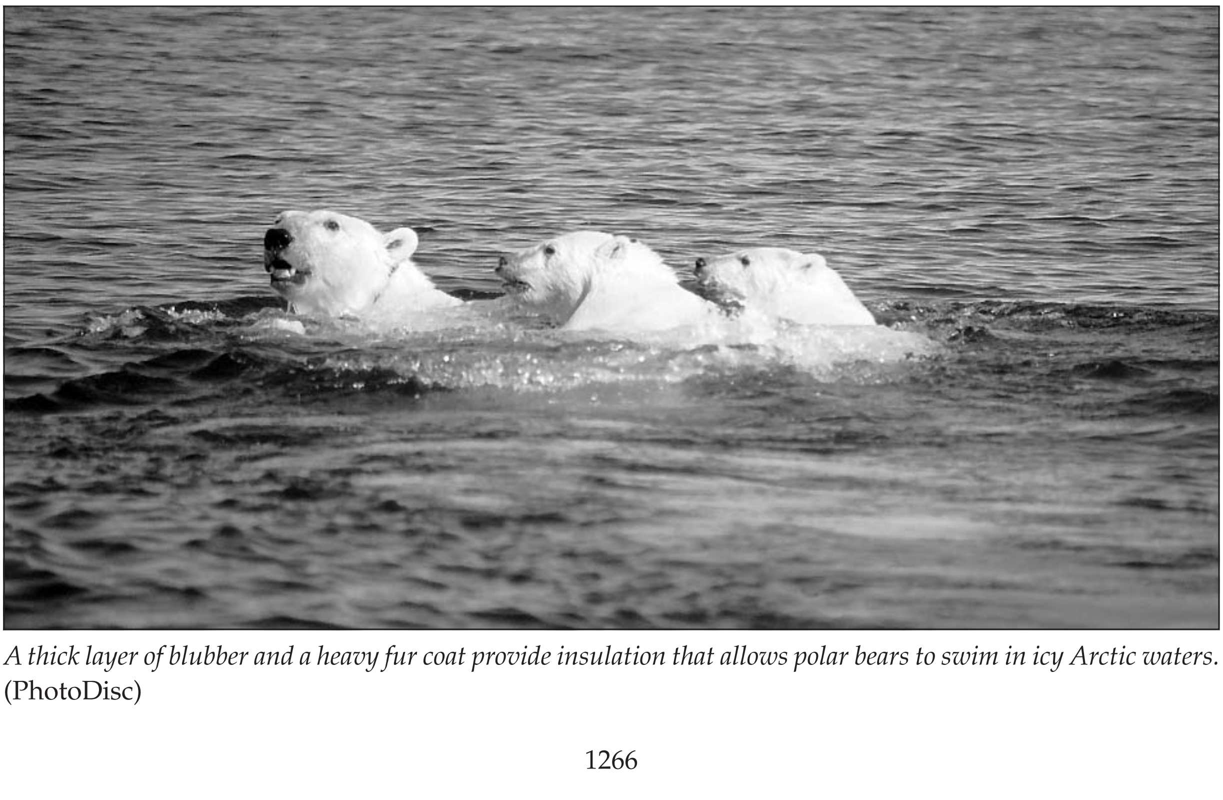
Type of animal science: Classification
Fields of study: Anatomy, conservation biology, evolutionary science, wildlife ecology, zoology

The polar bear lives in one of the harshest environments on earth: the Arctic. Yet it succeeds through a combination of hunting skill and the ability to store and conserve energy in the form of fat.

Principal Terms

BLUBBER: thick layer of fat under the skin
CARNIVOROUS: eating meat
GEOGRAPHICALLY ISOLATED: living in different habitats
PLANTIGRADE: walking on the entire foot, not just the toes
TERRESTRIAL: living on land

Protected from cold by a thick fur coat and a layer of blubber, the polar bear hunts seals in open areas in the Arctic sea ice. A strong swimmer, the polar bear uses its large front paws as paddles. Its white fur blends in with the ice and snow as it stalks or still-hunts seals. Ringed seals are the polar bear's primary food, but it also consumes bearded seals, and occasionally walruses, belugas, narwhals, musk oxen, and carrion (dead terrestrial and marine mammals). Although largely carnivorous, when on land the polar bear may eat grasses, kelp, berries, and lichens. Males and nonpregnant females do not make dens or hibernate, but spend the winter hunting on the sea ice.



A thick layer of blubber and a heavy fur coat provide insulation that allows polar bears to swim in icy Arctic waters. (PhotoDisc)

The polar bear evolved from the terrestrial brown bear about 100,000 to 200,000 years ago. In captivity, polar bears and brown bears have interbred and produced fertile offspring. This shows a high degree of genetic relatedness. In nature, however, these two species are geographically isolated from one another and would rarely meet.

Swimming in icy water among the ice floes of the Arctic, quietly stalking a resting seal, then killing it with a crushing blow of its forepaw, the polar bear is an impressive example of an animal's ability to adapt to and live in one of the harshest environments on earth.

Physical Characteristics of Polar Bears

Male polar bears are up to five feet high at the shoulder while on all fours and up to ten feet long. When standing on its hind legs, a male can be eleven feet tall. Adult males are generally much bigger than females: 1,100 to 1,770 pounds for males, 330 to 770 pounds for females. Like other bears, polar bears are plantigrade.

Mating takes place in late March to late May. This is the only time that the male is with the female. Other than family groups of females with their cubs, polar bears are solitary. Pregnant females dig snow or earth dens in which they will give birth to one to three cubs in late November to early January. The mother's milk is very rich, with an average fat content of 33 percent. The cubs, which weigh 1 to 1.5 pounds at birth, grow quickly and weigh 22 to 33 pounds when they emerge from the den with their mother in late February to early May. Polar bear cubs usually leave their mother at 2.5 years of age, at which time the mother is ready to breed again. Therefore, the female usually gives birth every third year.

Conservation

By the 1960's, polar bear populations were in serious decline due to sport hunting. In 1967, the five "polar bear nations" (the United States, Canada, Denmark, Norway, and the Soviet Union) limited hunting to the Inuit (Eskimo) people. By 2001, polar bears had recovered, and there were twenty thousand to forty thousand in the world.

A 1999 study by longtime polar bear biologist Ian Stirling and his colleagues shows that polar bears at Hudson Bay are 10 percent thinner and have 10 percent fewer cubs than they did twenty years ago. In 1999, the ice on Hudson Bay melted three weeks earlier than it did twenty-five years earlier. Polar bears must wait for ice to form each

Polar Bear Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Subclass: Eutheria
Order: Carnivora
Suborder: Fissipedia
Family: Ursidae
Subfamily: Ursinae
Genus and species: Ursus maritimus

Geographical location: Northern marine areas of Alaska, Canada, Greenland, Norway's Svalbard Archipelago, and Russia

Habitat: The sea ice and adjacent land areas of the circumpolar Arctic

Gestational period: About eight months

Life span: Up to thirty-two years in the wild, over forty years in captivity

Special anatomy: Fur, hide, and blubber providing effective insulation from the extreme arctic cold; white fur providing camouflage against the backdrop of ice and snow and greatly aiding in stalking seals; large paws used for paddling in water and which act like snowshoes on thin ice; pads of the feet covered with small, soft papillae that improve traction on ice; small ears and tail to reduce heat loss and a large body mass to conserve heat fall to hunt ringed seals, their main food source. Hudson Bay polar bears fast six to eight months each year and then hunt seals intensively during the ice season. The three-week reduction of hunting time has not yet resulted in significant decline of the polar bear population, but is expected to do so if the climate trend continues.

—Thomas Coffield

See also: Bears; Carnivores; Fauna: Arctic; Grizzly bears; Pandas.

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POLLUTION EFFECTS

Types of animal science: Ecology, geography, physiology, scientific methods
Fields of study: Conservation biology, ecology, environmental science, pathology, physiology

Pollutants in soil, water, and atmosphere have created enormous problems for the living world. Destroyed habitats and polluted food sources and drinking water for animals have caused deformations in animal growth, development, and reproduction, as well as a shortening of life span, all of which contribute to an accelerated decrease in biodiversity and the extinction of more species. Realization of the severity of pollution is the first step toward seeking a long-term remedy.

Principal Terms

ACID RAIN: the burning of primarily fossil fuels leads to an excessive release of nitrogen oxides or sulfur dioxide, which in turn combines with water to form nitric or sulfuric acid; when acids dissolve into rainfall, it is called acid rain

CHEMICAL POLLUTANTS: harmful chemicals manufactured and released to the environment; normally referring to those that contaminate ecosystems

CHLOROFLUOROCARBONS (CFCs): a group of very stable compounds used widely since their development in 1928 for refrigeration, coolants, aerosol spray propellants, and other purposes; once risen into the stratosphere, they cause ozone depletion

GREENHOUSE EFFECT: the process by which certain gases, such as carbon dioxide and methane, trap sunlight energy in the atmosphere as heat, resulting in global warming as more gases are released to the atmosphere by human activities

OZONE LAYER: the ozone-enriched layer of the upper atmosphere that filters out some of the sun's ultraviolet radiation, which causes skin and other types of cancer

During the last decade of the twentieth century, the environmental problems predicted by environmental scientists decades previously began to be aggravated in a variety of ways. These included population explosion, food imbalances, inflation brought about by energy resource scarcity, acid rain, toxic and hazardous wastes, water shortages, major soil erosion, a punctuated ozone layer, and greenhouse effects. The list goes on. As a result of pollution, decreases in biodiversity and the extinction of both plant and animal species have accelerated. The burning and cutting of thousands of square miles of rain forest not only destroyed habitats for numerous animal species, but also caused irreversible damage to ecosystems and climate. The recurring drought and famine in Africa are testimony to human mischief toward Mother Nature. The well-being of animals as well as humans will not be protected against the ecological consequences of human actions by remaining ignorant of those actions. Effective measures taken to reduce pollution and protect natural resources and the environment first come with a recognition of these problems. The ignorance and inaction of ordinary citizens will lead to disastrous consequences for the environment, threatening humanity's very existence.

Source and Types of Pollution

Industrialization and the expansion of the human population have left relatively few places on earth undisturbed. In simple terms, human interference in natural ecosystems is the single most important source of pollution. First, heavy dependence upon fossil fuels for energy, and on synthetic chemicals and materials helped to dump millions of metric tons of nonnatural compounds and chemicals into the environment. Among them are agrichemicals such as fertilizers, insecticides, fungicides, and herbicides, and home products. Application of excess chemical fertilizers to soil hampers natural cycling of nutrients, depletes the soil's own fertility, and destroys the habitat for thousands of small animals residing in the soil. Farm runoff carries priceless topsoil, expensive fertilizer, and animal manure into rivers and lakes, where these potential resources become pollutants. In the city, water pours from sidewalks, rooftops, and streets, picking up soot, silt, oil, heavy metals, and garbage. It races down gutters into storm sewers, and a weakly toxic soup gushes into the nearest stream or river. Many of these chemicals also seep through into the ground, contaminating groundwater.

Plants and factories manufacturing these chemical products are another source of pollutants and contamination. Burning fossil fuels releases greenhouse gases, carbon oxides, and methane. Coupled with deforestation in many regions of the world, carbon dioxide concentration in the atmosphere has steadily climbed, from 290 parts per million in 1860 to 370 parts per million in 1990, more than a 25 percent rise due to industrialization. The resultant global warming will have far-reaching effects on plants, animals, and humans in ways still not understood. Acid rain, a result of overcharging the atmosphere with nitric oxides and sulfur dioxide (two gases also released by burning of fossil fuels), has increased the acidity of soil and lakes to levels many organisms cannot survive. The most acidic rain is concentrated in the northeastern United States. In New York's Adirondack Mountains, for instance, acid rain has made about a third of all the lakes and ponds too acidic to support fish. First, much of the food web that sustains the fish is destroyed. Clams, snails, crayfish, and insect larvae die first, then amphibians, and finally fish. The detrimental effect is not limited to aquatic animals. The loss of insects and their larvae and small aquatic animals has contributed to a dramatic decline in the population

The Freshwater Crisis

Toxic chemicals are contaminating groundwater on every inhabited continent, endangering the world's most valuable supplies of fresh water, reports a study published in 2000 from the Worldwatch Institute, a Washington, D.C.-based research organization on the environment. This worldwide survey of groundwater quality shows that pesticides, nitrogen fertilizers, industrial chemicals, and heavy metals are contaminating groundwater everywhere, and that the damage is often worst in places where people most need water.

There are at least three essential roles of groundwater: providing drinking water, irrigating farmland, and replenishing rivers, streams, and wetlands. About one third of the world population relies almost exclusively on groundwater for drinking. Groundwater provides irrigation for some of the world's most productive farmland. Over 50 percent of irrigated croplands in India, and 40 percent in the United States, is watered by groundwater. Groundwater plays a crucial role in replenishing rivers, streams, and wetlands. It provides much of the flow for great rivers such as the Mississippi, the Niger, the Yangtze, and many more.

The range of groundwater contamination is stunning. Groundwater in all twenty-two major industrial zones surveyed by the Indian government in the late 1990's was unfit for drinking. In a 1995 study of four northern Chinese provinces, groundwater was contaminated in more than 50 percent of surveyed locations. One third of the wells tested in a California region in 1988 contained the pesticide 1,2-dibromo-3-chloropropane (DBCP) at levels ten times higher than the maximum allowed for drinking. The list goes on. There is a compelling urgency to prevent groundwater contamination.

Pollutants in water, from pesticides to acid rain, cause disruption and death all the way up the food chain. (PhotoDisc)

of black ducks that feed on them. The result is a crystal-clear lake, beautiful but dead.

Another serious problem created by the chemical industry is ozone depletion. CFC compounds contain chlorine, fluorine, and carbon. Since their development in the 1930's, these compounds have been widely used as coolants in refrigerators and air conditioners, as aerosol spray propellants, as agents for producing Styrofoam, and as cleansers for electronic parts. These chemicals are very stable and for decades were considered to be safe. Their stability, however, turned out to be a real problem. In gaseous form they rise into the atmosphere. There, the high energy level of ultraviolet (UV) light breaks them down, releasing chlorine atoms, which in turn catalyzes the breakdown of ozone to oxygen gas. As a result of the decline of ozone and the punctuation of the ozone layer, UV radiation has risen by an average of 8 percent per decade since the 1970's. This depletion of the ozone layer poses a threat to humans, animals, plants, and even microorganisms.

Pollution Effects of Chemicals

The degradation of air, land, and water as a result of the release of chemical and biological wastes has wide-ranging effects on animals. On a large scale, pollution destroys habitats and produces population crashes and even the extinction of species. Hazardous chemicals introduced into an environment sometime render it unfit for life (as at Love Canal, New York, or Times Beach, Missouri). At the individual level, pollution causes abnormalities in growth, development, and reproduction. Hazardous chemicals, introduced either intentionally (such as fertilizers, herbicides, and pesticides) or through neglect (as with industrial wastes), have a variety of detrimental, sometimes devastating effects on animals. They affect the metabolism, growth and development, reproduction, and average life span of many species.

A few examples will illustrate the effects of chemical pollution on animals. In the 1940's, the new insecticide dichloro-diphenyl-trichloroethane (DDT) was regarded as a miracle. It saved millions of lives in the tropics by killing the mosquitoes that spread deadly malaria. DDT saved millions more lives with increased crop yields resulting from DDT's destruction of insect pests. This miraculous pesticide, however, turned out to be a long-lasting nemesis to many species of wildlife and to the environment. In the United States, ecologists and wildlife biologists during the 1950's and 1960's witnessed a stunning decline in the populations of several predatory birds, especially fish-eaters, such as bald eagles, cormorants, ospreys, and brown pelicans. The population decline drove the brown pelican and bald eagle close to extinction. In 1973, the U.S. Congress passed the Endangered Species Act, which banned the use of DDT. The once-threatened species have somewhat recovered since. In the mid 1950's, the World Health Organization used DDT on the island of Borneo to control malaria. DDT entered food webs through a caterpillar. Wasps that fed on the caterpillar were first destroyed. Gecko lizards that ate the poisoned insects accumulated high levels of DDT in their bodies. Both geckos and the village cats that ate the geckos died of DDT poisoning. The rat population exploded with its natural enemy, cats, eliminated. The village was then threatened with an outbreak of plague, carried by the uncontrolled rats.

Although DDT has been banned in much of the world, there is a growing concern over the effects of a number of chlorinated compounds. These chemicals, described as "environmental estrogens," interfere with normal sex hormone functions by mimicking the effects of the hormone estrogen or enhancing estrogen's potency. High levels of chlorinated compounds, such as dioxin and polychlorinated biphenyls (PCBs), in the Great Lakes have led to a sharp decline in populations of river otters and a variety of fish-eating birds, including the newly returned bald eagles. These chemicals are also the cause of deformed offspring, or eggs that never hatch. In Florida's Lake Apopka, a spill of chlorinated chemicals in 1980 led to a 90 percent drop in the birth rate of the lake's alligators. These are only a few examples of the detrimental effects of synthetic chemicals on various animals.

Effects of Air Pollution

Air pollution leads to acid rain and the greenhouse effect, as well as damage to the ozone layer. Acid rain drops out of the skies onto areas at great distances from the source of the acids, and destroys forests and lakes in sensitive regions. As a result, fish populations are dwindling or being eliminated from lakes and streams by a lower pH caused by acid deposition. The strongest evidence comes from data collected from the past twenty-

Endangered Amphibians

Frogs and toads have been amazingly resilient throughout their evolution and hence have a wide distribution in ponds and swamps all over the planet. Their evolutionary longevity, however, appears to offer inadequate defense against the pollution to the environment brought about by human activities. During the 1990's, biologists around the world have documented an alarming decline in amphibian populations. Thousands of species of frogs, toads, and salamanders are experiencing dramatic decreases in numbers, and many have gone extinct or become endangered.

The specific causes of the worldwide decline in amphibians are not fully understood. All the likely factors, however, point at human modification of the biosphere, the portion of the earth that sustains life. The draining of wetland habitats, one type of habitat destruction, is a major cause of the decline. Amphibian bodies at all developmental stages are protected only by thin, permeable skins through which pollutants can easily penetrate. The double life on land and in water exposes their permeable skin to a wide range of aquatic and terrestrial habitats and hence a correspondingly wide range of environmental toxins.

Many amphibians' eggs and larvae develop in ponds and streams during spring, a time when acid rain causes an acidity increase in freshwater ecosystems. Increased ultraviolet (UV) light damages eggs and causes deformity among offspring. In addition, many amphibians are herbivores as larvae and insectivores as adults. Thus, they are vulnerable to both herbicides and insecticides in their food. Dramatic decline of amphibian populations provides an early warning of environmental degradation. It also depletes the food source for large carnivores that feed on them and may risk keeping insect populations in check.

five to forty-five years in Adirondack lakes and in Nova Scotia rivers. Studies during this period clearly show declines in acid-sensitive species. Similar results were obtained from analyzing fish population and water acidity in Maine, Massachusetts, Pennsylvania, and Vermont. The consensus is that fish populations would be eliminated if the surface waters were to acidify to between pH 5.0 and pH 5.5. The effects of acid rain on other animals are indirect, either through the dwindling fish population (as a food source for other animals) or stunted forest growth (disturbance to habitats).

The effect of global warming on the animal kingdom is also a serious and complex issue. As global temperature rises, ice caps in polar regions and glaciers melt, ocean waters expand in response to atmospheric warming, and thus the sea level elevates. The expected sea level rise will flood coastal cities and coastal wetlands. These threatened ecosystems are habitats and breeding grounds for numerous species of birds, fish, shrimp, and crabs, whose populations could be severely diminished. The Florida Everglades will virtually disappear if the sea level rises two feet. The impact of global warming on forests could be profound. The distribution of tree species is exquisitely sensitive to average annual temperature, and small changes could dramatically alter the extent and species composition of forests. This in turn could dramatically alter the population distribution of animals. A rise may make temperatures unsuitable for some species, hence reducing biodiversity.

The effect of the punctuated ozone layer on animals is yet to be fully understood. It is known that the high energy level of UV radiation can damage biological molecules, including the genetic material deoxyribonucleic acid (DNA), causing mutation. In small quantities, UV light helps the skin of humans and many animals produce vitamin D, and causes tanning. However, in large doses, UV light causes sunburn and premature aging of skin, skin cancer, and cataracts, a condition in which the lens of the eye becomes cloudy. Due to UV radiation's ability to penetrate, even animals covered by hair and thick fur cannot escape from these detrimental effects. Ozone damage costs U.S. farmers over $2 billion annually in reduced crop yields. All who depend on forestry and agriculture may bear a much higher cost if the emission of pollutants that destroy ozone is not regulated soon.

Possible Remedies

The various types of pollution all have serious effects on the plant and animal species that share this planet. It is all too easy to document the impacts of pollution on human health and ignore its effects on the rest of the living world. Any possible remedies to alleviate these problems should start with education, the realization of these problems at an individual as well as a global level. The tasks seem to be insurmountable, and no organization, no country can do it alone. It takes willingness to accept short-term inconvenience or economic sacrifice for the benefit of the long run. A couple of examples serve to illustrate what can be done to alleviate the problems of pollution.

Synthetic chemical pollutants that are poisoning both people and wildlife could be largely eliminated without disrupting the economy, as reported in a study published in 2000 by the Worldwatch Institute, a Washington, D.C.-based environmental organization. The report presents strong evidence from three sectors that are major sources of these pollutants—paper manufacturing, pesticides, and PVC plastics—to show that nontoxic options are available at competitive prices. Agricultural pollution can be mitigated, significantly reduced, or virtually eliminated through the use of proper regulation and economic incentives. Farmers from Indonesia to Kenya are learning how to use less of various chemicals while boosting yields. Since 1998, all farmers in China's Yunnan Province have eliminated their use of fungicides while doubling rice yields, by planting more diverse varieties of the grain. In most, if not all, cases, the question is not whether it is possible to alleviate pollution of the environment; rather, it is whether we realize the urgency and/or are willing to take a high road to do it. For the common well-being of generations to come, better approaches have to be taken to preserve the environment and biodiversity.

—*Ming Y. Zheng*

See also: Chaparral; Death and dying; Diseases; Ecology; Ecosystems; Endangered species; Extinction; Food chains and food webs; Forests, coniferous; Forests, deciduous; Grasslands and prairies; Habitats and biomes; Lakes and rivers; Marine biology; Mountains; Mutations; Rain forests; Savannas; Tidepools and beaches; Tundra; Urban and suburban wildlife; Wildlife management; Zoology.

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POPULATION ANALYSIS

Type of animal science: Ecology
Fields of study: Ecology, wildlife ecology, zoology

Many animal populations are becoming threatened or endangered, primarily due to loss of suitable habitat. Population analysis enables biologists to examine the factors which lead to declines in animal populations and thus is important in the management of wild species.

Principal Terms

CONTINUOUS GROWTH: growth in a population in which reproduction takes place at any time during the year rather than during specific time intervals

DENSITY-DEPENDENT GROWTH: growth in a population in which the per capita rates of birth and death are scaled by the total number of individuals in the population

DISCRETE GROWTH: growth in a population that undergoes reproduction at specific time intervals

POPULATION ANALYSIS: the study of factors that influence growth of biological populations

A population is a group of organisms belonging to the same species that occur together in the same time and place. For example, a wildlife biologist might be interested in studying the population of porcupines that inhabits a hemlock forest or the population of bark beetles that lives on a particular tree. Populations can change over time. They increase or decrease in size, and their change in size can depend on a wide variety of factors. Population analysis is the study of biological populations, with the specific intent of understanding which factors are most important in determining population size.

In order to conduct a population analysis, one must first determine whether the population of interest is best understood as discrete or continuous. A discrete population is one in which important events such as birth and death happen during specific intervals of time. A continuous population is one in which births, deaths, and other events take place continuously through time. Many discrete populations are those with nonoverlapping generations. For example, in many insect populations, the adults mate and lay eggs, after which the adults die. When the juveniles achieve adulthood, their parental generation is no longer living. In contrast, most continuous populations have overlapping generations. For instance, in antelope jackrabbits (*Lepus alleni*), females may give birth at any time during the year, and members of several generations occur together in space and time.

Modeling Animal Populations

The dynamics of animal populations is affected by a wide variety of demographic factors, including the population birth rate, death rate, sex ratio, age structure, and rates of immigration and emigration. In order to understand the effects of these factors on a population, biologists use population models. A model is an abstract representation of a concrete idea. The representation created by the model boils the concrete idea into a few critical components. By building and examining population models, population analysts investigate the relative importance of different factors on the dynamics of a given population.

A basic mathematical model of population size is as follows: $N_{t+1} = N_t + B - D + I - E$ (equation 1), where N_{t+1} equals the population size after one time interval, N_t equals the total number of individuals in the population at the initial time, B equals the number of births, D equals the number of deaths, I equals the number of immigrants into the population, and E equals the number of emigrants leaving the population. This simple model boils population size down to just four factors, B, D, I, and E. This model is not meant to be a true or precise representation of the population; rather, it is meant to clarify the importance of the factors of birth, death, immigration, and emigration on population size. To use the same model to examine the rate of growth of a population through time, it can be rearranged as follows: $N_{t+1} - N_t = B - D + I - E$ (equation 2). That is, the increase or decrease in the population size between time intervals t and t+1 is based on the number of births, deaths, immigrants, and emigrants.

When population biologists choose to focus specifically on the importance of birth and death in population dynamics, population models are simplified by temporarily ignoring the effects of immigration and emigration. In this case, the degree of change in the population between time intervals t and t+1 becomes: $N_{t+1} - N_t = B - D$ (equation 3). It is usually safe to assume that the total number of births (B) and deaths (D) in a population is a function of the total number of individuals in the population at the time, N_t. For example, if there are only ten females in a population at time t, it would be impossible to have more than ten births in the population. More births and deaths are possible in larger populations. If B equals the total number of births in the population, then B is equal to the rate at which each individual in the population gives birth, times the total number of individuals in the population. Likewise, the total number of deaths, D, will be equal to the rate at which the individuals in the population might die times the total number of individuals in the population. In other words, $B = bN_t$ and $D = dN_t$ (equation 4), where b and d represent the per capita rates of birth and death, respectively.

Given this understanding of B and D, the original model becomes $N_{t+1} - N_t = (bN_t) - (dN_t)$ or $N_{t+1} - N_t = (b - d)N_t$ (equation 5). It would be useful to find a variable which can represent per capita births and deaths at the same time. Biologists define r as the per capita rate of increase in a population, which is equal to the difference between per capita births and per capita deaths: $r = b - d$ (equation 6). Thus, the equation which examines the changes in population size between time intervals t and t+1 becomes: $N_{t+1} - N_t = rN_t$ (equation 7).

A numerical example works as follows. In a population that originally had 1000 individuals, a per capita birth rate of 0.1 births per year and a per capita death rate of 0.04 deaths per year, the net change in the population size between the year t and t+1 would be:

$$r = 0.1 - 0.04 = 0.06$$
$$N_{t+1} - N_t = 0.06(1000) = 60$$

In other words, the population would increase by sixty individuals over the course of one year.

This model works for populations in which events take place during discrete units of time, such as a population of squirrels in which reproduction takes place at only two specific times in a single year. In contrast, many populations are continuously reproductive. That is, at any given time, any female in the population is capable of reproducing. When these conditions are met, time is viewed as being of a more fluid than discrete nature, and the population exhibits continuous growth. Models of population growth are slightly different when births and deaths are continuous rather than discrete. One way to imagine the difference between a population with continuous rather than discrete growth is to imagine a population in which each time interval is infinitesimally small. When these conditions are met, the model for population growth becomes: $\delta N/\delta t = rN$ (equation 8), where $\delta N/\delta t$ represents the changes in numbers in the population over very short time intervals. The per capita rate of increase (r) can now also be called the instantaneous rate of increase because the population is one with minute time intervals.

How does a population biologist select the best model? Which model is best depends on exactly what it is that a scientist is trying to understand about a population. In the first model presented above (equation 1), the different effects of birth, death, immigration, and emigration can be compared relative to one another. In the second model, the effects of immigration and emigration are ignored and the effects of birth and death are summarized into one constant called the per capita rate of increase (equations 7 and 8). If the scientist is trying to understand the cumulative effects of *B*, *D*, *I*, and *E* on the population, then equation 1 would represent a good model. On the other hand, if the scientist is trying to understand how births and deaths influence the net changes in population size, equation 7 or 8 would be a better model.

Effects of Density on Population Growth

When dealing with a continuous rather than a discrete population, equation 8 represents the rate of population growth as a function of per capita births and per capita deaths in the population. Equation 8 represents a population that is growing exponentially without bound. In other words, regardless of the population size at any given time, the per capita rate of increase remains the same. It would be reasonable to assume that per capita rates of increase can actually change with changes in overall population size. For example, in a population of bark beetles inhabiting the trunk of a tree, many more resources are available to individual beetles when the population is small. Resources must be shared between more and more individuals as the population size increases, which can result in changes to the per capita rate of increase. A model of population growth that incorporates the effect of overall population density on the per capita rate of increase might look like: $\delta N/\delta t = r(1–N/K)N$ (equation 9), where K is equal to the carrying capacity, the maximum number of individuals in the population that there are adequate resources to support. The per capita rate of increase in equation 9 is not simply r by itself, but becomes $r(1–N/K)$. The per capita rate of increase is a function of rates of birth and death scaled by the population size and the carrying capacity of the habitat. If the population is very large relative to the number of individuals that the habitat can support, then $N \approx K$, and the expression $(1–N/K)$ becomes approximately equal to 0. When so, equation 9 takes the form $\delta N/\delta t = r(0)N = 0$ (equation 10) and the rate of population growth is zero. In other words, the population has ceased growing. On the other hand, if the population is very small relative to the number of individuals the habitat can support, then $N << K$ and the expression $(1–N/K)$ becomes approximately equal to 1. When so, equation 9 takes the form $\delta N/\delta t = r(1)N = rN$ (equation 11) and the rate of population growth remains a function of the rates of birth and death, but not the population size or carrying capacity. Thus, equa-

Declining Songbird Populations

Population biologists are interested in monitoring the status of migratory songbirds in the United States. The warbling vireo is a neotropical migrant that overwinters in Mexico and flies northward into the United States during the summer to breed. Population analysis has shown a decline in the coastal California population of warbling vireos over the last twenty-two years. Biologists examined the level of nest productivity and adult survivorship as indices of the per capita birth and death rates in the population, and found that declines in the population were most likely related to low reproductive success and not low survival rates. In terms of population models, this finding would indicate a population decline resulting from the low birth rate leading to an overall decline in numbers.

This example illustrates the importance of population analysis for conservation biology. By understanding the relative effects of birth and death on the warbling vireo population size, conservation biologists can develop the best strategies to sustain vireo populations. By determining that it is nest failure and not adult survivorship that is causing population declines, biologists can focus on eradicating factors that limit nest success and thereby increase the per capita birth rate in the population.

tion 9 represents what is called density-dependent growth.

Effects of Sex Ratio and Age Structure on Population Growth

The model set forth in equation 9 only takes into account the ways in which births, deaths, and population density relative to carrying capacity influence population growth. Sometimes it is helpful to understand how other factors such as the sex ratio and age structure in a population influence rates of growth. For example, deer hunters are not always allowed to take equal numbers of bucks and does from a population. Similarly, fishermen are often restricted in the size of fish they are allowed to keep when fishing. These wildlife management restrictions on the sex and size of animals that can be hunted arise from the fact that both age and sex can influence population growth rates. Models that incorporate the effects of age structure and population sex ratios will not be covered here. Suffice it to say that a population that consists mostly of young individuals yet to reproduce will grow more quickly than a population equal in size but consisting of mostly older individuals who have finished reproducing. Similarly, a population with a highly skewed sex ratio that has many more males than females will not grow as quickly as a population of equal size in which the numbers of males and females are equal.

Population analysis is the study of biological populations, with the specific intent of understanding which factors are most important in determining population size. Factors such as the per capita rates of birth and death, the population density, age structure, and sex ratio all contribute to population size. Understanding how these factors interact to influence population size is critical if biologists hope to manage populations of organisms at sustainable levels for hunting or fishing and if conservation biologists hope to prevent populations from going extinct.

—Erika L. Barthelmess

See also: Birth; Communities; Death and dying; Demographics; Groups; Herds; Migration; Packs; Population fluctuations; Population genetics; Population growth; Wildlife management.

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POPULATION FLUCTUATIONS

Type of animal science: Ecology
Fields of study: Genetics, population biology, reproduction science

The simplest realistic models of population growth produce populations that rise to some level and then stay there. These models cannot produce the complicated array of fluctuations observed in natural populations. Fluctuations vary in period from a few weeks to many decades and reach sufficient amplitude to threaten populations (and entire species) with extinction.

Principal Terms

ABUNDANCE: in ecology, the number of organisms living in a particular environment

ANTHROPOGENIC DISTURBANCE: a change (usually a reduction) in population size caused by human activities

DENSITY-DEPENDENT POPULATION REGULATION: the regulation of population size by factors or interactions intrinsic to the population; the strength of regulation increases as population size increases

IRRUPTION: a sudden increase in the size of a population, usually attributed to a particularly favorable set of environmental conditions

POPULATION: all the individuals of the same species in the same place at the same time

POPULATION DENSITY: the number of individuals in a population per unit of area or volume

QUADRAT: a sample plot of a specific size and shape used in one method of determining population size or species diversity

SESSILE: not free to move around; mollusks are sessile organisms

Every species on earth is composed of one or more populations. The number of organisms making up a population is never constant; it always changes over time. The populations of some species change in predictable or cyclical ways, whereas populations of other species frequently exhibit seemingly unpredictable and noncyclic changes. Fluctuations in population size may be caused by changes in the population's environment; for example, seasonal changes in temperature or moisture produce seasonal fluctuations in population size. Resource limitations may produce density-dependent reductions in the growth rate of a population, which, if the reduction is not instantaneous, can result in oscillations in population size. Interactions with other species also produce population fluctuations; mathematical models of predator-prey systems typically produce oscillations in the abundance of both predators and prey. Finally, natural or anthropogenic disturbances often reduce the size of a population, which then either recovers its former abundance over time or declines further to local (or global) extinction.

The Time Scales of Population Fluctuations

Population fluctuations occur over many different time scales. On a geological time scale (occurring over millions of years), species arise, increase to some level of abundance, and finally become extinct. These long-term patterns of species abundance provide a background for understanding population fluctuations that occur over ecological time (over days, weeks, years, or centuries). Fluctuations at these shorter time scales draw most of the attention of ecologists interested in population dynamics.

Many species of animals, including numerous insects and several small vertebrates, exhibit a more or less annual life cycle, characterized by increasing numbers and higher levels of activity during the summer (or wet season) and by dormancy or decreasing numbers during the winter (or dry season). Even highly mobile animals, such as birds, exhibit a strong seasonal pattern of abundance, if viewed from a local perspective; in North America, for example, most songbirds migrate to more tropical latitudes in the fall and to temperate latitudes in the spring, thereby producing a yearly cycle of abundance in each location. Yearly cycles of abundance are predictable and easily explainable in terms of seasonal patterns of temperature, moisture, and sunlight. Of more interest to ecologists are population fluctuations that appear to be random or unpredictable from year to year or those fluctuations that occur out of synchrony with climatic cycles.

Regular Fluctuations

Nonseasonal fluctuations are of two main types: those that exhibit more or less regular cycles of abundance over several years and those that seem to fluctuate irregularly or noncyclically. A three-to-four-year cycle of abundance is characteristic of several species of mice, voles, and other rodents found in far northern latitudes. Probably the best-known example of this type of cycle is that observed in lemming species in the northern tundra of Europe and North America. Lemming populations exhibit very high densities every three to four years, with such low densities in the intervening years that they are difficult to locate and study. This boom-or-bust cycle is apparently caused by alternating selection regimes. When lemmings are rare, high reproductive capacity and nonaggressive social behavior are favored, and the population grows rapidly. As the growing population becomes more crowded, aggressive individuals are favored, because they can hold territories, secure mates, and protect offspring better than passive individuals. The aggressive interactions, however, inhibit reproductive capacity, increase mortality attributable to fighting and infanticide, and expose more lemmings to predation as subordinate individuals are forced by dominants to occupy more marginal habitats. The behavioral changes that occur in response to crowding apparently persist for some time even as the density declines, so that aggressive interactions and a depressed birthrate continue until the lemming population reaches very low levels. Finally, passive individuals with high reproductive rates are again favored, and the cycle repeats.

Although the breeding cycles of many predators, including snowy owls, weasels, and foxes, are tied to lemming abundance, it appears that the regular fluctuation of lemming populations is a product of crowding and resource limitation rather than of a classical predator-prey cycle; that is, there is no tight coupling between the population fluctuations of lemmings and those of their predators. There is, however, a tight coupling between the population cycles of the snowshoe hare and the Canadian lynx. Since about 1800, the Hudson's Bay Company has kept records of furs produced each year. Both the hare and the lynx show a regular ten-year cycle, with the peaks in lynx abundance occurring about a year behind the hare's peak abundances. Since the hare is a major food source for the lynx in northern Canada, it is logical to assume that this is a coupled oscillation of population sizes, precisely as predicted by classical predator-prey theory.

Some regular cycles of abundance appear to have evolved as a means of avoiding predation rather than being a direct reduction caused by predation. There is a periodicity in the populations of cicadas and locusts. The hypothesized explanation is that predators cannot reproduce rapidly enough to increase their population sizes quickly in response to the sudden availability of a large food supply. When millions of adult cicadas appear above ground for a few weeks after surviving for seventeen years as nymphs in the soil, predators cannot possibly consume them all: No predator could specialize on adult cicadas unless it also had a seventeen-year cycle.

Several northern bird populations (such as crossbills, grosbeaks, and waxwings) fluctuate dramatically, in some years rising to several times their usual levels. This fluctuation may be a response to changing habitat quality. These bird populations always produce as many eggs as food availability and their natural fecundity allow, even though many offspring will not survive. In a good year, a higher proportion of the offspring survives, and the population experiences an irruption, often leading to intense competition and consequent expansion of the range of the population. In subsequent years, population size returns to preirruption levels. Thus, these fluctuations are entirely consistent with normal density-dependent processes responding to a fluctuating environment.

Irregular Fluctuations

Population fluctuations that occur irregularly or noncyclically often appear to be responses to natural disturbances rather than to density-dependent processes or predator-prey relationships. For example, blue grouse persist at a relatively low level of abundance in coniferous forests until a fire occurs. The species rapidly increases in number following a fire and gradually diminishes again as the forest regenerates over the next several decades.

The population fluctuations of some species are not easily attributed to disturbance or to any other single cause. For example, swarming locusts typically remain at low abundance in a restricted area for several years; then, apparently without warning, they may increase more than a hundredfold and swarm over large areas, consuming large amounts of vegetation. The locust outbreak lasts for several years, then the population declines as rapidly as it initially increased. In the early part of the twentieth century, it was discovered that locusts exhibit two phases: a solitary phase, corresponding to low abundance, and a gregarious phase, corresponding to an outbreak. While it is still not known how locusts transform from one phase to another, it is clear that several stages are involved and that weather conditions seem to initiate a transformation. Moisture seems to be the most important determinant, because of its influence on nymph development and survival, on egg development, and on predator abundance, but wind and plant nitrogen levels have also been implicated. Furthermore, it appears that environmental conditions are only effective in inducing a phase transformation if a certain concentration of locusts already exists and if the existing locusts are adequately sensitive to crowding.

Measuring Fluctuations

There are two parts to the study of population fluctuation: detecting and measuring the pattern of the fluctuation and identifying the underlying causes of the fluctuation. In general, any method designed for measuring population size can be used repeatedly over time to detect fluctuations in the population. Reference to a specialized textbook on ecological sampling techniques is strongly recommended when using any of these methods, in order to assure validity of the sampling for subsequent statistical analysis. The mark-recapture method is commonly used with animal populations. There are many variants of this technique, but they all involve capturing and marking some number of individuals, then releasing them; after some time period appropriate to the study, a second sample is captured and the proportion of marked individuals in the second sample (those that are "recaptured") is recorded. This proportion is used to estimate the size of the population at the time when the individuals were originally marked.

The quadrat method is used primarily with plants and other sessile organisms. Plots (called quadrats) are laid out, either randomly or in some pattern; all individuals within the plots constitute a sample. Quadrats are usually square, but any regular shape may be used. The appropriate size of each quadrat depends on the sizes of organisms to be sampled and on their spatial distribution. If nondestructive sampling techniques are used, the same quadrats may be sampled repeatedly; otherwise, new quadrats must be established for each sampling episode.

A variety of plotless techniques is available for sessile organisms, in lieu of the quadrat method. These techniques were developed to eliminate some of the uncertainties associated with selecting proper quadrat size and location. Most plotless methods locate points on the ground, then measure distances to nearby organisms; each plotless technique identifies the individuals to be measured in a slightly different way.

None of these techniques is adequate by itself to identify the origin or cause of any fluctuation in population size. Experimental manipulation of a population is necessary to elucidate the underlying mechanisms and determining factors. Populations of small, rapidly reproducing species (such as species of *Paramecium* or *Daphnia*) can be manipulated in the laboratory, and hypothesized causes of fluctuation can be tested under controlled conditions. This has been done primarily to develop theoretical predictions regarding environmental conditions (such as temperature, moisture, and humidity), resource limitations and fluctuations, and the effects of predators and competitors.

Identifying Causes of Fluctuation

The most interesting examples of population fluctuation, however, occur over spatial and temporal scales too large to handle in the laboratory. Their underlying mechanisms must be elucidated in the field. Because suites of factors typically produce the complex patterns of population fluctuation observed in nature, an effective field study must include all relevant factors. Generally, the most effective studies have been those that have sought to understand the complete life history of a species. Superb examples include the long-term studies of the wolves of Isle Royal National Park, by David Mech and colleagues, and the equally ambitious studies of the grizzly bears of Yellowstone National Park and surrounding areas by Frank and John Craighead and their many coworkers.

Most equilibrium models of population dynamics are capable of producing regular oscillations that mimic the patterns observed in nature. If the model parameters are properly manipulated, many of these models can produce apparently random fluctuation. More sophisticated models have been constructed that incorporate a mathematical equivalent of random environmental fluctuation, although they usually still assume that a population has a tendency to stabilize and that environmental change simply prevents stabilization. The underlying assumption of almost all these models is that species normally exist at equilibrium. This assumption is consistent with the long-held belief that there is a "balance of nature"—that species exist in harmony with their environments.

Image Not Available

If an entire species is considered, perhaps the assumption of equilibrium is warranted, at least for extended periods; yet at the level of the population, fluctuation is the rule—indeed, it may be that extreme fluctuation is the rule. As noted earlier, many populations fluctuate so markedly that they often disappear; they are reestablished only by colonization from large populations within dispersal range. If populations become too small or too isolated from one another, this colonization cannot occur. Additionally, because small populations are more subject to extinction associated with fluctuation, there is additional risk of species extinction if only small populations remain.

The problem of extinction is severe, since habitat destruction is occurring at an unprecedented rate on a global scale. The fragments of intact habitat that remain because of inaccessibility or preservation efforts contain populations that are smaller and more isolated than in the past. If an isolated population fluctuates markedly, resulting in its extinction from a habitat fragment, its replacement by recolonization is unlikely. Furthermore, the genetic variation maintained by a complex population structure within a species is reduced. As the genetic variation within a species is lost, the ability of a species to respond to environmental change is reduced, and extinction of the species is more likely.

Ultimately, if populations normally fluctuate severely enough that they can be expected to become extinct at frequent intervals, then effective conservation requires the maintenance of pathways for exchange and dispersal of individuals among populations within a species. It also requires the preservation of the largest population size possible to allow for normal fluctuation without extinction.

—Alan D. Copsey

See also: Competition; Demographics; Ecology; Endangered species; Extinction; Extinctions and evolutionary explosions; Habitats and biomes; Mark, release, and recapture methods; Migration; Population analysis; Population Growth; Predation; Punctuated equilibrium and continuous evolution; Rhythms and behavior.

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POPULATION GENETICS

Type of animal science: Evolution
Fields of study: Ecology, genetics, systematics (taxonomy)

Population genetics is the analysis of genes and genetic traits in populations to determine how much variability exists, what maintains the variability, how selection (natural or controlled) affects a population, and what the mechanisms of evolution are.

Principal Terms

DEOXYRIBONUCLEIC ACID (DNA): the chemical basis of genes

DOMINANT: requiring only one copy of a gene for expression of the trait

GENE: the unit of heredity; a short stretch of DNA encoding a specific product, usually protein

GENOTYPE: the gene makeup of an individual

INBREEDING: the mating of individuals more closely related than the population average

MEIOSIS: the two cell divisions leading to egg or sperm, during which the genes from the two parents are mixed

MUTATION: a sudden, unpredictable change in a gene

PHENOTYPE: a trait or combination of traits, the result of the genotype and environment

RANDOM GENETIC DRIFT: the random change of gene frequencies because of chance, especially in small populations

RECESSIVE: requiring two copies of a gene for the trait to be expressed

SELECTION: differential survival and reproduction rates of different genotypes

Population genetics is the description and analysis of genetic traits and their causative genes at the population level. Classical genetics deals with the rules of genetic transmission from parents to offspring, developmental genetics deals with the role of genes in development, and molecular genetics looks at the molecular basis of genetic phenomena. Population genetics uses information from all three fields and helps explain why populations are so variable, why some harmful traits are common, why most animals and plants reproduce sexually, how evolution works, why some animals are altruistic in a cutthroat world, and how new species arise.

The Sources of Variability

Simple observation tells us that animals are highly variable. Some dogs are big, others small; some wiry, others big boned; some long haired, others curly; some with special talents such as herding or retrieving, others with none; and some with diseases or defects, others normal. All of these are the results of various genes combined with environmental influences. Unless an animal is an identical twin, no one else shares that individual's genotype and no one ever will. Population genetics looks at variability in a population and examines its sources and the forces that maintain it.

Variability can come from genetic mutations. For example, about one child in ten thousand is born with dominant achondroplasia (short-legged dwarfism). Some children with the trait inherit the condition from an affected parent, but most have normal parents. They are therefore the result of a new mutation. Many mutations are deleterious and are eventually eliminated from the population by the lowered survival or fertility rates of those who have the mutation, but while they remain in the population, they add to its variability. Occasionally, a seemingly harmful mutation persists, for example, the gene that causes sickle-cell anemia, a severe disease characterized by red blood cells that become sickle shaped in certain laboratory tests. The causative gene is recessive, meaning that two copies are needed to produce the anemia, but the disease is very common in some parts of Africa. The harmful, anemia-causing gene persists in the population because if a person has only one gene with the trait rather than two, that gene confers resistance to malaria, the major cause of debility in that part of the world. Although the genes in these two examples have large and conspicuous effects, the great majority of mutations and the great bulk of genetic variability in the population are the result of a large number of genes with individually small effects, often detected only through statistics. The variability of quantitative traits such as size is due mainly to the cumulative action of many individual genes, each of which produces its small effect. The average size stays roughly constant from generation to generation because individuals who are too large or too small are at a disadvantage. However, such individuals continuously arise from new mutations.

The driving force in evolution is natural selection, that is the differential survival and fertility of different genotypes. New mutations occur continuously. Most of these are harmful, although usually only mildly so, but a small minority are beneficial. The rules of Mendelian inheritance ensure that the genes are thoroughly scrambled every generation. Natural selection acts like a sieve, retaining those genes that produce favorable phenotypes in the various combinations and rejecting others. Such a process, acting over eons of time, has produced the variety and specific adaptations that can be found throughout the animal kingdom.

The Forces Against Change

Although evolutionary progress is the result of natural selection, most selection does not accomplish any systematic change. Most selection is directed at maintaining the status quo—eliminating harmful mutations, keeping up with transitory changes in the environment, and eliminating statistical outliers (extremes of variation). Most of the time, evolutionary change is very slow.

In most populations, mating is essentially random in that mates do not choose each other because of the genes they carry. There are exceptions, of course, but for the most part, random mating can be assumed. This permits a great simplification known as the Hardy-Weinberg rule. This rule says that if the proportion of a certain gene, say A, in the population is p and of another, say a, is q, then the three genotypes AA, Aa, and aa appear in the proportions p_2, $2pq$, and q_2, respectively. (Remember that p and q are fractions between zero and one.) This is a simple application of elementary probability and the binomial theorem. Furthermore, after a few generations of random mating, genotypes at different loci also equilibrate, which means that the frequency of a composite genotype is the product of the frequencies at the constituent loci. The reason that this is so useful is that the number of genotypes is enormous, but a population can be characterized by a much smaller number of gene frequencies.

Genotypes are transient, but genes may persist unchanged for many generations. This has led the great theorists of population genetics, J. B. S. Haldane and R. A. Fisher in England and Sewall Wright in the United States, to make the primary units the frequency of individual genes and develop theories around this concept, making free use of the simple consequences of random mating. Such a gene-centered view has been described by scholar Richard Dawkins as the "selfish gene." A population can be thought of as a collection of genes, each of which is maximizing its chance of being passed on to future generations. This causes the population to become better adapted because those genes that improve adaptation have the best chance of being perpetuated.

An extension of this notion is kin selection. The concept holds that, to the extent that behavior is determined by genes, individuals should be protective of close relatives because relatives share genes. The fact that brothers and sisters share half their genes should lead a brother to be half as concerned with his sister's survival and reproduction as with his own. Evolutionists believe that altruistic behavior in various animals, including humans, is the result of kin selection. The degree of self-sacrifice to protect a close relative is proportional to the fraction of shared genes. Parents regularly make sacrifices for their children, and this is what evolutionary theory would predict.

One way in which populations depart from random mating is inbreeding, the mating of individuals more closely related than if they were randomly chosen. Related individuals share one or more ancestors; hence an inbred individual may get two copies of an ancestral gene, one through each parent. In this way, inbreeding increases the proportion of homozygotes. Because many deleterious recessive genes are hidden in the population, inbreeding can have a harmful effect by making genes homozygous. Similarly, if the population is subdivided into local units, mating mostly within themselves, these local units will be more homozygous than if the entire population mated at random. Small subpopulations will be more subject to purely random fluctuations in gene frequencies known as random genetic drifts. Therefore, subdivisions of a population often differ significantly, particularly with respect to unimportant genes.

The Argument Against Average Effects

The gene-centered view of evolution is not always accepted. Some evolutionists believe that it is simplistic to view an individual as a bag of genes, each trying to perpetuate itself. They emphasize that genes often interact in complicated ways, and that a theory that deals with only average gene effects is incomplete. Modern theories of evolution take such complications into account.

This different viewpoint has led to a major controversy in evolution, one that has not yet been settled. Wright emphasized that many well-adapted phenotypes depend on genes that interact in very specific ways; two or more genes may be individually harmful but when combined produce a beneficial effect. He argued that selecting genes on the basis of average effects cannot produce such combined effects. He believed that a population subdivided into many partially isolated units provides an opportunity for such interactions. An individual subpopulation, by random drift, might chance upon such a happy gene combination, in which case, the whole population can be upgraded by migrants from this subpopulation. Whether evolutionary advance results from gene interactions in subpopulations, from mass selection in largely unstructured populations, or from a combination of both is a question that remains unresolved.

Population genetics theory, along with the techniques of molecular genetics, has greatly deepened our knowledge of historical evolution. Everyone is familiar with tree diagrams of common ancestry that show, for example, birds and mammals branching off from early ancestors. In the past these had to be constructed using external phenotypes and fossils. These techniques for measuring the relatedness of different species and determining their ancestral relations have been replaced by DNA sequencing, which produces much surer results. It has long been suspected that genes can persist for very long evolutionary periods, changing slightly to perform new, often related but sometimes quite different functions. This belief has been confirmed repeatedly by molecular analysis. The similarity of the DNA sequences between some plant and animal genes is so great as to leave no doubt that they were both derived from a common ancestral gene a billion or more years ago.

Neutral Mutation and the Benefits of Sexual Reproduction

Most gene mutations have very small effects, and the smaller the effect, the less likely it is to be noticed. Molecular techniques have enabled scientists to detect changes in DNA without regard to the traits they cause or whether they have any effect at all. The Japanese geneticist Motoo Kimura has advanced the idea that most evolution at the DNA level is not the result of natural selection but simply the result of mutation and chance, a concept termed neutral mutation. In vertebrates, especially in mammals, most of the DNA has no known function. The functional genes make up a very small fraction of the total DNA. Many scientists believe that most DNA evolution outside the genes—and some within—is the result of changes that are so nearly neutral as to be determined by chance. How large a role random drift plays in the evolution of changes in functional proteins is still not certain.

A few animals and a large number of plants reproduce asexually. Instead of reproducing by using eggs and sperm, the progeny are carbon copies of the parent. Asexual reproduction has obvious advantages. If females could reproduce without males, producing only female offspring like themselves, reproduction would be twice as efficient. However, despite its inherent inefficiency, sexual reproduction is the rule, undoubtedly because of the gene-scrambling process that sex produces. The ability of a species to produce and try out countless gene combinations confers an evolutionary advantage that outweighs the cost of males. Another advantage of gene scrambling is that it permits harmful mutations to be eliminated from the population in groups rather than individually.

Population genetics is also concerned with the processes by which new species arise. Scientists believe that a population somehow becomes divided into two or more isolated groups, separated perhaps by a river, mountain range, or other geographical barrier. Each group then follows its own separate evolutionary course, and the groups' dissimilar environments accentuate their differences. Eventually so many differences between the two groups evolve that they are no longer compatible. The products of interspecies crosses, or hybrids, often do not develop normally or are sterile (like the mule). Sometimes the two species do not mate because they are so different.

Theory, Observation, and Experiment

Population genetics involves theory, observation, and experiment. Population genetics examines how genes are influenced by mutation, selection, population size, migration, and chance. Scientists develop mathematical models that embody these theories and compare the results obtained using the models with data from laboratory experiments or field observations. These genetic models have become more and more sophisticated to take into account complex gene interactions and increasingly realistic population structures. The models are further complicated by efforts to account for random processes. Often the mathematical geneticist relies on computers to perform complex analyses and computations.

One of the simpler models, which makes the assumption that mating is random, is the Hardy-Weinberg principle. If the proportion of gene A in the population is p and that of gene a is q, then the three genotypes AA, Aa, and aa appear in the proportions p_2, $2pq$, and q_2, respectively. The proportion of Aa is $2pq$ rather than simply pq because this genotype represents two combinations, maternal A with paternal a and paternal A with maternal a. This principle can be used to predict the frequency of persons with malaria resistance from the incidence of sickle-cell anemia. If one-tenth of the genes are sickle-cell genes and the other nine-tenths are normal, the frequency of two genes coming together to produce an anemic child is 0.1×0.1, or 0.01. The frequency of those resistant to malaria, who have one normal and one sickle-cell gene, is $2 \times 0.1 \times 0.9$, or 0.18. A slight extension of the calculation (using the rates of malaria infection and death from the disease) can be used to estimate the death rate from malaria. Another mathematical model can be formed based on the molecular genetics theory of neutral mutation. A neutral mutation, because it is not influenced by natural selection, has an expected rate of evolution that is equal to the mutation rate. Mathematical models embodying this theory are used to quantitatively predict what will happen in an experiment or what an observational study will find and act as a test of the theory. Neutral mutation theory is quite complicated and requires advanced mathematics.

Observational population genetics consists of studying animals and plants in nature. Evolution rates are inferred from the fossil record. Field observations can determine the frequency of genes in different geographical areas or environments. The frequency of self- and cross-pollination can often be observed directly. Increasingly, DNA analysis, which can detect relationships or alterations that are not visible, is being used to support field observations. For example, molecular markers have been used to determine parentage and relationship. DNA analysis revealed that certain birds that do not reproduce but care for the progeny of others are in fact close relatives, consistent with kin selection theory.

Increasingly, population genetics has begun to rely on experimentation. Plants and animals can be used to study the process of selection, but to save time and reduce costs, most laboratory experiments involve small, rapidly reproducing organisms such as the fruit fly, *Drosophila*. Some of the most sensitive selection experiments have involved the use of a chemostat, a container in which a steady inflow of nutrients and steady outflow of wastes and excess population permit a population to maintain a stable number of rapidly growing organisms, usually bacteria. These permit very sensitive measurements of the effects of mutation. Evolutionary studies that would require eons if studied in large animals or even mice can be completed in a very short time.

Explaining, Quantifying, and Predicting Evolution

The greatest intellectual value of population genetics has been to provide a theory of evolution that is explanatory, quantitative, and predictive. Population genetics places knowledge of mutation, gene action, selection, inbreeding, and population structure in a unified framework. It brings together Charles Darwin's theory of evolution by natural selection, Gregor Mendel's laws of inheritance, and molecular genetics to create a coherent picture of how evolution took place and is still occurring.

Population genetics has provided explanations for variability in a population, the prevalence of sexual rather than asexual reproduction, the origin of new species, and behavioral traits such as altruism. It has also provided an understanding of why some harmful diseases are found in the population. Population genetics has been used in animal and plant breeding to create rational selection programs. Using quantitative models, the results of various selection schemes can be compared and the best one chosen.

A particular telling example of a situation in which population genetics predicted an outcome that has become painfully obvious is the development of resistance to insecticides, herbicides, and antibiotics. As people used these products more and more, the insects, weeds, and bacteria they were trying to eliminate developed resistance, and new products had to be developed to replace those rendered ineffective. The development of resistance represents evolution by natural selection that took place not over hundreds or thousands of years but in just a few years. Probably the most problematic area of resistance is antibiotics because some treatable diseases are again threatening to move beyond the ability of medicine to cure. A major challenge to ecologists, microbiologists, physicians, and population geneticists is how to deal with the increasingly difficult problem of disease-producing microorganisms that are resistant to antibiotics.

—James F. Crow

See also: Aging; Asexual reproduction; Convergent and divergent evolution; Demographics; Development: Evolutionary perspective; Evolution: Historical perspective; Genetics; Hardy-Weinberg law of genetic equilibrium; Isolating mechanisms in evolution; Mutation; Natural selection; Neutral mutations and evolutionary clocks; Population analysis; Reproduction; Sex differences: Evolutionary origin.

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POPULATION GROWTH

Type of animal science: Ecology
Fields of study: Anthropology, ethology, genetics, population biology, reproduction science

Populations typically grow when they are found on sites with abundant resources, and biologists have developed two models to describe growth. In exponential growth, the population is exposed to ideal conditions, and new individuals are added at an ever-increasing rate. Logistic growth recognizes that resources are eventually depleted, however, and that the population density ultimately stabilizes at some level, which is defined as the carrying capacity.

Principal Terms

CARRYING CAPACITY: the number of individuals of a given species that a site can support

EMIGRATION: the process whereby individuals leave a site and move elsewhere, leading to a decrease in the size of the population

EXPONENTIAL GROWTH: a pattern of population growth in which the rate of increase becomes progressively larger over time

IMMIGRATION: the process by which new individuals arrive at a site from elsewhere, leading to an increase in size of the population

INTRINSIC RATE OF INCREASE: the growth rate of a population under ideal conditions, expressed on a per individual basis

LOGISTIC GROWTH: a pattern of population growth that involves a rapid increase in numbers when the density is low but slows as the density approaches the carrying capacity

POPULATION: a group of individuals of the same species that live in the same location at the same time

In nature, organisms of a particular species rarely occur by themselves. Instead, they usually exist with other individuals of the same species. Biologists use the term "population" to refer to an aggregation of organisms of a given species that live in the same general location at the same time. In some cases, populations can be well defined, such as herds of cattle or flocks of geese. In other cases, a population is not well defined, often because several species may be found in the same location. For example, a meadow may contain intermingled populations of several species, including daisies, timothy grass, earthworms, and grasshoppers.

Biologists have studied populations for many years. Many of those studies have been conducted to answer three separate but interrelated questions. First, how many individuals are there in a given population at a particular time? Second, how do those numbers change from one time to another? Third, what environmental factors are responsible for any population increases or decreases? Studies have shown that for most species of plants, animals, and microbes, the number of individuals in the population changes over time. Some populations increase steadily, other populations decrease, while still others fluctuate. Thus, populations are generally dynamic, rather than static, when viewed over time.

Population Behaviors

Most populations change so much through time because there is constantly turnover among individuals. That is, new individuals are constantly being born, hatched, or germinated, while others die. Moreover, animals are also able to enter a population by immigration and leave by emigration. Since the number of births and new immigrants hardly ever exactly matches the number of deaths and emigrants, the dynamic nature of populations should not be a surprise. Because changes in population size are common in nature, biologists have tried to understand the changes that are observed. One approach has been to model populations; the model is a simplified graphical or mathematical summary of the actual changes that are occurring in the species of interest. The relationship between a model and the actual population that it represents is similar to that between a map and the area of land that it represents. Because modeling is such an important aspect of population biology, a biologist who studies population must often have a good background in mathematics.

Perhaps the simplest model of population behavior is the difference equation, which states that the number of individuals in a population at some specified time in the future is equal to the number at present, plus the number of births, minus the number of deaths, plus the number of new immigrants, minus the number of emigrants. Thus, by knowing how many individuals are on a site at a given time and knowing the usual number of births, deaths, immigrants, and emigrants, one can predict the number of individuals on the site at some future time.

Obviously, the number of births, deaths, immigrants, and emigrants will vary from one place to another and from one time to another. For example, on a site with abundant food and space and with favorable physical conditions for growth and development, births and immigration will be much greater than deaths and emigration. Thus, the population will increase. Conversely, if food or space is limiting or if the physical conditions are more severe, losses to the population through death and emigration will equal or exceed gains through birth and immigration. Thus, the population will remain constant or decline.

Biologists often are concerned about what happens in extreme conditions, because such conditions define the limits within which the population normally operates. When conditions are very bad, a population normally declines rapidly, often to the point of local extinction; when conditions are very good, a population will increase. That increase is attributable to the fact that each individual normally has the capacity to produce many offspring during its lifetime. For example, a woman could produce more than forty children if she conceived every time that she was fertile. Other individual organisms, particularly many invertebrates and plants, can produce hundreds of thousands of offspring in their lifetimes.

Influences on Birth and Death Rates

At least three different traits influence the reproductive output of a given species. The first is the number of offspring per reproductive period (elephants produce only one child at a time, whereas flies can lay thousands of eggs). The second is the age at first reproduction (most dogs can reproduce when less than three years old, whereas humans do not usually become fertile until they reach an age of thirteen or fourteen). The third is the number of times that an individual reproduces in its lifetime (salmon spawn, that is, lay eggs, only once before they die, whereas chickens lay eggs repeatedly). Even under ideal conditions, death must also be considered when examining population growth. Most all organisms have a maximum life span that is determined by their innate physiology and cannot be exceeded, even if they are supplied with abundant food and kept free from disease.

Population biologists frequently express birth and death in the form of rates. This can be done by counting the number of new births and deaths in a population during a predetermined period of time and then dividing by the number of individuals in the population. That will give the per capita (per individual) birth and death rates. For example, suppose that during the course of a year there were thirty births and fifteen deaths in a population of one thousand individuals. That per capita birthrate would be 0.030 and the per capita death rate would be 0.015.

Next, one can subtract the death rate from the birthrate to find the per capita rate of population growth. That rate should be greatest under ideal conditions, when the birthrate is greatest and the death rate is least. That per capita rate of population growth is called the "maximal intrinsic rate of increase" or the "biotic potential" by population biologists, and it is a very important attribute. It is often symbolized as r_{max} or referred to as "little r." Normally, r_{max} is considered an inherent feature of a species. As one might expect, it varies greatly among different types of organisms. For example, r_{max}, expressed per year, is 0.02-1.5 for birds and large mammals, 4-50 for insects and small invertebrates, and as high as 20,000 for bacteria.

Exponential Growth

By knowing the intrinsic rate of increase and the number of organisms in a population, one can predict much about the behavior of a population under ideal conditions. The rate at which the population grows is merely the intrinsic rate of increase (r_{max}) multiplied by the number of individuals in the population. For example, suppose that there are ten individuals in a population whose annual r_{max} is 2. That population would increase by an annual rate of twenty (which would be a healthy increase). Next, suppose that one returned to that population at some later time when the population was fifty individuals. At that point, the annual rate of population increase would be one hundred new individuals (which would be an even healthier increase). If the rate of increase were measured when the population reached five hundred, the annual rate of increase would be one thousand individuals.

Under such circumstances, the population would keep on growing at an ever-increasing rate. That type of growth is called "exponential growth" by population biologists, and it typifies the behavior of many populations in ideal conditions. If the number of individuals in a population undergoing exponential growth is plotted as a function of time, the curve would resemble the letter J. That is, it would be somewhat flat initially, but it would curve upward, and at some point it would be almost vertical. Exponential population growth has been observed to a limited extent in many different kinds of organisms, both in the laboratory and under field conditions. Examples include protozoans, small insects, and birds. It should be obvious, however, that no species could behave in this manner for long. If it did, it would overrun the earth (and indeed the universe) in time. Instead, population growth is slowed by limited resources, accumulated wastes, behavioral stresses, and/or periodic catastrophes caused by the environment.

Logistic Growth

Biologists have created a second model to account for the behavior of populations under finite resources and have called it logistic growth. If the number of individuals in a population undergoing logistic growth is plotted as a function of time, the curve resembles a flattened S shape. In other words, the curve is initially flat, but then curves upward at a progressively faster rate, much like exponential growth. At some point (called the inflection point), however, the curve begins to turn to the right and flatten out. Ultimately, the curve becomes horizontal, indicating a constant population over time.

An important aspect of pure logistic growth is that the population approaches, but does not exceed, a certain level. That level is called the carrying capacity, and is represented by the symbol K in most mathematical treatments of logistic growth. The carrying capacity is the maximum number of individuals that the environment can support, based on the space, food, and other resources available. When the number of individuals is much fewer than the carrying capacity, the population grows rapidly, much as in exponential growth. As the number increases, however, the rate of population growth becomes much less than the exponential rate. When the number approaches the carrying capacity, new population growth virtually ceases. If the population were to increase above the carrying capacity for some reason, there would be a net loss of organisms from the population.

There are few studies that have documented logistic growth in nature. It would be necessary to

The study of population growth must consider how often an animal reproduces and how many offspring it produces at one time. Some animals, such as the elephant, have only one offspring with a long gestation period, while others, such as the fruit fly, lay thousands of eggs at a time. Significantly, elephants are an endangered species while fruit flies are not. (Corbis)

watch a species in a habitat from the time of its first introduction until its population stabilized. Such studies are necessarily of a very long duration and thus are not normally conducted. Logistic growth has been found in a number of experimental studies, however, particularly on small organisms, including protozoans, fruit flies, and beetles.

An important aspect of logistic growth is that, as the population increases, the birthrate decreases and the mortality rate increases. Such effects may be attributable to reduced space within which the organism can operate, to less food and other resources, to physiological and behavioral stress caused by crowding, and to increased incidence of disease. Those factors are commonly designated as being density-dependent. They are considered much different from the density-independent factors that typically arise from environmental catastrophes such as flooding, drought, fire, or extreme temperatures. For many years, biologists argued about the relative importance of density-dependent versus density-independent factors in controlling population size. It is now recognized that some species are controlled by density-independent factors, whereas others are controlled by density-dependent factors.

Classically, when a species undergoes logistic growth, the population is ultimately supposed to stabilize at the carrying capacity. Most studies that track populations over the course of time, however, find that numbers actually fluctuate. How can such variability be reconciled with the logistic model? On the one hand, the fluctuations may be caused by density-independent factors, and the logistic equation therefore does not apply. On the other hand, the population may be under density-dependent control, and the logistic model can still hold despite the fluctuations. One explanation for the fluctuations could be that the carrying capacity itself changes over time. For example, a sudden increase in the amount of food available would increase the carrying capacity and allow the population to grow. A second explanation relates to the presence of time lags; that is, a population might not respond immediately to a given resource level. For example, two animals in a rapidly expanding population might mate when the number of individuals is less than the carrying capacity. The progeny, however, might be born several weeks or months later, into a situation in which the population has exceeded the carrying capacity. Thus, there would have to be a decline, leading to the fluctuation.

Approaches to Studying Population Growth

Two main approaches can be used to investigate logistic and exponential population growth among organisms. One approach involves following natural populations in the field; the other involves setting up experimental populations. Each approach has its benefits and drawbacks, and, ideally, both should be employed. To study population growth in the field, it is important to study a species from the time that it first arrives on a site until its population stabilizes. Thus, any species already present are automatically eliminated from consideration unless they are brought to local extinction and a new population is then allowed to recolonize. Population growth studies can be profitably done on sites that are very disturbed and are beginning to fill up with organisms. Examples would be an abandoned farm field or strip mine, a newly created volcanic island, or a new body of water. Moreover, studies could also be done on a species that is purposely introduced to a new site.

In either case, one needs to survey the population periodically to assess the number of individuals that it contains. The size of the population can be determined directly or by employing sampling techniques such as mark-recapture methodologies. The number of individuals can then be plotted on a graph (on the y axis) as a function of time (on the x axis).

To study population growth in experimental conditions, one sets up an artificial habitat according to the needs of the species in question. For example, investigators have examined population growth in protozoans (unicellular animals) by growing populations in test tubes filled with food dissolved in known volumes of water. Others have grown fruit flies in stoppered flasks. Still others have grown beetles in containers filled with oatmeal or other crushed grain. In those cases, it was typically necessary to replenish the food to keep the population going. Whenever the population was placed into an artificial habitat with a nonrenewable food source, it would generally consume all the food and then die out.

More detailed experiments can be performed to test whether density-dependent mortality is occurring. Such experiments would involve setting up a series of containers with different densities of organisms and then following the mortality of those organisms. In theory, mortality rates should be highest in containers that have the greatest densities of organisms and lowest in containers with the sparsest populations. One could also examine the birthrate in those containers, with the expectation that birthrates should be highest in the sparsest containers and lowest in those that have the most organisms. The investigation should be long enough to allow the population to reach equilibrium at the carrying capacity. For short-lived organisms such as protozoans or insects, that could take days, weeks, or months. For longer-lived organisms such as fish or small mammals, one to several years may be required. For long-lived animals, a truly adequate study may take decades.

Another consideration in studying exponential and logistic population growth is that immigration and emigration should be kept to a minimum. Thus, organisms that are highly active, such as birds, large mammals, and most flying insects would be extremely difficult to study. Finally, one can set up numerous populations and expose each to a slightly different set of conditions. That would enable the researcher to ascertain which environmental factors are most important in determining the carrying capacity. For example, populations of aquatic invertebrates could be monitored under a range of temperature, salinity, pH, and nutrient conditions.

Implications of Logistic Growth

Since exponential growth is unrealistic in practical terms for almost all populations, its scientific usefulness is limited. The concepts derived from logistic growth, however, have important implications to biologists and nonbiologists alike. One important aspect of logistic growth is that the maximum rate of population growth occurs when the population is about half of the environment's carrying capacity. When populations are very sparse, there are simply too few individuals to produce many progeny. When populations are dense, near the carrying capacity, there is not enough room or other resources to allow for rapid population growth. Based on that relationship, those who must harvest organisms can do so at a rate that allows the population to reestablish itself quickly. Those who can apply this concept in their everyday work include wildlife managers, ranchers, and fishermen. Indeed, quotas for hunting and fishing are often set in a way that allows for the population to be thinned sufficiently without depleting it too severely. Unfortunately, there are two problems that biologists must confront when they try to use the logistic model to help manage populations. The first is that it is often difficult to establish the carrying capacity for a given species on a particular site. One reason is that the populations of many species are profoundly affected by density-independent factors, as well as by other species, in highly complex and variable ways. Further, for reasons unclear to most biologists, some species have a maximum rate of population growth at levels well above or well below the level (one half of the carrying capacity) that is normally assumed. Thus, the logistic model typically gives only a very rough approximation for the ideal size of a population. However, the logistic model is useful because it emphasizes that all species have natural limits to the sizes of their populations.

—Kenneth M. Klemow

See also: Biodiversity; Competition; Demographics; Ecology; Ecosystems; Mark, release, and recapture methods; Population analysis; Population fluctuations; Reproduction; Reproductive strategies.

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PORCUPINES

Types of animal science: Behavior, classification, ecology
Fields of study: Ecology, wildlife ecology, zoology

North American porcupines are large rodents who are vegetarians. These rather clumsy mammals are best known for their prickly quills that can inflict pain and suffering, and even result in death if the quill finds its way to a vital organ.

Principal Terms

ARBOREAL: living in or spending time in trees
DORSAL: the back portion of an animal
HERBIVORE: an animal that consumes vegetation for its diet
NOTOCHORD: a dorsal, flexible, rodlike structure extending the length of a vertebrate's body; serves as an axis for muscle attachment
PELAGE: a mammal's fur coat
PREDATOR: any animals that preys on another animal
QUILLS: sometimes referred to as spines; modified guard hairs; quills have barbed tips which can work themselves deeper into flesh once they have penetrated

Agile and armed, although they may seem slow, a porcupine is quick to make its point with its defensive quills. Porcupines do not throw or cast their quills into a potential predator; instead, quills penetrate a predator's body on contact with the porcupine's prickly body. The more than thirty thousand quills on a porcupine's back and sides are actually modified hairs (one of the characteristics of mammals). Other common names of porcupines are quillpig and pricklepig.

North American porcupines are arboreal or semiarboreal, spending much of their day climbing trees and consuming tree bark. These herbivores ingest a variety of plant materials, from buds to roots. On occasion, porcupines may eat shed antlers of deer or elk for the various minerals, such as calcium, that they contain.

Second in size only to the beavers in the class Rodentia, adults porcupines weigh between four and six kilograms, although much larger ones have been reported. The length attained by adults ranges from about sixty to one hundred centimeters. While color variations occur, most individuals have dark colored pelage. Porcupines are mostly nocturnal, but may be observed during the day either on the ground or in trees.

Porcupine Life Cycle

Adult porcupines are solitary mammals for most of the year, except during the breeding season, between September and November. Female porcupines begin reproductive activities at about 1.5 years of age. It is common to find several males around a female during her brief (eight- to twelve-hour) time of receptivity. Mating is brief and occurs on the ground, with the female raising her tail over her back. After the male has inseminated her, each porcupine goes its separate way.

Usually only one porcupette, as the young are sometimes called, is born after the lengthy gestation period. Weighing between four hundred and five hundred grams at birth, newborn porcupines are quite precocial. Their eyes are open and their quills are present, as are their incisors and premolar teeth. Although capable of consuming vegetation within a week of birth, the young are nursed by their mother through the summer months.

Porcupines consume the inner bark of trees and shrubs, especially in the fall and winter when the plants on the ground are becoming dormant or

Porcupine Facts

Classification:
Kingdom: Animalia
Phylum: Chordata
Class: Mammalia
Order: Rodentia
Family: Erethizontidae
Genus and species: Erethizon dorstaum

Geographical location: North American porcupines are found throughout Canada, extending into the northeastern and western United States; South American porcupines live in the tropical rain forests of South and Central America; various other porcupine species live in Africa and Asia

Habitat: Ranges from tropical rain forests to deserts; some inhabit coniferous and deciduous forests, while others live in grasslands

Gestational period: Averages 211 days

Life span: Five to six years in the wild, ten to twelve years in captivity

Special anatomy: Quills

dying. It is easy to observe porcupine feeding sites in the forests by observing the limbs and trunks of trees. If the outer bark has been stripped away, the whitish colored areas beneath are quite apparent. During the spring and early summer, porcupines spend more time on the ground feeding on tender shoots and buds of emerging plants.

While their vision is not acute, their olfactory (smell) and auditory (hearing) senses are well developed. Some researchers have reported observing porcupines standing up on their hind legs and sniffing their surroundings. If a porcupine detects a potential predator, it will form a defensive posture of lowered head and back, at the same time raising the tail for swinging. The heavy muscular tail can drive quills deep into a predator's face and head.

—Sylvester Allred

See also: Beavers; Defense mechanisms; Fur and hair; Mice and rats; Rodents; Squirrels.

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PRAYING MANTIS

Type of animal science: Classification
Fields of study: Ecology, entomology, ethology, invertebrate biology, physiology, population biology, systematics (taxonomy), zoology

All species of praying mantids (or mantises) are predators on other arthropods, but their importance in natural food webs is poorly understood. They have been models for a wide variety of experimental studies on behavior, neurophysiology, and ecology.

Principal Terms

ECOSYSTEM: the collection of all species and their abiotic environment in an area (habitat)

FOOD WEB: the feeding relationships among species in an ecosystem

HEMIMETABOLOUS: incomplete metamorphosis in which juveniles resemble wingless adults

NYMPH: the term for any of the juvenile stages of a hemimetabolous insect

SEX PHEROMONE: a volatile chemical released into the air by females to attract males

TROPHIC LEVEL: feeding position in the food web of an ecosystem

Praying mantis is the common name for any insect in the order Dictyoptera, suborder Mantodea. All of these insects are predators. The most important family in this group is Mantidae; hence, the general name for these insects often is given as "mantid," rather than "mantis." Mantids are closely related to cockroaches, termites, and grasshoppers. Approximately 1,800 species have been identified worldwide, most of which are tropical. The most common native species in the United States is the Carolina mantid, *Stagmomantis carolina*, which is found from New Jersey to the Gulf Coast in the eastern half of the United States. The most abundant and widespread species, the Chinese mantid, *Tenodera aridifolia sinensis*, was introduced from Asia at the end of the nineteenth century and can be found from South Carolina to Long Island east of the Mississippi, as well as in portions of the Midwest and West Coast. Another well-known imported species is *Mantis religiosa*, the distribution of which is limited to northern states and Canada because its eggs require cold winters before they will develop and hatch in the spring.

Mantid Physiology

The praying mantis has the most highly mobile head of any insect, attached to the front of an elongated prothorax (foremost midbody segment), and spiny front legs also attached to the prothorax. These specialized forelegs are folded when the animal waits motionless in ambush for its prey, giving it an attitude of prayer (hence, the common name for the group). Although most mantids are sit-and-wait ambush predators, some species actively hunt and chase their prey over short distances.

The sensory systems of mantids have been well studied. Mantids can integrate detailed information from their environments, and have exhibited a highly sophisticated array of responses to external stimuli, such as light, chemicals, and sound. They are able to use binocular vision to accurately estimate the striking distance to their prey, or the distance between perching sites in vegetation. Female mantids produce sex pheromones to attract males during mating season. Some species can hear ultrasound emitted by bats, and thus avoid predation when they fly at night.

Sexual behavior and cannibalism in mantids has been the subject of much folklore and scientific speculation. Females of many species sometimes eat males before, after, or even during copulation. The outcome of male-female encounters is mainly a function of hunger level in females, and males often escape to mate with other females later on. The reputedly suicidal behavior of males is not really a sacrifice, because a male cannot tell in advance the hunger state of his prospective mate, or whether her eggs have already been fertilized by an earlier encounter with another male.

Mantid Life Cycle

Mantids inhabiting temperate geographic zones generally live from spring to autumn, and the adults all die with the onset of cold weather, leaving the eggs to winter over. Development of mantids is hemimetabolous: Eggs hatch out into nymphs that are miniatures of the adults, except without wings. Nymphs grow through as many as seven stages (depending on species), increasing body length tenfold before developing wings as adults near the end of the season. The largest species in the United States, *Tenodera aridifolia sinensis*, may grow as large as ten centimeters (four inches), and often appears even larger to startled human observers. Very few hatchling nymphs survive the growing season to reach adulthood, most of them dying of starvation and the rest from predators such as spiders. Adults are large enough to escape predation by most other invertebrates, but vertebrate predators such as birds and lizards actively prey on them. Cannibalism between same-sized mantids is relatively rare except under crowded conditions in captivity where they cannot avoid one another, but larger nymphs will readily eat smaller ones. The variable feeding opportunities in natural ecosystems cause variable growth rates among nymphs within a season,

Image Not Available

Mantid Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Arthropoda
Subphylum: Uniramia
Class: Insecta
Order: Dictyoptera
Suborder: Mantodea (praying mantids)

Geographical location: Europe, Africa, Asia, the Americas, mainly in the tropics

Habitat: Open fields, forests, and deserts

Gestational period: Highly variable among species; most temperate zone species have a single generation each year, with eggs overwintering

Life span: Variable among species; temperate zone species die at the end of a single growing season; females of some tropical species survive until their eggs hatch

Special anatomy: Highly mobile head; elongated prothorax (first segment of thorax); raptorial front legs for grasping prey so cannibalism among different-sized individuals may be common in nature.

Praying mantids simultaneously occupy two trophic levels, feeding on both herbivorous and carnivorous arthropods. This makes their use in pest control problematic: If they eat grasshoppers they may be beneficial, but if they eat spiders they may be harmful. There is evidence that mantids can enhance plant growth by eating herbivorous insects, but their impact is likely to vary depending on the plants and other arthropod species present.

—Lawrence E. Hurd

See also: Arthropods; Cannibalism; Copulation; Insects; Mating; Metamorphosis; Reproductive strategies.

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PREDATION

Type of animal science: Ecology
Fields of study: Environmental science, evolutionary science, wildlife ecology

The relationships among predators and their prey in natural communities are varied and complex. These interactions provide clues as to how natural populations regulate one another, as well as to how to preserve and manage exploited populations more successfully.

Principal Terms

COMPETITION: the interaction among two or more organisms of the same or different species that results when they share a limited resource

FOOD WEB: the sum total of the feeding relationships (links) between trophic levels in ecosystems

FUNCTIONAL RESPONSE: the rate at which an individual predator consumes prey, dependent upon the abundance of that prey in a habitat

MIMICRY: the resemblance of one species (the model) to one or more other species (mimics), such that a predator cannot distinguish among them

NUMERICAL RESPONSE: the abundance of predators dependent upon the abundance of prey in a habitat

POPULATION REGULATION: stabilization of population size by factors such as predation and competition, the relative impact of which depends on abundance of the population in a habitat

TROPHIC LEVEL: a level at which energy is acquired in a food web—the herbivore level obtains energy from plants; the carnivore level from herbivores and other carnivores

Predation is an interaction between two organisms in which one of them, the predator, derives nutrition by killing and eating the other, the prey. Obvious examples include lions feeding on zebras and hawks eating rodents, but predation is not limited to interactions among animals. Birds that feed on seeds are legitimate predators since they are killing individual organisms (embryonic plants) to derive energy. There are a number of species of carnivorous plants, such as sundews and pitcher plants, that capture and consume small animals to obtain nitrogen in habitats lacking sufficient quantities of that nutrient. Most animals that feed on plants (herbivores) do not kill the entire plant and therefore are not really predators. Exceptions to this generalization are some insects that reach infestation levels, such as gypsy moths or locusts, and can kill the plants upon which they feed. The majority of herbivore-plant associations, however, are more properly described as parasite-host interactions in which the host plant may suffer damage but does not die.

There are special cases in which parasitism and predation may be combined. One of these is the interaction between parasitoid wasps and their hosts, usually flies. Adult female parasitoids attack and inject eggs into fly pupae (the resting stage, during which fly larvae metamorphose into adults), and the larvae of the wasp consume the fly. The adult parasitoid is therefore a parasite, while the larval wasp acts as a predator.

Predator-Prey Interactions

Predator-prey interactions can be divided into two considerations: the effects of prey on predators, and the effects of predators on their prey. Predators respond to changes in prey density (the number of prey organisms in the habitat) in two principal ways. The first is called numerical response, which means that predators change their numbers in response to changes in prey density. This may be accomplished by increasing or decreasing reproduction or by immigrating to or emigrating from a habitat. If prey density increases, predators may immigrate from other habitats to take advantage of this increased resource, or those predators already present may produce more offspring. When prey density decreases, the opposite will occur. Some predators, which are known as fugitive species, are specialized at finding habitats with abundant prey, migrating to them, and reproducing rapidly once they are established.

Cape May warblers are good at finding high densities of spruce budworms (a serious pest of conifers) and then converting the energy from their prey into offspring. This strategy allows the birds to persist only because the budworms are never completely wiped out; they are better at dispersing to new habitats than are the birds.

The second response of predators to changing prey density is called functional response. The rate at which predators capture and consume prey depends upon the rate at which they encounter prey, which is a function of prey density. If the predator has a choice of several prey species, it may learn to prefer one of them. If that prey is sufficiently abundant, this situation results in a phenomenon known as switching, the concentration by the predator on the preferred prey. It may entail a change in searching behavior on the part of the predator, such that former prey items will no longer be encountered as frequently.

Animals have evolved a number of defense mechanisms that reduce their probability of being eaten by predators. Spines on horned lizards, threatening displays by harmless snakes, camouflage of many cryptic animals, toxic or distasteful chemicals in insects and amphibians, and simply rapid movement—all are adaptations that may have evolved in response to natural selection by predators. A predator that can learn to prefer one prey item over another is smart enough to learn to avoid less desirable prey. That capability is the basis for a phenomenon—known as aposematism—among potential prey species which are toxic and/or distasteful to their predators. Aposematic organisms advertise their toxicity by bright coloration, making it easy for predators to learn to avoid them, which in turn saves the prey population from frequent taste-testing. Many species of insects are aposematic. Monarch butterflies are bright orange with black stripes, an easy signal to recognize. They owe their toxicity to the milkweed plant, which they eat as caterpillars. The plant contains cardiac glycosides, which are very toxic. The monarch caterpillar is immune to the poison and stores it in its body so that the adult has a high concentration of it in its wings. If a bird grabs the butterfly in flight, it is likely to get a piece of wing first, and this will teach it not to try orange butterflies in the future.

Some potential prey species that are not themselves toxic have evolved to resemble those that are; these are called Batesian mimics. Viceroy butterflies, which are not toxic, mimic monarchs very closely, so that birds cannot tell them apart. One limit to Batesian mimicry is that mimics can never get very numerous, or their predators will not get a strong enough message to leave them alone. Another kind of mimicry involves mimics that are as toxic as their models. The advantage with this type, Müllerian mimicry, is that the predator has to learn only one coloration signal, which reduces risk for both prey populations. In this relationship, the mimic population does not have to remain at low levels relative to the model population. A third type of mimicry is more insidious—aggressive mimicry, in which a predator resembles a prey or the resource of that prey in order to lure it close enough to capture. There are tropical praying mantids that closely resemble orchid flowers, thus attracting the bees upon which they prey. There are some species of fireflies that eat other species of fireflies, using the flashing light signal of their prey to lure them within range.

The Choice of Prey

What determines predator preference for prey? Since prey are a source of energy for the predator, it might be expected that predators would simply attack the largest prey they could handle. To an extent, this choice holds true for many predators, but there is a cost to be considered. The cost involves the energy a predator must expend to search for, capture, handle, and consume prey. In order to be profitable, a prey item must yield much more energy than it costs. Natural selection should favor reduction in energetic cost relative to energetic gain, the basis for optimal foraging theory. According to this theory, many predators have evolved hunting strategies to optimize the time and energy spent in searching for and capturing prey. Some predators, such as web-building spiders and boa constrictors, ambush their prey. The low energetic cost of sit-and-wait is an advantage in environments that provide plentiful prey. If encounters with prey become less predictably reliable, however, an ambush predator may experience starvation. Spiders can lower their metabolic energy requirements when prey is unavailable, whereas more mobile predators, such as boa constrictors, can simply shift to active searching. Probably because of the likelihood of facing starvation for extended periods of time, ambush predation is more common among animals that do not expend metabolic energy to regulate their body temperatures (ectotherms) than among those that do (endotherms). Some predators, such as wolves and lions, hunt in groups. This allows them to tackle larger (more profitable) prey than if they hunted alone. Solitary hunters generally have to hunt smaller prey.

Natural communities consist of food webs, constructed of links (feeding relationships) among trophic levels. Each prey species is linked to one or more predators. Most predators in nature are generalists with respect to their prey. Spiders, snakes, hawks, lions, and wolves all feed on a variety of prey. Some of these prey are herbivores, but some are themselves predators. Praying mantids eat grasshoppers (herbivores), but they also eat spiders (carnivores) and each other. Thus, generalist predators have a bitrophic niche, in that they occupy two trophic levels at the same time.

Predatory Relationships and Population Fluctuation

It is an open question whether predators and prey commonly regulate each other's numbers in nature. There are many examples of cyclic changes in abundance over time, in which an increase in prey density is followed by an increase in the numbers of predators, and then the availability of prey decreases, also followed by a decrease in predators. Are predators causing their prey to fluctuate, or are prey responding to some other environmental factor, such as their own food supply? In the second case, prey may be regulated by food, and in turn, may be regulating predators, but not the reverse.

Predators can sometimes determine the number of prey species that can coexist in a habitat. If a predator feeds on a prey species that could outcompete (competitively exclude) other prey species in a habitat, it may free more resources for those other species. This relationship is known as the keystone effect. Empirical studies have indicated that the number of prey species in some communities is directly related to the intensity of predation (numerical and functional responses of predators) such that at low intensity, few species coexist because of competitive exclusion; at intermediate intensity, the diversity of the prey community is greatest; and at high intensity, diversity decreases because overgrazing begins to eliminate species. This intermediate predation hypothesis depends upon competition among prey species, which is not always the case.

Studying Predation

The central question in the study of predation is: To what extend do predators and their prey regulate one another? Most studies suggest that predators are usually food limited, but the extent to which they regulate their prey is uncertain. It is one thing to observe predators in nature and another to assess their importance to the dynamics

In the course of evolution, predatory species must choose whether to expend small amounts of energy to capture large numbers of small prey or to expend a relatively large amount of energy to capture a few large victims, as this lion has done. (Digital Stock)

of natural communities. Like other aspects of ecology, studies of predation can be descriptive, experimental, and/or mathematical.

At the descriptive level, characteristics of both predator and prey populations are assessed: rates of birth and mortality, age structure, environmental requirements, and behavioral traits. Qualitative and quantitative information of this type is necessary before predictions can be made about the interactions between predator and prey populations. General lack of such information in natural ecosystems is largely responsible for failures at biological control of pests and management of exploited populations.

Experimental studies of predation involve manipulation of predator and/or prey populations. A powerful method of testing the importance of predation is to exclude a predator from portions of its accustomed habitat, leaving other portions intact as experimental controls. In one such experiment, excluding starfish from marine intertidal communities of sessile invertebrates resulted in domination by mussels and exclusion of barnacles and other attached species; in the absence of the predator, one prey species was capable of competitively excluding others. This keystone effect depends upon two factors—that the prey assemblage structure is determined by competition and that the predator preferentially feeds on the species that is the best competitor in the assemblage. Clearly, not all food webs are likely to be structured in this way.

Another method of experimental manipulation is to enhance the numbers of predators in a community. For complex natural communities, both additions and exclusions of predators have revealed direct (depression of prey) and indirect (enhancement) effects. Since generalist predators are bitrophic in nature, they may interact with other carnivores in such a way as to enhance the survival of herbivores that normally would fall victim. In one experiment, adding praying mantids to an insect community resulted in a decrease in spiders and a consequent increase in aphids, normally eaten by these spiders. Such results are not uncommon and contribute to the uncertainty of prediction. Mathematical models have been constructed to depict predator-prey interactions in terms of how each population affects the growth of the other. The simplest of these models, known as the Lotka-Volterra model for the mathematicians who developed it, describes a situation in which prey and predator populations are assumed to be mutually regulating. This model, which was developed for a single prey population and single predator species, has been modified by many workers to provide more realism, but it is far from predicting many competitive situations in complex natural communities.

As with the rest of modern ecology, these different approaches must be blended in order to build a robust picture of how important predators are in natural ecosystems. This knowledge would allow more successful prediction of the outcomes of human intervention and more intelligent management of exploited populations. Predation is a key interaction in natural ecosystems; understanding the nature of this interaction is central to any understanding of nature itself.

—*Lawrence E. Hurd*

See also: Altruism; Cannibalism; Carnivores; Communities; Competition; Ecological niches; Ecology; Groups; Herbivores; Herds; Omnivores; Packs; Population fluctuations; Symbiosis; Territoriality and aggression.

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PREGNANCY AND PRENATAL DEVELOPMENT

Types of animal science: Development, reproduction
Fields of study: Developmental biology, embryology, physiology, reproduction science

After conception, the life and normal development of the new individual depend on establishing a mutual relationship with its mother. Both mother and embryo must contribute to the success of the pregnancy.

Principal Terms

CORPUS LUTEUM (pl. CORPORA LUTEA): the structure on the ovary that is formed from the follicle after the egg has been released; it secretes progesterone

EMBRYO: a fertilized egg as it undergoes divisions from one cell to several thousand cells, but before the individual is completely differentiated into a fetus

ESTROGEN: a hormone secreted by the ovary and placenta for development of the uterus

FETUS: a differentiated but undeveloped individual with organ systems usually identifiable as a member of a species

OVARY: the female gonad that is the source of eggs to be fertilized and hormones to maintain pregnancy

OVIDUCT: a narrow, hollow tube which takes the newly ovulated egg from the ovary, provides the site for fertilization, and transports the new embryo to the uterus.

PLACENTA: the tissue providing contact for exchange of nutrients between the lining of the mother's uterus and the blood supply from the fetus

PROGESTERONE: the hormone, essential for maintenance of pregnancy, that is secreted by the corpus luteum

UTERUS: the hollow internal female organ that accommodates the embryo as it grows to term

Gestation is a period of intrauterine development in animals that are "viviparous," meaning "bearing live young." "Pregnant" comes from a Latin word meaning "to possess important contents." Intrauterine development is important for several reasons. The uterus provides a unique environment that not only permits development, but promotes it. A recently fertilized egg has little capability of living if not surrounded by the uterus. The pregnant female sustains a completely undifferentiated single cell in the form of a fertilized egg through the stages of embryonic differentiation to that of a fetus capable of living outside the uterus. Proper temperature is maintained, the necessary fluids and nutrients are provided, wastes are removed, attacks by microorganisms are prevented, oxygen is supplied in a form useful to the embryo, and other compounds essential for cell growth are present. The uterus is normally a safe haven with all the accommodations needed for the new potential animal. Because gestation takes place concealed inside the body, much myth and mystery have arisen over the process. Recent advances have dispelled some of the mystery, but much is still not completely understood. The present knowledge has been obtained from research and observations on laboratory and domestic animals, supplemented by observations on humans. The mechanisms of maintenance of pregnancy, number of young, length of gestation, anatomy of the uterus, and hormones vary considerably between species, thus preventing generalizations that might apply to more than a few species.

The Course of Pregnancy

Pregnancy begins when the recently ovulated egg is fertilized by a sperm in the upper segment of the oviduct. Depending on the species, the fertilized egg resides in the oviduct for forty to one hundred twenty hours before being transported to the uterus. At a particular time during that interval, upon the laying down of certain fundamental tissues, it is referred to as an embryo. The rate of passage is influenced by the concentration of hormones in the mother. Normally, estrogen production from the ovary is great before fertilization, when progesterone is not produced. After ovulation, the corpus luteum forms on the ovary, estrogen declines, and progesterone rises. This sequence permits the embryo to enter the uterus when the uterus is ready to support it. Progesterone will cause the oviduct to relax and allow the embryo to enter the uterus. Administration of large amounts of progesterone by injection will cause the oviduct to relax prematurely, and embryos will enter the uterus in eight or ten hours. High concentrations of estrogen, on the other hand, will cause the embryos to be retained in the oviduct for many days. Estrogen and progesterone also have a profound influence on the nature and function of the lining of the uterus. Estrogen causes rapid growth and, in synergism with progesterone, causes proliferation of glands lining the uterus. These glands secrete a complex of the compounds necessary for embryonic growth and development, called "uterine milk," for the nourishment of the young embryo before it becomes attached to the uterus.

The embryo must in some way make its presence known to the mother's constitution so that the uterus continues to be a hospitable environment for the entire gestation. There are a great variety of ways that have evolved in different species to maintain pregnancy. The act of mating will cause a female rabbit to ovulate and maintain a pseudopregnancy for about eighteen days. Signals from the fetus take over during the next thirteen days to maintain the corpora lutea. If the mating was not a fertile one, the rabbit will mate again about eighteen days after the first mating. Rats normally have recurrent periods of estrus every four or five days. Mating will delay the next estrus for about twelve days. When the mating is fertile, the fetus provides signals for maintenance for the remaining nine days of gestation. Even without mating, dogs will often become pseudopregnant. This pseudopregnancy can extend as long as the normal gestation period of about sixty-five days. In these cases of pseudopregnancy, the hormones present, changes in the uterus, and maternal behavior are very similar to a normal pregnancy that would produce live young.

In many animal species, the interval between ovulations is somewhat prolonged by the spontaneous formation of one or more corpora lutea if there is no pregnancy. Examples are: sheep, seventeen days; horse, pig, goat, cow, twenty-one days; and human, twenty-eight days. In each of these cases, the embryo must signal the mother to establish the pregnancy several days before the next expected ovulation. Embryos of some species produce estrogens that are thought not only to cause uterine growth and enlargement, so as to accommodate the growing fetus, but also to maintain the corpora lutea. In all species, the corpus luteum is necessary to produce progesterone during at least the first one-third of gestation. In the goat, pig, rabbit, and rat, the ovaries and the corpora lutea on them are essential throughout the gestation period. Progesterone is essential throughout gestation in all species, but in the sheep and human, the fetus and placenta supply progesterone for maintenance of pregnancy after about fifty-five days, even when the ovaries are removed. In summary, estrogen and progesterone are both essential for pregnancy for a number of functions. The source of these hormones can be either or both the ovaries and placenta, with variation among species.

The Uterine Environment

Embryos arriving in the uterus must have not only sustenance in the form of an ever-changing, compatible, fluid environment, but also a place and space to develop. In species with only one young born, this may not seem to be a problem, but in litter bearers (with as many as ten per birth), it is important that each embryo have sufficient space. In the pig, the uterus is V-shaped, with the ovaries at the tips. The two uterine horns form the sides of the V, and the body of the uterus and the birth canal consisting of the cervix and vagina are at the bottom. One uterine horn may be as long as 150 to 200 centimeters. The fetuses each occupy a segment of the uterus about 30 centimeters long; thus they are arranged like peas in pods in the two horns. The embryos enter the uterus forty-eight hours after ovulation at the four-cell stage. Embryos cannot move by themselves, so the motility of the uterus helps intrauterine migration. Embryos gradually move down each uterine horn during the period from day two to day nine when they reach the body of the uterus. From day nine to day twelve, some of the embryos continue to move into the other uterine horn. Some embryos arise from one ovary implant in the uterine horn on the side of the ovary of origin while others migrate through the body of the uterus to the other side. Movement stops at day twelve, when the embryos cannot move farther.

During this period of distribution, the embryo is dividing and growing. At day six, the embryo is about thirty-two cells and is still compact, resembling a tiny raspberry or morula about two hundred microns in diameter. The embryo forms a hollow ball of cells called a blastocyst, at days seven and eight. Some of the cells of the blastocyst are destined to become the new fetus and some will develop into the placenta. At around day twelve, the embryo is twenty to thirty centimeters in length—a very thin, fragile bit of tissue. It is at this stage that each embryo occupies the place and space in the uterus that it will grow within during the remaining 104 days of gestation. At this stage also the embryo histologically signals the mother of its presence so that the pregnancy may continue. The corpora lutea form and produce progesterone for about 14 days after ovulation, regardless of the presence of embryos. There is no need for a signal before day twelve. When embryos are present at day twelve and provide an adequate signal, the corpora lutea persist, maintaining the secretion of progesterone that maintains the pregnancy and prevents recurring ovulation and a new estrus cycle. In the event of an inadequate signal (as the result of no embryos or too few), the corpora lutea regress and a new ovulation occurs.

The pig is unique in that the proportion of the uterus that is occupied determines whether the signal is adequate. If half of the uterus is not occupied by embryos at day thirteen, the signal is inadequate and the corpora lutea will regress, even though there may have been some live embryos in some segment of the uterus. The anatomy of the uterus of the rat and rabbit is such that each horn is entirely separate and embryos cannot migrate between horns. In cows, sheep, and mice, intrauterine migration occurs infrequently. The embryos of the sheep and the cow signal the corpora lutea on the ovaries adjacent to the horns in which they are implanted. If an embryo is removed and placed in the opposite horn, the signal rarely goes from the uterine horn on one side to the ovary on the opposite side. The pregnancy will cease in that case in spite of the presence of an embryo. The uterus of the horse consists primarily of the body with no pronounced horns. Embryos of the horse do not migrate great distances and have only a local effect, influencing only the ovary on one side of the uterus.

The heart of the pig embryos begins to beat at about day sixteen. The uterus begins to expand at day eighteen and by day thirty the fetuses are about two centimeters long. The fetus is now surrounded by a round ball of fluid, the amnion. It will be floating in a zero-gravity environment for the next fifty days. The pig fetus grows roughly two centimeters every ten days until term. The first thirty days of gestation are critical for establishing systems and forming organs. It is during these embryonic stages that the embryo is very sensitive to toxins. The mother, the placenta, and the fetus all strive to protect the developing fetus from the harsh external environment.

Fetal Loss

Not all embryos and fetuses survive to term. For most species, only about 55 percent of the eggs finally end up as live fetuses. There are many potential causes for this prenatal loss. Some eggs are not fertilized because either the sperm or egg is faulty. Because the lives of an unfertilized egg and a sperm are both finite, limited to a matter of hours, the timing of the meeting of the sperm and egg at fertilization must be synchronized precisely, or a nonviable embryo will result. Even if fertilization occurs, the egg or sperm may have inherent chromosomal defects that produce a nonviable embryo. Any disruption of the rate of development of the embryo or in the rate of change in the uterus or composition of uterine milk will cause loss of the embryo. Synchronous, parallel development of mother's uterus and the embryo are absolutely essential for survival of the embryo. Factors such as toxic chemicals, estrogens, and severe dietary changes can greatly affect chances of survival. In some cases, the amounts of progesterone and estrogen and other hormones essential for pregnancy are slightly abnormal. In species that bear large litters, the uterine space available to each fetus is not always equal, with the result that some fetuses do not have sufficient uterine resources for survival. Considering these and other hazards, it is remarkable that the proportion of individuals that are normal at birth is as great as it is.

Not all embryos grow and implant within a few days of entering the uterus. The embryos of badgers, mink, lactating rats, seals, kangaroos, armadillos, and roe deer are among those that have a delayed implantation. The embryo develops to the early blastocyst, stops for several months until uterine conditions are favorable, and then completes the normal development. When a lactating rat with delayed implantation weans the pups, the embryos resume growth. In mink and some other species, the ratio of light to dark each day seems to influence the time of resumption of growth. The knowledge of this phenomenon goes back more than one hundred years, as indicated by the records of roe deer collected by the physician of a noble on a large estate. He had an opportunity to examine the uteri of roe deer killed for meat. He had noted the dates of mating but found no fetuses even after several months. This led to the discovery that the blastocyst's development had been arrested for a prolonged period before resumption.

The Study of Gestation

The accumulation of knowledge on pregnancy and prenatal development has taken place over a long period. From the early superficial, gross observations of dead animals to the recent sophisticated and detailed techniques of observation of both mother and embryo or fetus, methods of exploring the changes that take place have developed. One procedure in current practice has its origin in antiquity. A cesarean section is a surgical procedure in which the fetus is brought out of the uterus through an incision in the abdominal wall and the uterus. (The term derives the name from the belief that Julius Caesar was delivered by that procedure.) Currently, embryos can be removed very early and still survive. The ability to recover embryos and keep them alive outside the body for several days during the first six or seven days after fertilization has been a major step in study of embryos. The culture fluid must have many characteristics similar to uterine milk to be compatible with living embryos. Temperature, the ratio of gases, the osmotic pressure of the fluid, and chemical composition must all be near those of the normal uterine environment. Each component may be modified slightly to achieve optimum livability at different stages of development and in different species. Embryos from several species may now be frozen and preserved for many years. This creates many possibilities for studies but also creates ethical and moral dilemmas.

The transfer of embryos between mothers of the same species has provided a means of separating the maternal genetic influence from the effect of intrauterine environment on the fetus. Embryos from smaller breeds of rabbits grow larger than normal when transferred to a larger breed. Zebra foals have been born to horse mares as the result of transferring zebra embryos to the horse. The use of ultrasound to obtain an image of the fetus, the uterus, and surrounding tissue by noninvasive means has been very helpful. Now it is possible to get a frequent picture of the course of events in the uterus to monitor development of the fetus. Nuclear magnetic resonance imaging can generate a picture of the uterus and contents noninvasively. By nuclear magnetic resonance spectroscopy, chemical reactions can be measured in very small segments of the uterus and placenta. Optical systems inserted into the amniotic cavity with the fetus permit direct visualization of the fetus. Perfection of surgical techniques has permitted insertion of cannulas into blood vessels of experimental fetuses to monitor the concentration of hormones. The development of the brain of fetuses has been measured by use of minute electrodes and cannulas placed in specific points.

The concentration of hormones circulating in the mother and fetus can be measured, often and with great precision and specificity, by radioimmunoassay of very small quantities of blood. These hormones change with different stages of gestation. The normal changes and concentrations have been determined for a wide variety of animals. An interesting aspect of the emerging picture of the various species studied is the great variety of mechanisms by which pregnancy exists. No two species have the same mechanism even though they may appear to be very similar. As this rapidly growing area of knowledge expands, humans will be able to shed light on the inside of the uterus, which has been called one of the darkest places on earth.

Fostering Optimal Pregnancies

Humankind has entered into an era of unprecedented ability to understand the complexities of pregnancy in animals. The efficiency of the animals related to human consumption—in production of food, fiber, recreation, and companionship—depends largely on the efficiency of pregnancy. Among cows, horses, pigs, sheep, and goats, the proportion of mated females that conceive and bear young is less than 100 percent. The proportion of the fertilized eggs that develop into differentiated embryos is less than 100 percent. The proportion of embryos that develop into full-term fetuses born alive is less than 100 percent. Of those fetuses born alive, less than 100 percent survive more than a few days because of problems that had occurred prenatally. As an example, the runt of the litter often cannot compete successfully and perishes. Often, these animals were stunted in the uterus because of inadequate space or other resources, such as energy and gas exchange. Some of the inadequacies of resources may be avoided by proper prenatal care.

Avoiding adverse effects on embryos and fetuses of all species should be humanity's aim; it may be possible to correct both maternal and fetal problems by judicious prenatal monitoring and treatment. A problem anticipated is half-solved. A sheep with twins needs different feeding and management from one with a single lamb. Prenatal monitoring can anticipate a problem, and treatment may prevent it.

—Philip J. Dziuk

See also: Asexual reproduction; Cleavage, gastrulation, and neurulation; Determination and differentiation; Fertilization; Marsupials; Parthenogenesis; Placental mammals; Reproduction; Reproductive system in female mammals; Reproductive system in male mammals.

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PREHISTORIC ANIMALS

Types of animal science: Anatomy, classification, ecology, evolution
Fields of study: Anatomy, evolutionary science, paleontology, zoology

Prehistoric animals are those ancient animals that lived before modern humans described them in writing. The vast majority of prehistoric animals are now extinct.

Principal Terms

ARTHROPODS: the phylum of invertebrate animals having clearly segmented bodies and appendages (legs, antennae, and mouth parts) with many segments and joints

CHORDATES: the phylum of animals that have a stiff, rodlike structure called the notochord running their length; chordates include the boneless fishlike animals similar to amphioxus, as well as fish, amphibians, reptiles, birds, and mammals

EVOLUTION: the science that studies the changes in astronomical bodies, the earth, and living organisms and creates explanations of how changes occur and how entities and events are related

GEOLOGICAL PERIODS: the twelve divisions in successive layers of sedimentary and volcanic rocks, which are differentiated by the distinctive fossils present within each division; because of many recently discovered fossils and careful dating, the beginning and ending dates for these periods tend to vary somewhat among different references

PALEONTOLOGY: the branch of geology that deals with prehistoric forms of life through the study of fossil animals, plants, and microorganisms

The fossil record indicates that eubacteria evolved as long as 3,800 million years ago, whereas a comparison of ribosomal ribonucleic acid (RNA) suggests that cells with nuclei probably diverged from archaebacteria as long as 2,800 million years ago. Although cells with respiratory and photosynthetic organelles (mitochondria and chloroplasts) evolved much later, about 1,500 million years ago, no trace of animals has been found in the fossil record before 1,000 million years ago. The fossil record of microscopic animals is nearly nonexistent between 1,000 and 600 million years ago. All of our knowledge of prehistoric animals comes from the fossil record that formed during the last 600 million years.

Near the end of the Precambrian period (540 million years ago), a few sponges, jellyfish, colonial filter feeders, wormlike animals, early mollusks, and primitive arthropods are found in the fossil record. One or more minor extinction events that eliminated up to 50 percent of all species brought the Precambrian period to an end. Animals whose body plan was based on segmentation quickly diversified into a myriad of forms.

How Did So Many Animals Develop So Quickly?

The Cambrian period (540 to 500 million years ago) is characterized by the "sudden" appearance (in 1 to 10 million years) of a large number of morphologically different animals. One of the most innovative body plans that evolved near the end of the Precambrian period was that associated with the many wormlike animals that developed segmented bodies. Segmentation allowed for rapid evolution of all sorts of animals simply by changing the number of segments, their size and shape, as well as the associated appendages. Evolution of homeotic genes and the genes they regulate altered not only segment number and segment characteristics but also appendages. For example, legs could be easily changed into preening, mating, and sensory appendages. During the Cambrian period, all kinds of marine worms, caterpillar-like animals, arthropods, and chordates made their appearance. Some of these caterpillar-like animals had broad legs (*Aysheaia*) and resembled velvet worms of today, whereas others had long, sharp spikes for legs (*Hallucigenia*) and are unrelated to any other known animals.

Many of the early arthropods vaguely resemble today's sow bugs, shrimp, centipedes, and horseshoe crabs. A very successful group of marine arthropods that superficially resemble sow bugs were the trilobites. A trilobite had a prominent, centrally located, segmented, concave, dorsal ridge running the full length of its body. The trilobites differentiated and evolved for over 300 million years until the few remaining forms went extinct during the Permian-Triassic mass extinction (250 million years ago) that wiped out nearly 90 percent of all species. A trilobite had a head, thorax-abdomen, and tail (pygidium). The segments of the head were fused but the thoracic-abdominal and tail segments were varied. Depending upon the trilobite, thoracic-abdominal segments ranged from nine (low of six) to thirteen (high of twenty-two) in number, whereas tail segments varied from six to sixteen (high of twenty-two). Legs and other specialized appendages protruded ventrally from the segments. Gills were also associated with a number of the segments. Although some of the first trilobites had "eyes," their compound nature is not clear because of their size. Most of the later trilobites developed compound eyes that closely resemble the compound eyes seen in extant insects.

One of the most unusual arthropod-like creatures of the Cambrian period was the enormous predator known as *Anomalocaris*, which ranged up to three feet in length. It had a long, oval, dorsoventrally flattened head with compound eyes on short stalks near the back of the head. Protruding from the ventral region at the front of the head were two grasping feeding appendages that for many years were mistaken for separate shrimplike organisms. Just behind the feeding appendages was a circular mouth resembling a cored pineapple slice. This mouth had been misinterpreted as a jellyfish by early discoverers. Saw-shaped "teeth" lined the inside of the mouth and most likely contracted around animals that were positioned in the mouth by the feeding appendages. A number of fossil trilobites have been found with missing chunks that appear to have been torn away by *Anamalocaris*. No arthropods of today have any sort of mouth like that of *Anamalocaris*. This creature was a specialized swimmer, propelled by winglike flaps that appear to consist of numerous overlapping flaps originating from most of the body segments.

The Evolution of Fish

The oldest fossils of jawless fish, referred to as the Agnatha, are about 470 million years old. The jawless lampreys and hagfish of today are most closely related to the ancient Agnatha of the Ordovician period (500 to 440 million years ago). These prehistoric Agnatha attached to larger animals through their whorls of "teeth" and rasped the flesh of the host. Lamprey teeth are horny, sharp structures devoid of calcium, derived from the skin. Because the teeth contained enamel-like proteins, they are considered to be precursors to modern teeth, which consist of enamel over dentine.

The more advanced Agnatha that developed in the Silurian and Devonian periods did not survive the Devonian-Carboniferous mass extinction. Yet they are important because they suggest when the evolution of mineralized teeth, bone, body armor, eyes, and paired limbs occurred. The jawed fish first evolved in the Devonian period (410 to 360 million years ago) but did not dominate until after the Devonian-Carboniferous mass extinction. The earliest jawed fishes were sharks. The discovery of fossilized shark teeth dated to the Devonian period suggest that they evolved during this period.

The earliest fossil skeletons of sharks discovered to date, however, are from the Carboniferous period (360 to 290 million years ago).

The First Terrestrial Vertebrates

The first land-dwelling vertebrates were amphibians that evolved from freshwater, lobe-finned fishes closely related to *Eusthenopteron*, a crossopterygian that lived midway through the Devonian period (410 to 360 million years ago). Most amphibians are tetrapods that begin life in a watery environment but turn to a terrestrial life as adults. Extant amphibians include frogs, toads, salamanders, and the legless, snakelike caecilians.

An unusual prehistoric amphibian was *Ichthyostega*, a three-foot-long crocodile-like animal that lived somewhere between 350 and 370 million years ago. Its jaws were lined with two rows of teeth. Along the front was a row of large teeth and behind them was a row of densely packed, small, sharp teeth bounded by a couple of very large canine teeth. The skull was similar in some respects to the lobe-finned fish that lived during the Devonian. Its neck was only two to three vertebrae long and the pectoral bones were attached to the skull and backbone by muscle.

External gills were a prominent feature of the juvenile or larva. The adult however, lost the external gills when it underwent metamorphosis and developed primitive lungs. The aquatic juvenile amphibians depended on gills to breath, but when they metamorphosed into terrestrial adults they developed primitive lungs out of part of the swim-bladder. Air was swallowed into the intestine-swim bladder tract. A high concentration of capillaries in the wall of these simple lungs carried oxygen to the heart.

The pelvic bones were attached to the spinal chord through muscles. *Ichthyostega* had a heavy rib cage to support its weight out of water, in contrast to other contemporaneous vertebrates. In general, the early amphibians had very short leg bones compared to the primitive reptiles that evolved from them. *Ichthyostega* had seven digits on both its front and back feet, whereas *Acanthostega* had eight digits. Other ancient amphibians had variations in the number of digits. Living amphibians generally have four to five digits on the front feet and five digits on the back feet. *Ichthyostega*'s diet was mainly fish, but on land it may have consumed arthropods and smaller amphibians.

Mastodonsaurus giganteus, another crocodile-like animal, lived 230 million years ago, during the early Triassic period (250 to 205 million years ago). It was the largest amphibian that ever existed, growing to nearly thirteen feet in length. Like *Ichthyostega*, two rows of pointed teeth lined the jaws of this amphibian, making it a formidable match for the early reptiles.

A small group of amphibians lost their legs and took on the appearance of snakelike animals. Today these legless amphibians are highly segmented, making them look more like giant earth worms than snakes. One of the largest extant caecilians is *Caecilia thompsoni*, which lives in Colombia and grows to a length of five feet.

Reptile Diversity

The first reptiles evolved from amphibians during the early Carboniferous period (360 to 290 million years ago). Early reptile skeletons can be distinguished from amphibian remains by the skull and jaw characteristics, the number of neck vertebrae, the absence of external gills, the length of the leg bones, and the number of foot and toe bones.

Prehistoric amphibians had dorsoventrally flattened skulls and skull bones similar to their crossopterygian fish relatives. Amphibians had no nasal holes in their skulls because they breathed through their gills or through their mouths. Reptiles, however, had anterior nasal openings in the snout. The diapsid reptiles had two additional holes behind the eye openings for muscle attachment, whereas synapsid reptiles had one hole, and anapsid reptiles had none. The early amphibians had necks with two to three vertebrae, whereas reptiles generally had necks with more than six vertebrae. The early amphibians generally had very short front and rear leg bones and feet with six to eight digits, whereas early reptiles had front and rear feet with only five digits. Later amphibians reduced the number of digits to four in the front and five in the rear, similar to what is found in extant frogs. Early amphibians had digits that varied considerably, whereas early reptiles usually had digits with two, three, four, five, and three bones (moving from thumb to little finger).

The evolution of reptiles required the development of a new type of egg. The new egg provided a watery environment in which the embryo and juvenile could develop. An amniotic sac evolved to contain the developing reptile and its watery environment, the yolk sac developed to provide the nutrients needed for growth, and the allantoic sac was acquired to help eliminate wastes. The evolution of a tough, membranous egg covering allowed oxygen and carbon dioxide exchange but prevented water loss. Fish and amphibians have to lay their eggs in water because they never evolved the adaptations needed to lay their eggs on land. Reptiles, dinosaurs, birds, and mammals are all amniotes and can lay their eggs on land because their eggs have amniotic sacs, yolk sacs, or allantoic sacs.

Although amphibians' skin was protected by thick layers of secreted mucous, it was always in danger of drying or burning under the sun if the animal strayed too far from water. Reptiles and dinosaurs evolved thick scales to prevent drying and burning, whereas birds and mammals evolved feathers and hair to protect their skin.

Flying Reptiles

The oldest flying reptiles are dated to the late Triassic period (250 to 205 million years ago). The first of these pterosaurs (flying lizards) had long, thin tails, often more than half the length of their bodies. The wings consisted of a leathery skin that was supported along its anterior margin by the pterosaurs' front legs and a highly elongated fourth digit. Digits one, two, and three were tipped with claws. The wings were attached to the body and hind legs, and the wingspan ranged from one to six feet. Their elongated jaws were lined with numerous sharp teeth that they used to grab surface fish, like some present day birds. In the late Jurassic and Cretaceous period, pterosaurs lost their long tails. Some became quite large. *Pteranodon* had a wingspan of up to twenty-five feet, whereas the largest *Quetzalcoatlus* had a wingspan of nearly forty feet. Toothless *Pteranodon* fished on the move, scooping up surface fish, whereas *Quetzalcoatlus* hunted much like the vultures of today, but swooping down on a dead dinosaur instead of the carcass of a wildebeest. Both these large flying reptiles were consummate soaring reptiles, able to take advantage of the slightest updraft of air because of their long, narrow wings.

Reptiles Returned to the Sea

Some reptiles became adapted to living most of their lives in the sea. *Nothosaurus* lived near the beginning of the Triassic period (250 to 205 million years ago) and grew up to ten feet long. Its neck and tail each accounted for a third of its length. *Nothosaurus* used its legs and webbed feet to swim and to drag itself onto beaches, where it laid its eggs.

By the end of the Triassic period, marine reptiles such as *Liopleurodon* and *Plesiosaurus* had flippers instead of legs and feet. *Liopleurodon* sometimes grew to lengths of seventy-five feet and achieved weights of nearly one hundred tons. It was twenty times heavier than *Tyrannosaurus rex* and had teeth twice as long. Long necks and tails were characteristic of the plesiosaurs, which had anywhere from twenty-eight to seventy neck vertebrae, depending upon the genus. The small mouth and teeth of *Plesiosaurus* were adapted to capturing small fish and squid.

Over a period of millions of years, ichthyosaurs evolved an extremely long, thin snout. The leg bones of these reptiles shortened and the digits were remodeled to form flippers. A dorsal and tail fin appeared. Some of these reptiles have the distinction of having the largest eyes of any animal that ever lived. Fully grown *Temnodontosaurus* had eyes with diameters of nearly eleven inches. (In comparison, adult elephants have eyes that are two inches in diameter, and those of blue whales are six inches wide.) These reptiles became so adapted to their marine lives that they could not return to land to lay eggs. Ichthyosaurs solved the

An Early Chordate Related to the Vertebrate Ancestor

A large number of soft-bodied chordates from the Cambrian period have been studied. *Haikouella* is a 530-million-year-old fishlike animal up to 1.25 inches long. The bulbous head had a ventral mouth cavity surrounded by short tentacles. "Teeth" in the pharyngeal cavity of *Haikouella* represent one of the earliest known biomineralizations in chordates. A single ventral artery and paired dorsal arteries were connected by six branchial arches, each with gill filaments. A heart was located at the end of the ventral aorta, more than a third of the way along the body. The narrow tuberous body was strengthened by a notochord that began less than a third of the way along the body and extended nearly to the tail. A small brain headed the spinal chord, which stretched to the tail just above the notochord. Some of these chordates may have had primitive eyes. A gut ran from the mouth cavity ventrally along the animal to the anus, very near the tail. The dorsal rear two-thirds of the body consisted of a muscular, finlike structure. The vertical muscle groups of this vertical fin allowed the animal to undulate from side to side through its watery environment. The extant lancelet, *Branchiostoma*, appears to be most closely related to *Haikouella*.

problem of producing the next generation by giving birth to live babies. A fossil of *Stenopterygius* illustrates a baby exiting the reptile's birth canal much like the marine mammals of today.

All these marine reptiles had nasal openings and lungs that had to be filled with air from time to time. This need for oxygen required them to surface just like extant marine mammals. Even though the marine reptiles were highly adapted to the sea, none survived the Cretaceous-Tertiary extinction, 65 million years ago.

Dinosaurs

Dinosaurs evolved from reptiles sometime after the Permian extinction, 250 million years ago. Dinosaurs developed legs and a skeleton that supported them from beneath, in contrast to most reptiles, which supported themselves on legs that protruded from the sides of their bodies. Dinosaurs were slow to diversify during the Triassic (250 to 205 million years ago) and early Jurassic (205 to 145 million years ago) periods. Even so, many distinctive animals evolved from four major groups present near the beginning of the Jurassic.

Evolution of animals in the Eurypoda led to tetrapods such as *Stegosaurus*. These huge vegetarians up to thirty feet in length had large, diamond-shaped plates that protected their necks and backs from predators. It is believed that these large dinosaurs were cold-blooded and also used the plates to rapidly cool or heat their bodies.

Animals in the Euornithopoda were mostly tetrapods. *Iguanosaurus* was a large vegetarian with big, hornlike claws on its thumb and toes that ended in "hoofs." *Hadrosaurus* was a large vegetarian with a long, hollow, head crest along the top of its skull that protruded up to 1.5 feet behind the head. *Parasaurolophus* grew up to thirty feet in length and had a head crest over 5 feet long. These animals could blow air through the head crest to create various trumpeting sounds. *Triceratops* was another large vegetarian that grew up to nine feet long. It had a sharp, horny beak, a rhinoceros-like horn above and somewhat posterior to its nostrils, two long horns above its eyes, and a bony neck frill protruding from the back of its skull to protect its neck from predators. *Styracosaurus*, a relative of *Triceratops*, grew to lengths of seventeen feet. A number of smaller horns on either side of two long horns extended the neck frill to make *Styracosaurus* appear larger and to protect its neck.

Certain Sauropoda evolved into some of the largest land animals that ever existed. The vegetarian tetrapods *Titanosaurus* weighed up to seventy tons, while *Supersaurus* ranged up to fifty-five tons, *Brachiosaurus* forty-five tons, and *Seismosaurus* thirty tons. Some scientists argue that these reptiles must have been cold-blooded, because they could not possibly process enough vegetation to maintain a constant temperature. In comparison, warm-blood mammals such as elephants often reach weights of six to eight tons, whereas warm-blooded blue whales may attain weights of up to ninety tons.

Archaeopteryx, the Dinosaur That Flew

Theropod dinosaurs were warm-blooded, bipedal animals that came in a myriad of sizes and superficially resembled *Tyranosaurus rex*. Approximately 155 million years ago, a number of therapod dinosaurs were developing feathered coats. Most of the feathers were similar to down feathers that superficially resemble a tuft of hair. A tuft of hair, however, consists of hairs derived from many hair follicles, whereas a down feather is a single unit in which each hairlike barb attaches to the base of the feather. Some theropod dinosaurs also produced vaned feathers having a distinct shaft and barbs attached along the length of the shaft. Like scales, feathers develop from the differentiation of certain epithelial cells. The earliest stages of feather development resemble the first stages of reptilian scale formation. This suggests that one or more genes evolved that blocked scale development in favor of feather development.

During the late Jurassic period, many of the small, bipedal theropod dinosaurs related to the ancestor of birds evolved long arms, three-fingered hands with claws, fused clavicles (the beginnings of a wishbone), feet with three toes for running, first toes protruding from the back of the foot, and hollow bones.

The first primitive bird, *Archaeopteryx*, is dated to the late Jurassic, about 150 million years ago. Fossil remains suggest that *Archaeopteryx* had primary, secondary, and tertiary flight feathers originating from its palm, forearm, and upper arm, respectively. These flight feathers were covered at their base by other feathers known as main coverts and lesser coverts. The three clawed digits of the hand appear not to have supported primary feathers; instead they protruded three-quarters of the way along the wing.

In modern birds, the palm and first digit bones have fused and greatly diminished so that a single, small thumb bone protrudes near the wrist. This first finger supports feathers that run parallel to the front of the wing. The palm bones associated with the second and third digits have partially fused at their ends to become a bone that roughly resembles a fused miniature radius and ulna. The second digit that supports the primary feathers that extend the wing and compose the wing tip has shortened and thickened. The third finger has been reduced to a single, tiny bone.

Modern flying birds have large, keel-like sterna for attaching the muscles that move the wings up and down. Although *Archaeopteryx* had wings that suggest it was capable of performing intricate maneuvers in flight, its tiny sternum indicates it probably lacked the power to take off from the ground. It probably launched itself by running rapidly until it developed sufficient lift. Its feet are similar to those on fast-running dinosaurs. The first digit is high on the foot, suggesting that *Archaeopteryx* did not depend upon trees or high bushes to launch itself.

Archaeopteryx inherited a long, bony tail from its dinosaur ancestors. The tail supported numerous vaned feathers along its length. In modern birds, the bony tail has been greatly reduced by the loss of numerous segments at the end and the fusion of segments at the base. The short, bony tail in modern birds is called the pygostyle. Most of the tail in modern birds consists of long feathers that extend toward the rear from the pygostyle.

Archaeopteryx also inherited a head that closely resembled that of its dinosaur ancestors. The skull and mandible are light because of cavities in the bones, whereas its elongated snout, not yet a true beak, has a mouth lined with teeth. Although *Archaeopteryx* and many primitive birds of the Cretaceous period did not survive the Cretaceous-Tertiary extinction, 65 million years ago, a few did. These survivors gave rise to the myriad bird species of today.

—Jaime Stanley Colomé

See also: *Allosaurus*; *Apatosaurus*; *Archaeopteryx*; *Brachiosaurus*; Dinosaurs; Evolution: Animal life; Extinction; Fossils; Hadrosaurs; Ichthyosaurs; Mammoths; Neanderthals; Paleoecology; Paleontology; Pterosaurs; Sauropods; Stegosaurs; *Triceratops*; *Tyrannosaurus*; Velociraptors.

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PRIMATES

Type of animal science: Classification
Fields of study: Anthropology, human origins, systematics (taxonomy)

The primates are an order of mammals that includes monkeys, apes, lemurs, tarsiers, and humans. Many primates live in trees and have adaptations which include freely movable limbs, grasping hands and feet with opposable thumbs, reliance on vision, a high degree of intelligence, and complex, learned behavior patterns.

Principal Terms

ARBOREAL: tree-dwelling, or pertaining to life in the trees

BINOCULAR VISION: vision using two eyes at once, with overlapping visual fields

BRACHIATION: a form of locomotion, also called arm-swinging, in which the body is held suspended by the arms from above

CATARRHINI: a primate group including Old World monkeys, apes, and humans, with reduced tails and only two pairs of premolar teeth

CLAVICLE: the collarbone, connecting the top of the breastbone to the shoulder

OPPOSABLE: capable of rotating so that the fingerprint surface of the thumb or big toe approaches the corresponding surfaces of other fingers or toes

PLACENTALS: mammals whose unborn young are nourished within the mothers' uteri

STEREOSCOPIC VISION: vision with good depth perception

VISUAL CORTEX: the part of the cerebral cortex concerned with vision

VISUAL PREDATION: catching prey (such as insects) by sighting them visually, judging their exact position and distance, and pouncing on them

The primates are an order of mammals that includes monkeys, apes, lemurs, tarsiers, and humans. The other primates are thus the nearest relatives to human beings. Anatomically, primates have many similarities to the earliest placental mammals. Primitive features retained by primates, but lost in many other mammals, include five-fingered hands and feet with individually mobile fingers and toes, a collarbone (clavicle), a relatively simple cusp pattern in the molar teeth, and the freedom of movement within the forearm that allows the wrist to rotate without moving the elbow.

Many primates live in trees; those that do not, have anatomical features showing that their ancestors were tree-dwellers. These include features directly concerned with arboreal locomotion, those concerned with vision and intelligence, and those concerned with reproduction. Arboreal locomotion, the ability to climb trees, has many direct consequences in primate anatomy. Most primates, for example, possess long, agile arms and legs. Grasping hands and feet give them the ability to hold objects and to climb by wrapping the fingers around branches. This is different from the many other arboreal animals that dig their claws into the bark. The primate grasp is aided by the development of opposable thumbs and big toes. If a primate grasps an object, the fingerprint surface of the thumb faces the corresponding surfaces of the other fingers. This is possible because the bone supporting the thumb can rotate out of the plane of the other fingers. Most primate thumbs and big toes are opposable; human feet are unusual. Individual mobility of all fingers and toes is a primitive mammalian ability that primates have kept but which many other mammals have lost through evolution. Combined with the grasping ability of hands and feet, this characteristic allows primates to manipulate objects of all sizes rather skillfully.

Primates also have hairless friction-skin on their palms and soles, which are supplied with a series of parallel ridges in complex patterns (fingerprints). These ridges provide a high-friction surface, which helps in grasping objects—or in holding branches without slipping. Claws, which could get in the way and cause injury, have generally been reduced to fingernails that rub against things and thus stay short. The clavicle (collarbone), which strengthens the shoulder region, is present in primitive mammals. Many modern mammals have lost this bone, but in primates, it has been retained and often strengthened.

Primate Vision

Primates are primarily visual animals. Whereas many other animals rely strongly on smell, primates rely on sight, and particularly on color vision. One reason for this visual orientation of primates is that the exact position of the next branch can best be judged visually, and good depth perception is essential for avoiding a fall. Primates often hunt by visual predation, stalking an insect or other small prey, judging its exact position and distance, and then pouncing on it.

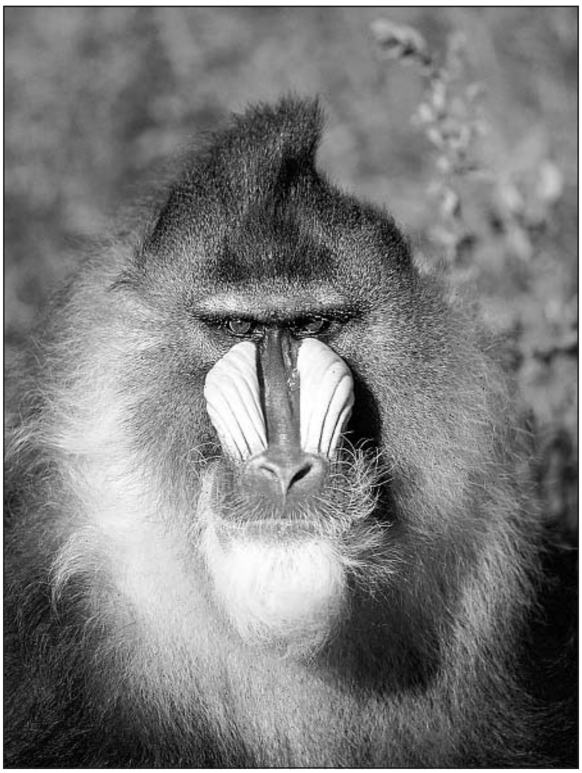
Vision in depth (stereoscopic vision) requires two eyes with overlapping visual fields (binocular vision). Each eye sees the same objects from slightly different angles; the brain combines the two images into a single three-dimensional image. Binocular vision is made possible by the forward position of the eyes. The eyes need protection in this position, and it is furnished in most primates by a bony structure called the postorbital bar. A complex organization of the brain is required for binocular vision. The cerebral cortex of the brain is therefore expanded, especially the part known as the visual cortex. The surface of the brain develops a large number of folds—primate brains are more heavily folded than any others. One characteristic fold is called the calcarine fissure, a characteristic feature of all primates.

Primates can pick up unfamiliar objects with the fingers and bring them in front of the face for closer visual inspection. This behavior requires coordination of eye, brain, and hand in a very complex interaction. It is through this behavior that young primates learn to manipulate and understand their environments and to investigate them with a characteristic curiosity. Primates rely heavily on learned behavior, including exploratory play. Primates are the most intelligent animals, and the great expansion of the cerebral cortex reflects this. Most primates grow up in social groups, where they interact in complex ways with other individuals. They have a curiosity about the world, especially about other primates.

Primate behavior is complex, and most of it is learned. The price paid for reliance on learned behavior is youthful inexperience. Infant primates have much to learn, and they have not yet had much time to learn it; they therefore depend significantly on their parents. A long and extended period of intensive parental care of offspring characterizes nearly all primates. This would not be possible if primates were born in large litters, because their mothers would be too busy caring for so many babies at once. Furthermore, infant primates are carried frequently, placing a burden on their mothers, some of whom need both arms free for climbing. Accordingly, primates are usually born one at a time. Twins and other multiple births are uncommon. There are several related features in primate reproductive systems. Female primates need only one uterus to carry their young and one pair of nipples to nourish them after birth. The right and left uteri, paired in other mammals, are fused into a single uterus called a uterus simplex. Unlike female dogs or pigs, which have many nipples in parallel rows, female primates have only a single pair, located high in the chest region.

Primate Classification

There are many different types of primates and several ways of classifying them. The classification followed here divides primates into the suborders Paromomyiformes, Haplorhini, and Strepsirhini. The suborder Paromomyiformes contains the earliest primates, all now extinct. They lived from about fifty to eighty million years ago (from the Cretaceous period to the Eocene epoch). They are known mostly from fossilized teeth, but the genus *Plesiadapis* is known from nearly complete skeletons. All these primates were small, from roughly the size of a mouse to that of a cat. Their limbs were long and agile, with hands and feet showing the grasping ability typical of arboreal primates. The teeth, which differed among the three families of Paromomyiformes, were modified for a diet of mostly fruits but also some insects. A postorbital bar was not present; the eyes had not yet shifted forward. The visual fields overlapped much less than they do in modern primates, showing that these animals were not efficient visual predators. Some paleontologists have suggested excluding them from the order Primates for this reason.



Primates are visually oriented animals, with forward-facing eyes to optimize binocular vison. (PhotoDisc)

Suborder Haplorhini

The majority of primates belong to the suborder Haplorhini and possess relatively large brains and relatively short faces. The noses of all Haplorhini are dry and have no external connection to the mouth; the upper lip goes straight across the mouth and is not divided by a groove, as it is in the Strepsirhini. The structures of the ear region, the placenta, and certain other anatomical features show that the Haplorhini are closer to the ancestral mammals than are the Strepsirhini. The geologic record of haplorhines extends from the Paleocene to the Recent (or Holocene) epoch.

There are three subgroups of Haplorhini: Tarsioidea, Platyrrhini, and Catarrhini. Of these, the Tarsioidea are the oldest and most primitive. The tarsioids are small primates with rounded heads. The eyes are rotated forward and protected from behind by a postorbital bar; visual fields overlap significantly. Tarsioids flourished during the Eocene epoch, about forty to fifty million years ago. They lived across Europe, Asia, and North America, all of which then had subtropical climates. Tarsioids disappeared from Europe and North America as climates became colder, but they survived in Asia. The living genus *Tarsius* now inhabits the East Indies from Borneo to Celebes. *Tarsius* is a big-eyed, nocturnal primate with an elongated ankle. It has a peculiar form of locomotion called vertical clinging and leaping. It clings to vertical bamboo stalks much of the time, then uses its hind legs to jump to the next perch. At least one extinct tarsioid had similar adaptations.

The Platyrrhini include the South and Central American primates. They are characterized by nostrils that open directly forward, three pairs of premolar teeth, and tails that are strong and sometimes assist in locomotion. Platyrrhines probably evolved from tarsioid primates that reached South America prior to Miocene times. Included in the Platyrrhini are the small forest primates called marmosets (*Callithricidae*). Male marmosets often have striking white or yellowish facial markings (such as tufted ears, eyebrows, and mustaches) which may be useful in mate recognition. The other Platyrrhini are the New World monkeys (*Cebidae*). Familiar ones include squirrel monkeys (*Saimiri*), capuchin monkeys (*Cebus*), and howler monkeys (*Alouatta*). All these monkeys are arboreal, and several of them are skilled acrobats. A few species, including the squirrel monkeys, can hang by their tails.

The Catarrhini include the Old World monkeys, apes, and humans. All Catarrhini are characterized by noses that protrude from the face with the nostrils opening downward, as human noses do. There are only two pairs of premolars. The tails are weak or absent and are useless in locomotion. Two very early catarrhine species occurred in Burma, but they are poorly known and of uncertain relationships. The oldest undoubted Catarrhini occur as fossils in the Fayum deposits of Egypt, which are Oligocene in age—about thirty-five million years old. Fayum primates are thought to be of tarsioid ancestry. One type, *Apidium*, has definite tarsioid resemblances. Other Fayum primates include several small apes, such as an early gibbon, a possible ancestor of Old World monkeys, and *Aegyptopithecus*.

Living Catarrhini include the Old World monkeys, or cercopithecoids, along with apes and humans. Familiar cercopithecoids include baboons (*Papio*), guenons and vervet monkeys (*Cercopithecus*), macaques (*Macaca*), langurs (*Presbytis* and *Pygathrix*), and colobus monkeys (*Colobus*); there are many others. The large and complex social groups of macaques and baboons have been studied repeatedly. There are dominance relationships within these primate societies, but they are usually expressed by gestures and displays instead of by fighting.

The family Pongidae includes the apes. The smaller, more lightly built apes are called gibbons (Hylobates and Symphalangus). These skillful acrobats are often placed in a family by themselves, the Hylobatidae. The more typical "great" apes include the orangutans (*Pongo*) of Asia, the gorillas and chimpanzees (*Pan*) of Africa, and several fossil apes, such as *Dryopithecus*. Modern apes have long arms and shorter legs. They exhibit a variety of locomotor patterns: arm-swinging (brachiation) in gibbons, knuckle-walking in gorillas and chimpanzees, and a four-handed type of clambering in the orangutan.

The family Hominidae includes humans, who walk upright and communicate using language. All living humans belong to the single species *Homo sapiens*.

Suborder Strepsirhini

The Strepsirhini, or Lemuroidea, include lemurs and their relatives. Once thought to be "lower" on the evolutionary scale, the lemuroids are now known to be separately specialized in many ways. Their placentas, for example, are of a peculiar type not found among other primates or among primitive mammals. The ear regions of their skulls show certain anatomical peculiarities; the same is true of the brain and the facial muscles.

All true lemurs live on the island of Madagascar, off the eastern coast of Africa. Most lemurs have the lower front teeth modified to form a comblike structure used in cleaning the fur. Other lemuroids include the small, agile galagos of mainland Africa and four types of slower-moving lorises in Africa and southern Asia. Many fossil lemuroids are known from the Eocene epoch.

Genetic Comparisons

For many years, the classification of primates was based largely on anatomy, physiology, and paleontology. Now, however, the molecular structure of proteins and other types of biochemical evidence are used to make additional comparisons. Closely related primates have proteins with similar or identical sequences. For the most part, family trees based on protein sequences confirm the traditional classifications, with some exceptions; the separateness of gibbons from other apes is based largely on such biochemical evidence.

Geneticists have compared the chromosome sequences of humans and apes. They have found that the sequences of banding patterns in chimpanzee and gorilla chromosomes are nearly identical and that fewer than twenty chromosomal inversions (end-to-end changes) separate chimpanzees and humans.

Types of Primate Study

Primates are studied by different specialists, each using different methodologies. Primate anatomists and functional morphologists dissect primates and compare their structures to those of other species. Morphologists may also take numerous measurements and analyze the results statistically, often with the aid of a computer.

Primate ethologists and sociobiologists study the behavior of living primates, both in the field and in the laboratory. Field studies have been conducted among the chimpanzees in the Gombe Stream Reserve in Tanzania, the rhesus macaques of India, the Japanese macaques of Japan, the howler monkeys of Barro Colorado Island in the Panama Canal Zone, and the baboons of the East African savannas. Studies have confirmed that these primates have diverse locomotor patterns, varied diets, and complex and flexible social organizations that help them find food, avoid predators, and survive under difficult circumstances.

Molecular biologists and geneticists analyze the structures of important proteins and of deoxyribonucleic acid (DNA). This information provides important evidence of the relatedness of one group of primates to another. It was through such studies that molecular biologists were able to show that chimpanzees and gorillas are nearly identical, that humans are very closely related to these African apes, and that the gibbons of Asia are much more distantly related. In general, the findings of molecular biology and genetics have tended to confirm the earlier findings based on comparative anatomy and paleontology, but with occasional exceptions.

Observations on living species are supplemented by studies of fossil primates. Paleontologists are always trying to connect living and extinct species into common family trees. Some molecular biologists have made estimates, based on biochemical differences, of the time of evolutionary divergence between apes (Pongidae) and humans (Hominidae). These estimates are somewhat controversial because they place the hominid-pongid split at less than five million years ago—in contrast to earlier estimates of ten million years or more made by paleontologists in the 1960's. Reinterpretations of the fossil primate *Ramapithecus* and other fossils from Asia support the biochemists' view that the hominid-pongid split took place less than five million years ago.

Many scientists with other fields of interest use nonhuman primates as experimental subjects for medical or biochemical research, including cancer research, space exploration, and the testing of new drugs. These scientists also make important additions to knowledge of how similar these primates are to humans. In particular, monkeys and apes are subject to nearly all the same diseases as are humans. Many drugs and surgical procedures designed to aid in the fight against these diseases are first tested in monkeys or apes because the physiological responses of these primates to the drugs or other medical procedures are nearly always the same as they are in humans. One case of particular importance is acquired immunodeficiency syndrome (AIDS). This disease, which attacks the immune system, does not occur in rats and mice, but it does occur in monkeys and apes. For these reasons, monkeys and apes are used extensively in tests on the AIDS virus and on possible treatments or cures for this disease.

Humans and Other Primates

Since the nonhuman primates are *Homo sapiens*' closest relatives, most studies of primates involve inevitable comparisons with humans. Most of the knowledge that is gained in studying the primates helps scientists understand the human species better. Primates, especially macaques, are commonly used in medical and behavioral research. New drugs, for example, are often tested in monkeys because the physiological reactions of these primates are likely to be more similar to those of humans than would be the case in rats or mice.

Chimpanzees are used when an even closer approximation to human anatomy or human intelligence is important to the experiment. From the use of these and other primates in medical research, knowledge of human health and human diseases has been greatly enhanced.

Scientific understanding of human behavior and other aspects of human biology is similarly enhanced by studies of other primates. Studies of sign language among apes, for example, have greatly increased the understanding of human language and the ways in which it is learned. Both gorillas and chimpanzees have successfully been taught American Sign Language (ASL), a gesture-language commonly used by deaf people. Many researchers who have worked with these apes believe that they show true language skills in their use of ASL, although some linguists disagree. Apes who use sign language can converse about past, present, and future events, faraway places, hypothetical ("what if?") situations, pictures in books, and individual preferences. These apes apparently can use language to lie, to play games or make puns, or to create definitions, such as "a banana is a long yellow fruit that tastes better than grapes."

Studies on the social organization of baboons, langurs, and other nonhuman primates have greatly increased understanding of how human social organization might have originated. Most nonhuman primates have social groups based on friendships and dominance relationships. Larger and stronger individuals tend to get their way more often, but usually by gesturing or threatening rather than by actually fighting. Even this observation, however, must be qualified, because encounters involving three or more individuals are generally very complex, and less dominant individuals can often manipulate these complex situations to their advantage.

—Eli C. Minkoff

See also: Apes to hominids; Baboons; Chimpanzees; Evolution: Historical perspective; Gorillas; Hominids; *Homo sapiens* and the diversification of humans; Human evolution analysis; Lemurs; Mammalian social systems; Mammals; Monkeys; Neanderthals; Orangutans.

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PROTOZOA

Type of animal science: Classification
Fields of study: Cell biology, evolutionary science, pathology, systematics (taxonomy)

The protozoa are a heterogeneous group of organisms the only common characteristic of which is that they are all unicellular. Otherwise, they are extremely diverse in their structures and habits: Some are animal-like and others plantlike; some are free-living, while others are parasitic and cause pernicious diseases.

Principal Terms

AUTOTROPH: any organism capable of synthesizing its own food by using either solar or chemical energy

CILIATE: a protozoan that uses short, hairlike structures called cilia for locomotion

FLAGELLATE: a protozoan that uses long, whiplike structures called flagella for locomotion

HETEROTROPH: any organism that must consume other organisms or organic substances to obtain nutrition

NUCLEUS: a cellular organelle that coordinates the cell's activities and contains the genetic information

ORGANELLE: any of several structures found inside an individual cell, analogous to the organs of multicellular organisms

PHAGOCYTOSIS: obtaining food by engulfing it

PSEUDOPODS: cytoplasmic extensions of a protozoan's body, used for locomotion and the engulfing of food

UNICELLULAR: consisting of only one cell

The protozoa are a vast assemblage of extremely diverse organisms whose only common characteristic is that they are all unicellular. They were previously classified as members of the animal kingdom but are now recognized as a distinct group and occupy a kingdom of their own, Protista.

Protozoa have been known only since the seventeenth century, when Dutch naturalist Antoni van Leeuwenhoek observed them with simple microscopes of his own making. Leeuwenhoek's discovery was accidental; he was simply curious about the microscopic nature of such common substances as rainwater and scrapings from his mouth and teeth. His observations of small, active creatures associated with these substances were the first recorded descriptions of microscopic life. Although Leeuwenhoek made no effort to classify protozoa (which he called "little beasties"), his observations were later confirmed by scientists who recognized the importance of his discoveries.

Protozoan Diversity

The diversity of protozoan types cannot be overemphasized. Though some have a close evolutionary relationship, others have followed very different paths. Some protozoa are animal-like, obtaining energy by consuming food from external sources, and others resemble plants in that they contain chlorophyll and use the energy of the sun to manufacture food.

Protozoa occur in salt water and freshwater, in the soil, and inside larger organisms. In short, they are wherever moisture is present. Most are motile, although some are sessile (attached), and others, like volvox, form colonies. The great majority of protozoa are microscopic, although the very largest are just visible to the naked eye. The blood parasite *Anaplasma* is only one-sixth to one-tenth the size of a human red blood cell, while the ciliate *Spirostomum* (a freshwater protozoan that uses tiny hairlike cilia for locomotion) is up to three millimeters long and can be seen without a microscope.

An individual protozoan, because it consists of only one cell, does not contain any organs. Instead, it harbors analogous structures called organelles, which enable it to carry out its life functions. Central among these organelles is the nucleus, which contains the genes and serves as a sort of control center for cell activities. The cells of protozoa contain from one to many nuclei, depending on the species. Other organelles that distinguish the protozoa are those used for locomotion. These include whiplike flagella, hairlike cilia, and flowing extensions of the cell called pseudopodia, or false feet, which are generated in the direction of movement. Locomotory organelles are important in the classification of the protozoa. Many protozoa, especially freshwater species, possess an organelle called the contractile vacuole, which serves to pump excess water out of the cell. This organelle is especially important in freshwater protozoa, which tend to accumulate water by osmosis because their bodies contain more dissolved substances than the water in which they live. As water flows into these protozoa, the contractile vacuole absorbs it, expands, and finally contracts to flush the water through the cell membrane and into the surrounding environment.

Protozoa can be divided into two groups based on how they get their food: autotrophic and heterotrophic. Autotrophic protozoa contain chlorophyll and are able to convert solar energy into usable energy. The freshwater *Euglena* are autotrophs. Heterotrophic protozoa must capture their food, either funneling it through mouthlike openings or, like the amoeba, engulfing food particles with their pseudopods. This latter method of obtaining food is called phagocytosis.

Gas exchange in protozoa occurs through simple diffusion of gases across the cell membrane. Some protozoa live in environments such as stagnant water or the guts of animals where little oxygen is present. These protozoa are called facultative anaerobes, which means they can live with or without oxygen.

Protozoan Reproduction

Most protozoa reproduce asexually: a single parent produces offspring that are identical genetic copies of itself. Asexual reproduction in protozoa is accomplished in two ways, through fission and budding. In fission, the parent cell simply divides into two offspring cells of equal size. In budding, the offspring is a smaller cell that grows off the larger parent cell. Some protozoa carry out sexual reproduction, in which two parent cells release smaller sex cells called gametes. Two gametes fuse and grow into a new protozoan that is genetically different from either parent.

Conjugation is an interesting process that occurs in ciliate protozoa and may be linked to the reproductive process. It involves the temporary linking of two cells, followed by an exchange of nuclei, after which the cells separate. However, no offspring are formed. It is thought that conjugation is a means of renewing the nuclei of certain protozoa so that they may continue to reproduce asexually. Another process that many protozoa undergo is called encystment, in which the protozoa secrete a thickened sheath around themselves and enter a period of dormancy. Encystment enables protozoa to survive adverse environmental conditions such as drought or cold. When conditions become favorable again, the protozoa emerge from their cysts and resume their normal activities.

Protozoan Phyla

The kingdom Protista is subdivided into five groups, or phyla: Mastigophora, Sarcodia, Sporozoa, Cnidospora, and Ciliophora. The phylum Mastigophora contains the flagellates: protozoa that move by means of one or more whiplike flagella. The mastigophorans are of two types: phytoflagellates, which contain chlorophyll and are primarily autotrophic; and zooflagellates, which are primarily heterotrophic. Many zooflagellates are parasites of insects and vertebrates. The flagellates of the phylum Mastigophora show such a high degree of structural diversity that it is impossible to describe a typical representative. However, among the more interesting of the phylum members are the dinoflagellates, which occur in both marine and freshwater environments. They have two flagella, one of which points away from the cell and the other of which lies transversely around the cell. Many dinoflagellates contain a golden-brown photosynthetic pigment called xanthophyll and are therefore autotrophic, but others are unpigmented and are heterotrophic. These protozoa are encased in a cellulose sheath, or pellicle, which is often highly ornamented with spikes, hooks, or other prominences. Certain marine species are responsible for red tides, a population explosion that is responsible for massive fish kills and causes paralytic poisoning in humans who consume shellfish taken from red tide waters.

The protozoa in the phylum Sarcodina move about and engulf their food by means of pseudopodia. Amoebas belong to this phylum, as well as many marine, freshwater, and terrestrial species. The members of this phylum are the simplest protozoa and have few organelles. Some have exquisitely crafted external skeletons. The radiolarians, which are restricted to the marine environment, have beautifully sculptured exoskeletons made of silicon dioxide or strontium sulfate. The skeleton is riddled with tiny pores through which the living organism within is able to extrude thin filaments of cytoplasm for purposes of feeding, locomotion, and anchorage. Radiolarians exist in great numbers in the surface waters of the ocean and, upon dying, sink to the bottom where in some areas their skeletons form a large proportion of ocean bottom sediments.

Two phyla are closely related: the Sporozoa and Cnidospora. These are parasitic protozoa collectively referred to as sporozoans because some members of both groups go through sporelike infective stages. The phylum Sporozoa contains parasites that infect cells of the intestine and blood and are responsible for causing malaria in humans. These sporozoans belong to the genus *Plasmodium*, a group containing more than fifty species, four of which infect humans. All require a mosquito for transmission of the disease-causing protozoan. When the mosquito bites a person, the parasite is introduced into the blood with the saliva of the insect. From the blood, the protozoan travels to the individual's liver, where it reproduces, then escapes to invade red blood cells. Once in the red blood cells, it consumes hemoglobin, reproduces, and escapes to invade additional red blood cells. This cycle of invasion and escape is responsible for the debilitating chills and fever characteristic of malaria. The phylum Cnidospora contains amoeboid parasites of fishes and insects. This phylum's members are separated from those in Sporozoa based on differences in the nature of the infective spores.

The largest phylum is Ciliophora, which has more than eight thousand species. Of all the phyla, this one has the most homogeneous members as far as their evolutionary relationships are concerned. They all appear to have arisen from a common ancestor. Members of this phylum are commonly referred to as ciliates because they use cilia for locomotion and for sweeping food particles into the cytostome (cell mouth). They are also characterized by the presence of two nuclei, a small micronucleus and a larger macronucleus whose sole purpose is the synthesis of deoxyribonucleic acid (DNA, the genetic material). Although some ciliophorans are sessile, or attached, many are nimble, quick, and carnivorous and are therefore perhaps the most animal-like of all the protozoa. They reproduce either asexually by fission or through sexual conjugation, but they never release free gametes into the surrounding environment. Ciliophorans are common in fresh and salt water. Some are parasitic.

Protozoology

Although Antoni van Leeuwenhoek had little sense of what he was looking at when he first observed protozoa in the seventeenth century, he used the same tool that later scientists did, the microscope. Protozoology—the study of organisms too small to be observed with the naked eye—has become an area of specialization within microbiology.

Protozoa are best examined while alive, as specimens that have been killed, fixed, and stained often become distorted. Some of the smaller species can be viewed under the cover slip of a microscope slide; others, especially the larger specimens, must be viewed under less restrictive conditions: in a petri dish with a dissecting microscope or under a raised cover slip with corners that have been supported with paraffin or some other material.

One of the challenges of studying protozoa with the microscope is the speed with which they move and the tedium of keeping track of them by constantly adjusting the position of the slide. For this reason, a solution of methyl cellulose is often added to the slide preparation to increase the viscosity of the water and slow down the organisms.

As many protozoa are almost transparent, it is necessary to highlight their features by using dyes or stains that will not kill them. Such substances, called vital stains, render various structures in the protozoa visible under the microscope. For example, the vital stain janus green b selectively stains mitochondria, the energy-producing organelles, while neutral red has an affinity for vacuoles, the organelles that contain engulfed food particles. In studying protozoan structure, scientists use an assortment of vital stains and regular stains, which are used when protozoa are killed and preserved on a slide. Electron microscopy, used to examine the extremely fine structure of protozoa, has special stains and fixatives of its own for maintaining the structure of these organisms under the sustained electron bombardment required to illuminate the specimen.

Protozoa are ideal subjects of study for cytologists, geneticists, and developmental biologists because they reproduce asexually and therefore provide the researcher with an endless succession of clones, or genetically identical individuals. Scientists can subject these clones to various environmental conditions and observe the effects in their offspring.

The primary method of maintaining protozoa in a laboratory is a culture, which usually consists of one species of protozoa and the bacterium on which it feeds. The object is to exclude other organisms that might harm the protozoan. As toxic waste products build up in the culture dish, a small number of protozoa are transferred to a clean culture medium. This procedure is called subculturing and continues as long as the culture is maintained. There are two types of cultures: monoxenic and axenic. In monoxenic cultures, a single species of protozoa is maintained with a single species of bacteria. In axenic cultures, a single species of protozoa lives in isolation from any other organisms. The axenic culture is of value in certain types of nutritional studies.

Parasitic protozoa can be examined separate from their hosts in a laboratory but only when kept under conditions that provide them with a chemical and physical environment that will keep them alive for as long as necessary. For example, some parasitic protozoa of warm-blooded animals must be kept in a warm culture medium to prevent their being distorted by cooling.

The Base of the Food Chain

Protozoa are of first and foremost importance to ecology. These organisms make up the lowest links of the food chain that eventually leads to humans. Autotrophic protozoa are called producers because, like plants, they are able to use the energy of sunlight to manufacture food substances. Other protozoa are heterotrophs, or consumers, and must take food from their environments. Dinoflagellates are a group of autotrophs with a notorious role in the marine environment. These organisms, which are responsible for red tides, can pass their potent toxins up the food chain to cause paralytic shellfish poisoning in humans. The toxic materials they release into the ocean during periods of intense reproductive activity also lead to massive fish kills, which mean losses for the fishing industry.

Foraminifers are a type of shelled amoeba in the phylum Sarcodina. Some foraminifers existed millions of years ago, when the earth's fossil fuel deposits were being generated. Therefore, the presence of their fossil remains in drill cores helps indicate where oil is likely to be found.

An interesting relationship exists between protozoa and termites. Cellulolytic (cellulose-breaking) protozoa inhabit the guts of termites and are the organisms actually responsible for digestion of the wood that termites eat. Without these protozoa, the termites would not be able to feed on wood and would no longer be able to damage homes and other structures.

Protozoan Infections

In people, protozoa cause numerous infections, generally limited to four sites in the body: the intestines, the genital tract, the bloodstream and tissues, and the central nervous system (brain and spinal cord). Not all parasitic protozoa cause death in humans, but they are responsible for untold misery in wide areas of the world, especially underdeveloped countries where preventive medicine is unknown and too expensive for these societies to employ.

The two most common protozoan infections are malaria and amoebic dysentery. The malarial parasite is transmitted through the bite of the *Anopheles* mosquito and eventually destroys the body's red blood cells, causing anemia and recurrent debilitating chills and fever. Malaria is a major health problem in parts of Africa, Asia, and Central and South America. More than one hundred million people are afflicted at any given time, and about one million die of the disease each year. Amoebic dysentery flourishes in overcrowded, unsanitary conditions. The disease gradually erodes the inner lining of the intestines, causing ulcers. Amoebic dysentery is entirely avoidable when food and water are handled carefully to prevent their contamination or are purified if contamination is suspected.

Other protozoa of medical importance are *Trichomonas vaginalis*, which parasitizes the genital tract; *Giardia lamblia*, a parasite of the small intestine; and *Toxoplasma gondii*, which infects the fetus and can cause congenital abnormalities.

Protozoa play an important role in the degradation of both human and industrial wastes in the environment. In sewage treatment, for example, anaerobic protozoa (those that flourish in the absence of oxygen) and bacteria play a role in the degradation of raw sewage. After they have done their work, the effluent is passed to a set of tanks with aerobic (oxygen-requiring) protozoa for further processing. Autotrophic protozoa have been used to deal with industrial wastes containing high levels of nitrates and phosphates. The settling tanks are illuminated to promote the growth of the autotrophs, which absorb and metabolize the industrial chemicals as part of their normal life processes.

—Robert T. Klose

See also: Deep-sea animals; Ecosystems; Food chains and food webs; Histology; Marine animals; Marine biology.

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PTEROSAURS

Type of animal science: Classification
Fields of study: Evolutionary science, paleontology, physiology

Pterosaurs were the flying reptiles of the Mesozoic. Pterosaurs are part of the group Archosauria, and the first of only three vertebrate groups to have evolved active flight. Pterosaurs were contemporaries of the Mesozoic dinosaurs, and quite closely related to them.

Principal Terms

ARCHOSAURS: diapsid reptiles whose skeletal evolution distinguishes them from the diapsid lepidosaurs

MESOZOIC ERA: the middle era of the Phanerozoic eon, 250 million to 65 million years ago

PATAGIUM: a soft, flexible membrane

Pterosaurs ("winged reptiles") were flying reptiles of the Mesozoic Era, and the first of only three vertebrate groups known to have evolved active flight. Pterosaurs first appear in the paleontological record about 225 million years ago, during the late Triassic Period, and persist to the terminal Cretaceous extinction event, about 65 million years ago. Pterosaurs are recognized as being members of the group Archosauria, a group including thecodonts, crocodiles, birds, and dinosaurs. While pterosaurs were contemporaries to the great Mesozoic dinosaurs, and often confused with them, pterosaurs were not dinosaurs.

The origin of pterosaurs is a subject of great debate. Pterosaurs share some physical characteristics in the hips and legs with early dinosaurs. It has also been suggested they could run bipedally and took to the air by the energy-consuming method of running and flapping their wings. Another view suggests pterosaurs pursued a tree-dwelling way of life, and developed parachuting, gliding, and eventually flight as an energy-saving byproduct of their lifestyle. Another debate surrounds whether pterosaurs were warm-blooded or cold-blooded creatures. Some fossil remains suggest certain pterosaurs may have been covered with short, thin fur, or even very fine feathers. This, combined with the energy-consuming activity of flying, leads many researchers to favor warm-blooded pterosaurs.

The first pterosaur fossils were discovered in the Solnhofen Limestone Formation in Germany, in 1784. Pterosaur fossils range in size from those of *Pterodactylus*, whose forty-centimeter wingspan was about that of a modern song bird, to *Quetzalcoatlus*, whose fifteen-meter wingspan was as big as a modern private aircraft wing. Pterosaurs had light, bony skeletons made of hollow, tubular bones, and compact bodies to improve wing support. The pelvis and hind limbs were small, yet long and slender when compared to the fore limbs and shoulders. The fore limbs were exaggerated in comparison to the hind limbs, with their great length derived from the extended fourth finger, which alone supported the flight patagium. The pterosaur patagium was a soft membrane thought to have been tougher and thicker than a bat's wing, and divided into three anatomical segments. One short segment stretched from the torso to the elbow end of the humerus; a second, longer segment stretched from the radius and ulna and the bones of the wrist and palm; and the third, longest segment was an elongated fourth finger supporting the wing membrane to its tip. The segments of the wing were progressively longer as they got farther from the trunk. The first, second, and third fingers were not involved in membrane support

Image Not Available

but were free to grasp and cling; there was no fifth finger. This "finger-wing" configuration is quite different from the wing support structure seen in bats and birds.

Types of Pterosaurs

Pterosaurs are generally divided into two groups: The rhamphorhynchoids first appear during the Triassic, and the pterodactyloids appear some 108 million years later. The Rhamphorhynchoidea had teeth, long tails, short metacarpals, long fifth toes, and a head held in front of and slightly above the torso. The Pterodactyloidea had no tail or fifth toe, an elongated metacarpus forming the largest support structure of its wing, a more "birdlike" neck posture with the neck curving in an S-shape entering the cranium from below rather than from behind, holding the head higher above the torso, and many had evolved toothless beaks. Pterodactyloidea, such as *Pteranodon*, also evolved extreme head crests, and like many later pterosaurs, lacked well- developed teeth. Many other pterosaur fossils exhibit well-developed and specialized teeth: *Eudimorphodon* and *Dorygnathus* had teeth designed to spear and hold prey; *Dsungaripterus* had bony jaws and broad, flattened teeth to winkle out shellfish and snails; and *Pterodaustro* had a comblike array of teeth, ideal for sieving plankton.

The majority of pterosaur bones have been recovered from marine sedimentary rock deposits, suggesting these flying reptiles took advantage of the atmospheric updraft conditions of gentle and constant breezes along shorelines, as well as the abundant food of the marine environment. Pterosaur aerodynamics and flight characteristics have been studied in great detail, and they suggest pterosaurs were active, wing-flapping fliers, but also better gliders than are most modern bird species. Pterosaur anatomy suggests they were able to glide and soar over great distances and for extended periods of time under calm conditions, but that they were not well adapted for staying aloft under turbulent conditions. It is estimated that the pterosaur *Pteranodon*, who represents one of the high points in pterosaur evolution with a wingspan of over seven meters, could soar at speeds in excess of 30 kilometers per hour, continue gliding aloft for nearly twenty hours, and possibly cover distances of over 750 kilometers without landing.

The greatest number of pterosaur bones have been recovered from the Kansas marine chalk deposits of North America. Over eight hundred skeletal fragments have been found there. While many of the remains suggest these Kansas pterosaurs died nonviolently, other bones suggest the pterosaurs were eaten by marine reptiles. Apparently, pterosaurs swooping low to snatch prey from the ocean's surface were often in turn preyed upon by larger marine reptiles or sharks.

—Randall L. Milstein

See also: *Allosaurus*; *Apatosaurus*; *Archaeopteryx*; Dinosaurs; Evolution: Animal life; Extinction; Fossils; Hadrosaurs; Ichthyosaurs; Paleoecology; Paleontology; Prehistoric animals; Sauropods; Stegosaurs; *Triceratops*; *Tyrannosaurus*; Velociraptors.

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PUNCTUATED EQUILIBRIUM AND CONTINUOUS EVOLUTION

Type of animal science: Evolution
Fields of study: Evolutionary science, genetics, systematics (taxonomy)

According to classical evolutionary theory, new species arise by gradual transformation of ancestral ones. Speciation theory of the 1950's and 1960's, however, predicted that new species arise from small populations isolated from the main population, where they diverge rapidly. In 1972, Niles Eldredge and Stephen Jay Gould applied this concept to the fossil record, predicting that species should arise suddenly ("punctuated" by a speciation event) rather than gradually, and then persist virtually unchanged for millions of years in "equilibrium" before becoming extinct or speciating again.

Principal Terms

ALLOPATRIC: populations of organisms living in different places and separated by a barrier that prevents interbreeding

GRADUALISM: the idea that transformation from ancestor to descendant species is a process spanning millions of years

MACROEVOLUTION: large-scale evolutionary processes that result in major changes in organisms

MICROEVOLUTION: small-scale evolutionary processes resulting from gradual substitution of genes and resulting in very subtle changes in organisms

SPECIATION: the process by which new species arise from old species

SPECIES SELECTION: a higher level of selection above that of natural selection is postulated to take place on the species level

STASIS: the long-term stability and lack of change in fossil species, often spanning millions of years of geologic time

SYMPATRIC: populations of organisms living in the same place, not separated by a barrier that would prevent interbreeding

Although Charles Darwin's most influential work was entitled *On the Origin of Species* (1859), in fact it did not address the problem in the title. Darwin was concerned with showing that evolution had occurred and that species could change, but he did not deal with the problem of how new species formed. For nearly a century, no other biologists addressed this problem either. Darwin (and many of his successors) believed that species formed by gradual transformation of existing ancestral species, and this viewpoint (known as gradualism) was deeply entrenched in the biology and paleontology books for a century. In this view, species are not real entities but merely arbitrary segments of continuously evolving lineages that are always in the process of change through time. Paleontologists tried to document examples of this kind of gradual evolution in fossils, but remarkably few examples were found.

The Allopatric Speciation Model

By the 1950's and 1960's, however, systematists (led by Ernst Mayr) began to study species in the wild and therefore saw them in a different light. They noticed that most species do not gradually transform into new ones in the wild but instead have fairly sharp boundaries. These limits are established by their ability and willingness to interbreed with each other. Those individuals that can interbreed are members of the same species, and those that cannot are of different species. When a population is divided and separated so that formerly interbreeding individuals develop differences that prevent interbreeding, then a new species is formed. Mayr showed that, in nature, large populations of individuals living together (sympatric conditions) interbreed freely, so that evolutionary novelties are swamped out and new species cannot arise. When a large population becomes split by some sort of barrier so that there are two different populations (allopatric conditions), however, the smaller populations become isolated and prevented from interbreeding with the main population. If these allopatric, isolated populations have some sort of unusual gene, their numbers may be small enough that this gene can spread through the whole population in a few generations, giving rise to a new species. Then, when the isolated population is reintroduced to the main population, it has developed a barrier to interbreeding, and a new species becomes established. This concept is known as the allopatric speciation model.

The allopatric speciation model was well known and accepted by most biologists by the 1960's. It predicted that species arise in a few generations from small populations on the fringe of the range of the species, not in the main body of the population. It also predicted that the new species, once it arises on the periphery, will appear suddenly in the main area as a new species in competition with its ancestor. These models of speciation also treated species as real entities, which recognize one another in nature and are stable over long periods of time once they become established. Yet, these ideas did not penetrate the thought of paleontologists for more than a decade after biologists had accepted them. In 1972, Niles Eldredge and Stephen Jay Gould proposed that the allopatric speciation model would make very different predictions about species in the fossil record than the prevailing dogma that they must change gradually and continuously through time. In their paper, they described a model of "punctuated equilibrium." Species should arise suddenly in the fossil record (punctuation), followed by long periods of no change (equilibrium, or stasis) until they went extinct or speciated again. They challenged paleontologists to examine their biases about the fossil record and to see if in fact most fossils evolved gradually or rapidly, followed by long periods of stasis.

In the years since that paper, hundreds of studies have been done on many different groups of fossil organisms. Although some of the data were inadequate to test the hypotheses, many good studies have shown quite clearly that punctuated equilibrium describes the evolution of many multicellular organisms. The few exceptions are in the gradual evolution of size (which was specifically exempted by Eldredge and Gould) and in unicellular organisms, which have both sexual and asexual modes of reproduction. Many of the classic studies of gradualism in oysters, heart urchins, horses, and even humans have even been shown to support a model of stasis punctuated by rapid change. The model is still controversial, however, and there are still many who dispute both the model and the data that support it.

Implications of Punctuated Equilibrium

One of the more surprising implications of the model is that long periods of stasis are not predicted by classical evolutionary theory. In neo-Darwinian theory, species are highly flexible, capable of changing in response to environmental changes. Yet, the fossil record clearly shows that most species persist unchanged for millions of years, even when other evidence clearly shows climatic changes taking place. Instead of passively changing in response to the environment, most species stubbornly persist unchanged until they either go extinct, disappear locally, or change rapidly to some new species. They are not infinitely flexible, and no adequate mechanism has yet been proposed to explain the ability of species to maintain themselves in homeostasis in spite of environmental changes and apparent strong natural selection. Naturally, this idea intrigues paleontologists, since it suggests processes that can only be observed in the fossil record and were not predicted from studies of living organisms.

The punctuated equilibrium model has led to even more interesting ideas. If species are real, stable entities that form by speciation events and split into multiple lineages, then multiple species will be formed and compete with one another. Perhaps some species have properties (such as the ability to speciate rapidly, disperse widely, or survive extinction events) that give them advantages over other species. In this case, there might be competition and selection between species, which was called species selection by Steven Stanley in 1975. Some evolutionary biologists are convinced that species selection is a fundamentally different process from that of simple natural selection that operates on individuals. In species selection, the fundamental unit is the species; in natural selection, the fundamental unit is the individual. In species selection, new diversity is created by speciation and pruned by extinction; in natural selection, new diversity is created by mutation and eliminated by death of individuals. There are many other such parallels, but many evolutionary biologists believe that the processes are distinct. Indeed, since species are composed of populations of individuals, species selection operates on a higher level than natural selection.

If species selection is a valid description of processes occurring in nature, then it may be one of the most important elements of evolution. Most evolutionary studies in the past have concentrated on small-scale, or microevolutionary, change, such as the gradual, minute changes in fruit flies or bacteria after generations of breeding. Many evolutionary biologists are convinced, however, that microevolutionary processes are insufficient to explain the large-scale, or macroevolutionary, processes in the evolution of entirely new body plans, such as birds evolving from dinosaurs. In other words, traditional neo-Darwinism says that all evolution is merely microevolution on a larger scale, whereas some evolutionary biologists consider some changes too large for microevolution. They require different kinds of processes for macroevolution to take place. If there is a difference between natural selection (a microevolutionary process) and species selection (a macroevolutionary process), then species selection might be a mechanism for the large-scale changes in the earth's history, such as great adaptive radiations or mass extinctions. Naturally, such radical ideas are still controversial, but they are taken seriously by a growing number of paleontologists and evolutionary biologists. If they are supported by further research, then there may be some radical changes in evolutionary biology.

Patterns of Evolution

Determining patterns of evolution requires a very careful, detailed study of the fossil record. To establish whether organisms evolve in a punctuated or gradual mode, many criteria must be met. The taxonomy of the fossils must be well understood, and there must be large enough samples at many successive stratigraphic levels. To estimate the time spanned by the study, there must be some form of dating that allows the numerical age of each sample to be estimated. It is also important to have multiple sequences of these fossils in a number of different areas to rule out the effects of migration of different animals across a given study area. Once the appropriate samples have been selected, then the investigator should measure as many different features as possible. Too many studies in the past have looked at only one feature and therefore established very little. In particular, changes in size alone are not sufficient to establish gradualism, since these phenomena can be explained by many other means. Finally, many studies in the past have failed because they picked one particular lineage or group and selectively ignored all the rest of the fossils in a given area. The question is no longer whether one or more cases of gradualism or punctuation occurs (they both do) but which is predominant among all the organisms in a given study area. Thus, the best studies look at the entire assemblage of fossils in a given area over a long stratigraphic interval before they try to answer the question of which tempo and mode of evolution are prevalent.

Since the 1940's, evolutionary biology has been dominated by the neo-Darwinian synthesis of genetics, systematics, and paleontology. In more recent years, many of the accepted neo-Darwinian mechanisms of evolution have been challenged from many sides. Punctuated equilibrium and species selection represent the challenge of the fossil record to neo-Darwinian gradualism and overemphasis on the power of natural selection. If fossils show rapid change and long-term stasis over millions of years, then there is no currently understood evolutionary mechanism for this sort of stability in the face of environmental selection. A more general theory of evolution may be called for, and, in more recent years, paleontologists, molecular biologists, and systematists have all been indicating that such a radical rethinking of evolutionary biology is on the way.

—Donald R. Prothero

See also: Evolution: Animal life; Evolution: Historical perspective; Convergent and divergent evolution; Extinction; Gene flow; Isolating mechanisms in evolution; Natural selection.

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RABBITS, HARES, AND PIKAS

Type of animal science: Classification
Fields of study: Anatomy, ecology, evolutionary science, physiology, reproduction science, systematics, wildlife ecology, zoology

At least eighty species of rabbits, hares, and pikas have been identified in the order Lagomorpha. Lagomorphs constitute approximately 2 percent of the known four thousand mammalian species.

Principal Terms

ALTRICIAL: born naked, with eyes and ears closed for several days (rabbits)
DIGITIGRADE: walking on toes
FENESTRATION: a latticework of openings on the sides of the skull
PRECOCIAL: born fully haired, with functional eyes and ears (hares)
RUDIMENTARY: short or small

Lagomorphs have two families: Leporidae (rabbits and hares) and Ochotonidae (pikas). Lagomorphs range in size from pikas, which are six inches in length and 3.5 ounces in weight, to hares which are almost twenty-eight inches in length and 10 pounds in weight. Most lagomorphs have coats that are brownish or reddish brown above and lighter brown to white below. There are color differences according to species, location, and season. Lagomorphs are well adapted to a herbivorous diet. Rabbits and hares are not known to store food, while pikas not only store food but also dry or cure vegetation for winter. Rabbits and pikas burrow or inhabit abandoned burrows, and hares shelter in natural depressions.

Physical Characteristics of Rabbits, Hares, and Pikas

Lagomorph incisor teeth are long and grow throughout life. They are extremely effective for severing plant stems and for gnawing on bark. Behind the long incisors is a tiny peglike incisor. There are no canine teeth. Cheek teeth, located further back in the jaw, also grow throughout the animal's life, wearing away as they grind abrasive vegetation. The upper tooth rows are more widely separated than the lower rows, and chewing is done with a transverse movement. Vegetation

Lagomorphs have fused bones in their hind limbs that allow them to hop with great rapidity. (Corbis) passes through the small intestine, which has a spiral valve, providing greater surface area for digestion. A large cecum is located at the point of attachment of the large intestine, which contains bacteria that aid in digestion. Lagomorphs have the ability to produce two types of fecal material, one that is wet and eaten again for further nutrient absorption, and one that is dry and discarded.

The bones of the hind limb are fused where they move against the calcaneuni, resulting in increased leverage in locomotion. Lagomorphs are digitigrade, with five digits on the forefoot and five on the hind foot.

Rabbits and hares have a rudimentary tail, while pikas have none at all. Folds of skin on the lips can meet behind the incisors so that gnawing can take place with the mouth cavity closed. Other flaps of skin are able to close the nostrils. The skull is peculiarly fenestrated. The ears are usually long. The testes are located in front of the penis rather than behind.

Rabbits and hares usually vocalize only when frightened or injured. Pikas express themselves with a whistle or bark and a chattering call.

Lagomorphs can yield two or more litters during each breeding season, with two or three litters common among hares and pikas and three to six among rabbits. Litter size ranges between two and eight. Young rabbits are altricial and are cared for in a nest. Hares are born in the open and are precocial, able to run soon after birth.

Destructive and Beneficial Lagomorphs

Lagomorphs can be vectors for disease, as well as pests to human agriculturists. Rabbits eat flowers and vegetables in spring and summer, causing problems in flowerbeds, gardens, and fields. In the fall and winter, they may damage and kill valuable woody plants. Lagomorphs are the dietary staple of many carnivorous mammals and birds, among them wolves, foxes, bobcats, weasels, predatory hawks, and owls. They are therefore an important link in the food chain.

—*Jason A. Hubbart*

See also: Home building; Mammals; Reproductive strategies; Teeth.

Rabbit, Hare, and Pika Facts

Classification:
Kingdom: Animalia
Subkingdom: Deuterostomia
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Subclass: Eutheria
Order: Lagomorpha
Family: Leporidae (hares and rabbits), Ochotonidae (pikas)
Genera: Bunolagus (bushman hares), *Caprolagus* (hispid hares), *Lepus* (hares, twenty-one species), *Oryctolagus* (European rabbits), *Nesolagus* (Sumatran hares), *Pentalagus* (amami rabbits), *Poelagus* (Bunyoro rabbits), *Pronolagus* (red rock hares, three species), *Romerolagus* (volcano rabbits), *Sylvilagus* (cottontails, thirteen species); *Ochontona* (pikas, fourteen species)

Geographical location: All continents except Australia and Antarctica; absent from southern South America and most islands; especially diverse in North America and Eurasia, the only continents where pikas are found

Habitat: Range from tropical forest to arctic tundra

Gestational period: Rabbits, approximately twenty-eight days; hares, up to forty-seven days; pikas, approximately thirty days

Life span: In the wild, rarely more than nine months; up to fifteen years in captivity

Special anatomy: Flaps of skin able to close the nostrils; peculiarly fenestrated skull; long incisors that grow throughout life; generally long hind feet, with the hind legs strong and positioned for leaping; usually long ears; testes located in front of the penis rather than behind; lagomorphs produce two types of fecal material, one that is wet and eaten again for further nutrient absorption and one that is dry and discarded

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RACCOONS AND RELATED MAMMALS

Types of animal science: Anatomy, classification, reproduction
Fields of study: Anatomy, zoology

The raccoon family—raccoons, coatimundis, kinkajous, and pandas—are agile arboreal mammals. Most are nocturnal omnivores.

Principal Terms

ARBOREAL: living in trees
CARRION: dead animals
DIURNAL: active during the day
GESTATION: duration of pregnancy
NOCTURNAL: active at night
OMNIVORE: an animal that eats plant and animal foods
PREHENSILE: able to grip things
SOLITARY: living alone

The raccoon family, Procyonidae, includes raccoons, coatimundis, kinkajous, and red pandas. (Giant pandas are part of the bear family, rather than the raccoon family.) All are arboreal. Except for pandas, found in the southeastern Himalayas at elevations up to twelve thousand feet, procyonids occur only in the New World. Most are mammals living in the lower elevations of temperate and tropical regions, in areas rich in water and trees.

Procyonids are omnivores, eating insects, crayfish, crabs, fishes, amphibians, reptiles, birds, small mammals, nuts, fruits, roots, and young plants. Procyonids eat what is available, including carrion, depending on season, locale, and availability. Red pandas eat bamboo, honey, grass, vines, other plants, and some meat.

The raccoon family is nocturnal, except coatis and red pandas. They mate at different times of the year. Gestation is about three months. Life spans of procyonids are up to thirty years in captivity but only ten years in the wild.


Raccoons have distinctive facial markings that look like masks. (Corbis)

Raccoons

All members of the raccoon family have small bodies, long tails, ringed tails, and facial markings. Kinkajous lack markings, but have prehensile tails that aid arboreal movement. Raccoons are carnivores of the genus *Procyon*. They are common throughout the United States and also inhabit southern Canada, Central America, and South America. They are foxlike in appearance, with a broad head, a pointy muzzle, and short, erect ears. Raccoons have long fur and bushy tails. They are gray to brown above and lighter beneath. Black cheek patches and white whiskers adorn their heads. Their tails are marked with dark rings. Each paw has five toes, and most raccoons are about 3.5 feet long, including a 1-foot tail. The crab-eating raccoon, a species of Central and South America, is larger than common raccoons and has dark gray fur with yellow patches.

Common U.S. raccoons inhabit trees near ponds and streams, or near human homes. They hunt at night for poultry, rodents, bird eggs, insects, fish, frogs, carrion, nuts, and fruit. Those that live near human habitations are particularly fond of scavenging in garbage cans and raiding bird feeders. In northern areas, raccoons winter in dens, rarely emerging. Males are solitary except for mating, while females and young live in groups. Raccoons mate in winter. The following spring, they give birth to up to six young, born in tree dens. Young raccoons depend on their mothers for five months. Mothers and offspring stay together for a year.

Raccoon Family Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Carnivora
Family: Procyonidae (raccoons and related animals)
Genus and species: Ailurus fulgens (lesser or red panda); *Procyon lotor* (common raccoon), *P. cancrivorous* (crab-eating raccoon), *P. insularis* (Tres Marías raccoon), *P. gloveranni* (Barbados raccoon), *P. pygmaeus* (Cozumel Island raccoon), *P. minor* (Guadalupe raccoon); *Nasua nasua* (ringtailed coatimundi), *N. narica* (white-nosed coati), *N. nelsoni* (island coati); *Nasuella olivacea* (mountain coati)

Geographical location: North, Central, and South America, and the Himalayas

Habitat: Mostly lower elevations of temperate and tropical regions, in areas well supplied with water and trees, although some inhabit mountains twelve thousand feet high

Gestational period: Raccoons, 2 months; coatis, 2.5 months; red pandas, 3 months

Life span: Ten to thirty years, depending on species

Special anatomy: Dexterous five-toed front paws; sixth, thumblike toe; prehensile tail

Coatimundis

Coatimundis inhabit South American lowland forests and grasslands, and dry, high-altitude forests. They have long, furry, ringed tails, are fine climbers, and live in trees and on the ground. Unlike most Procyonidae, they are diumal. Their bodies look like those of other raccoons, and their front limbs have long claws. Males grow to 4 feet long and weigh fourteen pounds, while females are 3.5 feet long and weigh ten pounds. They are a yellow-red color on their bodies, while their faces are black, with white spots around each eye and on each cheek. Their throats and bellies are also white. Coatis eat insects and other arthropods, crabs, frogs, lizards, mice, and reptile eggs.

Adult males are solitary but females and young live in bands of up to twelve members. Mating occurs in February or March, when a visiting male impregnates each adult female in a band. Gestation is 2.5 months, and about a month before birthing, each female leaves the band and builds a tree nest. There, she gives birth to up to five babies, each weighing six ounces. Babies are nestbound for six weeks. Then mother and young rejoin the band. Life spans of coatis are seven to nine years in the wild and up to fourteen years in captivity.

—Sanford S. Singer

See also: Fauna: North America; Fauna: South America; Omnivores; Pandas; Urban and suburban wildlife.

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RAIN FORESTS

Types of animal science: Ecology, geography
Fields of study: Conservation biology, ecology, environmental science

A forest growing in a region that receives over one hundred inches of rain annually is considered to be a rain forest. Rain forests can be found in both tropical and temperate climates, and are noted for their remarkable biodiversity. Thousands of different animal and plant species can be found within only an acre or two of a rain forest.

Principal Terms

HERBIVOROUS: a plant-eating animal

TEMPERATE ZONE: the regions of the earth north of the Tropic of Cancer but south of the Arctic Circle, or south of the Tropic of Capricorn but north of the Antarctic Circle

TOLERANCE: ability of a tree to grow in the shade of other trees

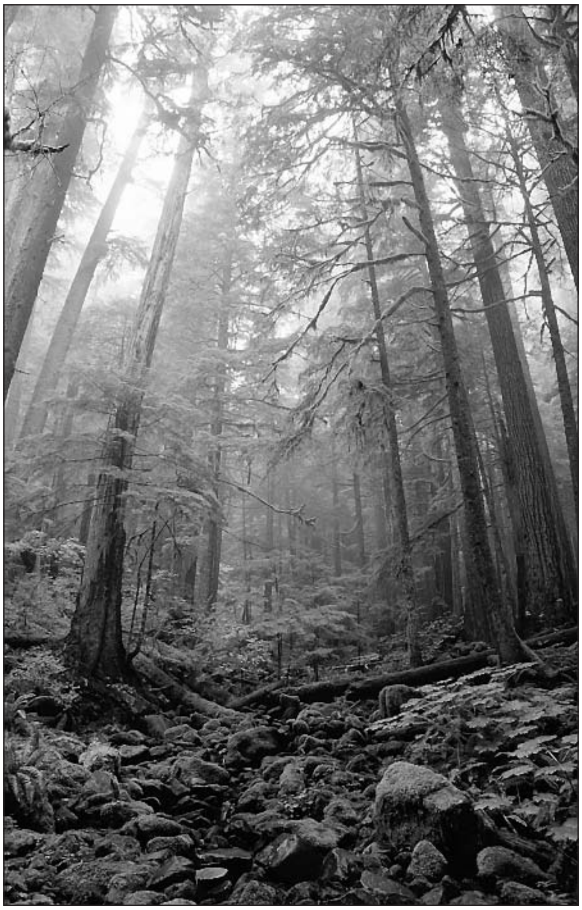
TROPICS: the region of the earth lying between the Tropic of Cancer and the Tropic of Capricorn

Rain forests are forests found in regions of the world that receive large amounts of precipitation annually. Rain forests present an incredibly diverse range of habitats, as they exist both at low elevations and high in mountain ranges. Many unusual and seldom-seen creatures inhabit the world's rain forests, including spiders so large they eat small birds, and colorful but highly poisonous tree frogs. The enigmatic sloth, an animal that spends its entire life hanging upside down from tree limbs and moving so slowly that moss grows on its fur, is found in the rain forests of South America.

Although tropical rain forests such as those in the Amazon River drainage system of South America are perhaps the best known, rain forests do exist in temperate regions as well. Olympic National Park in the state of Washington preserves a temperate climate rain forest, while much of the coast of British Columbia and southeastern Alaska also receives well over one hundred inches of rain annually. The primary difference between temperate and tropical rain forests is that in a temperate rain forest, often one or two species of trees will become dominant. In the coniferous rain forest of the Pacific Northwest, for example, Douglas fir and western red cedar are the dominant species, while other trees are found in much smaller numbers. In a tropical rain forest, in contrast, several hundred species of trees may grow side by side within a very small geographic area. The majority of trees found in tropical rain forests tend to be broad-leaved, such as the rubber tree, while temperate rain forests are dominated by conifers. The leaves of many plants in rain forests have a waxy texture or come to a point to help shed water more quickly and prevent the growth of fungi or mold.

Characteristics of Rain Forests

Although rain forests are remarkably diverse, they do share a few characteristics in common. The abundant moisture in a rain forest gives the woodland a lush, fertile appearance. This is particularly true in tropical regions. Even in the understory, close to ground level where light is limited, vegetation may be dense. This appearance of fertility is often deceptive. Dead plant matter decays rapidly in a tropical forest, but the nutrients are used quickly by the numerous competing plants. In addition, the trees in tropical forests are evergreen, which means the litter that does fall to the forest floor does so irregularly, unlike temperate broadleaf forests, where trees lose



The rain forests of the Pacific Northwest are largely composed of coniferous trees. (Corbis)

their leaves annually as the seasons change. Leaves will remain indefinitely on tropical species, such as fig and rubber trees, which is one reason small specimens of these trees are popular as houseplants. As a consequence of this lack of mulch, topsoil is often thin and the root systems of the trees are quite shallow.

One reason tropical rain forests are evergreen is that in the tropics there is little seasonal variation in the hours of daylight. The closer to the equator a forest lies, the less change there is from season to season. In temperate climates, many plants have evolved to bloom, set seeds, or lose their leaves based on the number of hours of sunlight available each day. As the seasons change annually, plants bloom in the spring or early summer; fruit ripens in the fall, photosynthesis slows, and leaves change color and die. In the tropics, where the number of hours of daily sunlight never varies, plants follow a different schedule. Many tropical plants bear new flowers and mature fruit simultaneously. The evergreen foliage and continuous supply of certain fruits has led to the adaptation of some animals to a very restricted diet: koalas, for example, which feed exclusively on eucalyptus leaves, or parakeets that eat only figs. Exceptions to this pattern are the forests where rainfall is seasonal, such as regions of the world like southeast Asia, where much of the rain comes in the form of annual monsoon storms. In those cases, flowering and setting fruit will coincide with the seasonal rains.

Forest Zones

A rain forest can be divided into four zones, each of which has its own distinct characteristics. The lowest level, the forest floor, is often dark and gloomy. Little sunlight penetrates to this level, and there is little air movement. Numerous insects, such as beetles, cockroaches, and termites, live in the decaying litter and provide food for larger animals and birds. Many of the insects, birds, reptiles, and amphibians that live in the lower levels of the rain forest are brightly colored. Scientists speculate that the animals have evolved in this fashion to more easily attract potential mates. Other scientists believe that colors warn potential predators to stay away. In either case, the vivid colors make the animals more easily seen in what is otherwise a dark environment.

Just above the forest floor is the understory. Many of the plants in the understory have large, dark leaves to maximize their light-collecting ability. Because there is little natural air movement within the lower levels of a rain forest due to the canopy blocking any natural breezes, the flowering plants in the understory often have strongly scented or vividly colored flowers to help attract insects or birds to assist with pollination. Lizards, snakes, amphibians such as tree frogs and salamanders, small birds, and mammals as large as the jaguar all call the understory home. The plants found only in the understory seldom exceed fifteen to twenty feet in height. The coffee shrub is an example of a small, shade-tolerant, tropical tree. Until horticulturalists developed strains of coffee for use in plantations where the coffee bushes are the only plants grown, coffee grew naturally in the understory of tropical forests.

The densest layer of plant life is the canopy. High above the rain forest floor, the branches of mature trees form a dense intertwined zone of vegetation extending up as much as 150 feet above the ground. Numerous plants sprout in the crotches of trees, where debris may collect. Tree limbs are festooned with vines and mosses, and bromeliads and orchids grow on the rough bark of tree trunks. Even other trees may start their life cycles a hundred feet above the ground: The strangler figs of Borneo are a relatively shade-intolerant species. A fig seed that lands and sprouts on the ground will probably not survive due to low light levels on the forest floor. Strangler figs have adapted so that their seedlings do best high in the canopy. The figs begin life in the crotches of other trees. The roots of a young fig will gradually creep down the trunk of the tree on which it sprouted. Over time, the strangler fig's roots will completely encircle the host tree, as well as penetrating the forest floor. The fig thrives, but the host tree dies, choked off by the strangler fig. Primates such as gibbons, orangutans, and lemurs spend much of their lives in the canopy, feeding on the fruit of trees such as the strangler fig, as do the sloth and other herbivorous mammals.

The emergent layer of the rain forest consists of the tallest trees, some of which exceed two hundred feet in height. The tops of these trees provide a habitat for large, predatory birds, such as eagles, as well as being home to assorted snakes, monkeys, and other animals. Every layer of the rain forest teems with life, and often what can be found at ground level gives no hint of the diversity that exists two hundred feet above in the tree tops.

Rain Forest Conservation

Many of the trees found in rain forests are valued for their commercial use as lumber, while others have been exploited for their fruits or other products, causing much habitat loss. Tropical hardwoods, such as teak and mahogany, for example, have long been used in construction and in furniture. Teak resists rotting and as a result is often used for products that are going to be exposed to the weather, such as garden furniture. Due to teak's desirability as lumber, timber companies are increasingly planting it in plantations for a sustainable yield rather than relying solely on natural forests as a source.

Activists hoping to preserve the tropical rain forest have encouraged indigenous peoples to collect forest products, such as nuts or sap, as a way to create a viable economy while at the same time discouraging industrial clear-cutting of the forest. Native people tap rubber trees in Amazonia, for example, to collect latex. Rubber trees are native to the rain forests of South America, although they are also grown in plantations in other tropical regions of the world, such as Southeast Asia.

The biggest threat to the world's rain forests may not come from commercial logging, however. In many regions of the world, rain forests have fallen victim to population pressures. Forests continue to be clear-cut for agricultural use, even when the farmers and ranchers know the exposed soil's fertility will be quickly exhausted. In some cases, the cleared land becomes an arid wasteland as the tropical sun bakes the soil too hard to absorb rain water. In others, the land is farmed for a year or two and then abandoned. Given enough time, the rain forest may regenerate, but the process will take hundreds of years.

—Nancy Farm Männikkö

See also: Ecosystems; Food chains and food webs; Forests, coniferous; Forests, deciduous; Habitats and biomes; Lakes and rivers; Mountains; Tidepools and beaches.

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REEFS

Type of animal science: Geography
Fields of study: Ecology, invertebrate biology, marine biology, oceanography

Coral reefs are the largest structures constructed by living organisms and have been around for hundreds of millions of years. The importance of these marine habitats extends far beyond their aesthetic beauty.

Principal Terms

- ATOLL: a remnant horseshoe or ring-shaped barrier reef surrounding a sunken island
- BARRIER REEF: a reef that is separated from land by a lagoon
- FRINGING REEF: a reef that is directly adjacent to land, lacking a lagoon
- HERMATYPIC CORAL: reef-building coral species, belonging to the Cnidarian order of Scleractinia
- LAGOON: shallow, sandy, protected areas located behind the reef flat of barrier reefs and atolls
- PATCH REEF: a small, isolated reef that is typically found in lagoons

Reefs are hard, rocky habitats typically found in shallow seas or along coasts. When people speak of reefs, they are typically referring to coral reefs, which are the largest structures ever built by living organisms. Coral reefs have been around for hundreds of millions of years. Hermatypic, or reef-building, corals are small animals that excrete a calcium carbonate shell that forms most of the structure of reefs. Calcareous seaweeds and some other animals also contribute calcium carbonate to reefs. Carbon dioxide is removed from water (and eventually the atmosphere) when reef organisms form calcium carbonate. The formation of calcium carbonate removes seven hundred billion kilograms of carbon every year, which is tied up as rock and not easily released back into the atmosphere. Coral reefs are typically found between thirty degrees north and south latitude in warm, shallow, clear, nutrient-poor seas, where hermatypic corals grow best. Some species of ahermatypic (nonreef building) corals can live outside these latitudes, but their growth rates are too slow to build reef structures.

Rain Forests of the Sea

Coral reefs are beautiful, but they are important for environmental reasons as well. Despite occupying just 0.17 percent of earth's surface, coral reefs house an estimated 5 percent of all known species. Nearly every phylum of organism can be found on coral reefs. This high degree of biodiversity found on coral reefs is why they have been called "the rainforests of the sea."

Most of the species that contribute to the beauty of reefs are poorly studied because of the difficulty of visiting marine habitats. However, with the use of scuba gear, underwater laboratories, and ships, scientists are beginning to explore the rich array of reef organisms. Because predation is so intense on reefs, many reef creatures produce unique chemical defenses. Scientists study these chemicals with hopes of finding ones that can be useful to humans. Compounds with anti-inflammatory, antibiotic, antifungal, and anticancer properties have been isolated from reef organisms and are in various stages of clinical testing. These compounds might also be useful as shark repellents, as antifoulants, or as agrochemicals. Protecting species because they might someday benefit humans is one of many good reasons for the conservation of biodiversity.

Earth's Most Productive Habitats

Coral reefs are one of the few places where animals are more abundant than plants. Despite the lack of conspicuous plants on reefs, these habitats are the most productive places on earth. Their productivity is about twice that of agricultural fields. Single-cell algae called zooxanthellae that live within the tissues of coral animals are responsible for the coral's dark coloration and much of the photosynthesis that contributes to high reef productivity. The relationship between corals and zooxanthellae is mutualistic, meaning both organisms benefit. The zooxanthellae protect corals from ultraviolet (UV) radiation and provide them with energy-rich sugars, while the corals offer zooxanthellae a place to grow and fertilizer from the corals' metabolic wastes.

"Bleaching" is a process by which corals expel their zooxanthellae and take on a white coloration. Coral bleaching has been happening with greater frequency in recent years and may be a signal that environmental changes are harming the health of corals.

Small, inconspicuous seaweeds are responsible for the remainder of reef productivity. The basal portions of these seaweeds are protected from herbivores by being located in the abundant crevices of reefs. As soon as the top portions grow beyond this protective shelter, however, they are rapidly consumed by fishes, sea urchins, or other herbivores. Scientists have counted as many as 150,000 bites per square meter per day being taken out of some areas of reefs. This intense herbivory benefits the reef by maintaining seaweeds in a fast growing state with little seaweed biomass. When herbivores are removed from reefs, the seaweeds grow to large size and smoother the corals within weeks. This problem has been observed on reefs where too many fish have been harvested.

Types of Coral Reefs

Coral reefs are generally grouped into one of four catagories: fringing, barrier, atoll, and patch reef. When coral animals colonize a new volcanic island and form a coral reef along the fringes of that island, it is called a fringing reef. The island slowly sinks into the ocean as it cools, while the reef continues to grow upward through the building activity of the coral animals. After millions of years, the original fringing reef is then located away from the shores of the existing island because the island has, in essence, shrunk. At this point, the reef is considered a barrier reef because there is now a lagoon between the reef and the island. Barrier reefs get their name because they serve as a barrier to waves heading toward land. Eventually, the island will sink completely below the water's surface and the atoll is the ring of reef left behind. This is how atolls form, and because the Indo-Pacific is the oldest ocean, atolls are most common here. If the oceanic island sinks at a rate greater than the reef can grow, then the reef will eventu-

Coral reefs offer habitats for many varieties of marine life. (Digital Stock) ally die as the water becomes too deep and dark to support the hermatypic corals. Scientists have found deep undersea reefs on top of seamounts that apparently grew too slowly to remain near the water surface. Finally, the fourth category of reefs is patch reefs, which are small patches of corals that dot lagoons.

Not all barrier reefs are found off islands. Barrier reefs that grow along continents are the largest reefs, with the Great Barrier Reef along eastern Australia being over two thousand kilometers long and up to seventy kilometers wide. The second largest reef is a barrier reef located off the coast of Belize. These reefs can be used to describe different zones of a reef that one encounters as they move from the sea toward land. Approaching the reef from the sandy ocean floor, the reef slope is the first zone encountered. The reef slope is the steepest part of the reef and can be fifty meters deep. It extends from the base of the reef to the reef crest, located at about five meters depth. Most waves crash near the reef crest, protecting shoreward zones from severe wave energy. The slope of the reef changes drastically at the reef crest, resulting in a gradually sloping zone, a reef flat that extends from the reef crest to the lagoon. Shoreward from the reef flat is a lagoon of shallow, calm water. The bottom of the lagoon is typically covered with fine, white calcium carbonate sand, with an occasional patch reef providing a hard structure for organisms. The lagoon extends to the shore where white beaches usually occur. The calm, crystal clear blue water and white beaches that make these locations popular destinations for tourists are the result of coral reef ecosystems.

—Greg Cronin

See also: Chaparral; Ecosystems; Food chains and food webs; Forests, coniferous; Forests, deciduous; Grasslands and prairies; Habitats and biomes; Lakes and rivers; Marine biology; Mountains; Rain forests; Savannas; Tidepools and beaches; Tundra.

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REFLEXES

Type of animal science: Ethology
Fields of study: Biophysics, neurobiology

Reflexes are simple, unlearned, yet specific behavioral responses to particular stimuli. Virtually all animals, from protozoa to primates, exhibit reflexes.

Principal Terms

AXON: that part of a nerve cell through which impulses travel away from the cell body

EFFECTOR: that part of a nerve which transmits an impulse to an organ of response

FIXED ACTION PATTERN (FAP): a complex motor act involving a specific, temporal sequence of component acts

INTERNEURON: central neurons often interposed between the sensory and motor neurons

MOTOR NEURON: a nerve cell body and its processes which carry impulses from the central nervous system to a muscle, producing motion

NEURONS: the structural and functional units of the nervous system, each consisting of the nerve cell body and all its processes, as the dendrites and axon

RECEPTOR: a nerve ending specialized for the reception of stimuli

REFLEX ARC: the entire nerve path involved in a reflex action

SPINDLE: in a muscle, the bundle of nuclear fibers formed during one stage of mitosis

SYNAPSE: the point of contact between adjacent neurons, where nerve impulses are transmitted from one to the other

That there are immediate motor responses to sensory stimulation is a fact that has been apparent in the thinking and writing of many scholars for centuries. Yet the term "reflex" actually did not appear until the eighteenth century. Georg Prochaska of Vienna, one of the first to use the term (1784), stated that "the reflexion of sensorial into motor impressions . . . takes place in the *sensorium commune* (common sensory center). . . . This reflexion may take place either with consciousness or without."

The word "reflex," then, originates from the idea that nerve impulses are "reflected" in the central nervous system. Current use of the term dates from the earliest experimental investigations of the role of the spinal cord in mediating muscle responses to sensory stimuli. These studies, conducted in the 1820's by Charles Bell in England and François Magendie in France, first established that sensory fibers are contained in the dorsal (upper) roots and motor fibers in the ventral (underside) roots of the spinal cord.

Response to Stimuli

Reflexes are types of action consisting of relatively simple segments of behavior usually occurring as direct and immediate responses to particular stimuli uniquely correlated with them. In addition to other, more complex stimulus-bound responses such as fixed action patterns, reflexes account for many of the behavioral patterns of invertebrates. In higher animals, such as primates, learned behavior dominates; however, reflexes remain a significant component of total behavior.

Reflexes are genetically determined. No effort is needed to acquire reflexes; they simply occur automatically, usually taking place beneath the conscious level. Although heart rate and ventilation rate, for example, are constantly regulated by reflexes, most people are unaware of these modifications. In like manner, pupillary diameter and blood pressure are regulated reflexively, without conscious knowledge. Other reflex responses, however, such as perspiring, shivering, blinking, and maintaining an upright position, are more apparent, although they also occur without conscious intervention.

Only one neuron (or even an absence of neurons) is required for the simplest known reflexes. For example, ciliated protozoa, single-celled animals having no neurons, exhibit what appear to be reflex actions. When a paramecium collides with an object, it reverses the stroke of the cilia (hairlike outgrowths), backs away a short distance, turns, and again moves forward. When touched caudally (at or near the tail), the animal moves forward. In this instance, the animal's cell membrane itself serves as the receptor of the stimulus, and the cilia act as effectors for directed movement. Very simple reflexes also occur in higher animals. For example, when human skin is injured sufficiently to stimulate a single pain neuron, an unknown substance is released, causing small local blood vessels to dilate. In contrast to these simple responses, however, most reflexes require a vast sequence of neurons.

In most reflexes, the neurons involved are connected by specific synapses to form functional units in the nervous system. Such a sequence begins with sensory neurons and ends with effector cells such as skeletal muscles, smooth muscles, and glands, all controlled by motor neurons. Interneurons, or central neurons, are often interposed between the sensory and motor neurons. This sequence of neurons is called a reflex arc. The sensory aspect of the reflex arc conveys specificity regarding the particular reflex to be activated. That is, the sensory cells themselves determine which environmental change is sensed, either inside or outside the body. The remainder of the reflex response is regulated by the specific synaptic connections that lead to the effector neurons.

Types of Reflexes

One visible and familiar reflex is the knee-jerk or stretch reflex. This reflex involves the patellar (kneecap) tendon and a group of upper leg muscles. While other muscle groups exhibit similar reflexes, this one is described here because of its widespread clinical use. This reflex involves a relatively simple reflex arc in which the terminals of the sensory cells synapse directly on the effector neurons. It is thus an example of a monosynaptic reflex. When the patellar tendon is tapped, a brief stretch is imposed on the attached muscles (quadriceps femoris), including the muscle spindles that are embedded within the quadriceps. This stretch causes the sensory neurons of the spindles to fire impulses, which return to the spinal cord. Within the spinal cord, excitatory synapses are then activated on the specific motor neurons supplying the same muscles that were stretched (the quadriceps). A series of impulses occurs in the motor neurons, which activate a brief contraction of the quadriceps, which in turn extends the leg. Another component of this reflex causes the central inhibition of the flexor motor neurons. A possible function of stretch reflexes is to oppose sudden changes in the length of skeletal muscle.

The stretch reflex, as well as other more complex reflexes, involves the inhibition of antagonistic muscle groups. This activity requires the activation of inhibitory interneurons in the spinal cord, which synapse upon the motor neurons of antagonistic muscles. In other complex reflexes, there is a sweep of activity to higher and lower levels of the spinal cord and to the opposite side of the body. Examples of reflexes with these characteristics include the flexor reflex and accompanying crossed extensor reflex. These reflexes are commonly initiated by a painful stimulus. The returning sensory signals excite the motor neurons of the leg flexor muscles, which inhibit those of the leg extensor muscles on the same side as the stimulus. This behavior assures that the foot is quickly removed from the harmful stimulus. Balance, however, must also be maintained, which is accomplished by exciting the leg extensors of the opposite limb—thus the term "crossed extensor reflex." The flexor reflex is a prime example of a protective response, and it takes place so rapidly that the pain is felt only after the withdrawal response is complete. Speed of response is particularly important when the severity of the injury is time-dependent, such as in response to a chemical exposure or burn.

Many thousands of neurons are usually involved in flexor and extensor responses. From only a few to many sensory neurons may activate several hundred to several thousand motor neurons, depending upon the reflex involved. Each motor neuron, in turn, branches to synapse on as many as a thousand muscle cells. In addition, in reflexes with bilateral effects, another thousand or more interneurons may become involved.

The Functions of Reflexes

The functions of reflexes are numerous and varied. As previously mentioned, reflexes adjust many important biological functions rapidly and efficiently without conscious effort, while other reflexes are largely protective. For example, the eye and the ear, the most delicate and sensitive sensory systems, can be damaged or destroyed by overstimulation or by accident. The amount of light admitted to the retina is controlled by the pupillary reflex, which in humans can effect a change in pupillary diameter from approximately eight millimeters in darkness to two millimeters in bright light. A sudden flash of intense light, for example, can evoke the reflex closing of the eyelids, further protecting the delicate retina. The eyeball itself is protected from drying by the blink reflex and from mechanical injury by the eyelid closure reflex. The latter reflex is triggered when an object approaches the eye or when the lashes or cornea are touched. The ear is also protected from potentially damaging sounds through the reflex contraction of middle-ear muscles in response to loud noise. This reflex functions to lower the efficiency with which sound vibrations are transmitted through the bones of the middle ear and thus reduces the possibility of damage to the delicate hair cell receptor of the inner ear.

Another category of protective reflexes exhibited by many animals is stereotyped escape responses. For example, a startled squid takes evasive action by contracting its mantle muscles (the membranous flap or folds of the body wall), forcing a jet of water through its siphon. Fish respond to vibrations carried through water by contracting the muscles on one side of their bodies; the reflex contraction occurs on the side opposite the source of vibration, and the result is a sudden move away from potential danger.

Equally essential for survival are the numerous feeding reflexes exhibited by animals. For example, flies as well as many other insects possess chemoreceptors located on their feet, mouth parts, and antennae. Thus, when a hungry fly walks on a surface moistened with nutrients, a set of reflexes is triggered. A reflex extension of the proboscis occurs. If the proboscis receptors are favorably stimulated, then the animal begins to drink. Drinking continues until the crop is sufficiently distended to stimulate its stretch receptors. Finally, this stimulus initiates the reflex termination of feeding.

Instinctive or innate behaviors, such as courtship rituals, nest-building, aggression, and territorial behaviors, demonstrate many similarities to reflexes. Although generally more complex, they are, like reflexes, unlearned, species-specific, genetically determined, and stereotypic in nature. Importantly, fixed action patterns such as these are similar to reflexes in that they are initiated by a specific stimulus, called a sign stimulus or a releaser. Generally, both forms of behavior are also comparable in that they are thought to be controlled by specific sets of neurons that underlie each behavior. Like the more complex learned behaviors, however, the neural basis of instinctive behaviors remains largely unknown.

Modification of Response

Normally, the degree of reflexive response depends upon the intensity of the stimulus; many reflexes tend to weaken gradually if the stimulus is applied repeatedly. This phenomenon, termed habituation, allows an animal to ignore a familiar or repeated stimulus. If a strong, unexpected stimulus is introduced along with a reflex-evoking stimulus, however, the strength of the reflex is often enhanced. This process, called sensitization, causes the animal to detect a potentially threatening situation by responding forcefully to its environmental cues.

Similarly, reflexes may be modified by classic (Pavlovian) conditioning, a form of associative learning. For example, in dogs, the sight and smell of food causes the reflexive secretion of saliva. A light or the sound of a bell does not. Ivan Pavlov (1849-1936) demonstrated that linking the sight and smell of food (unconditioned stimuli) with a light or bell caused the animal to associate the light or bell with food. Thus, after several training sessions, introduction of the light or bell alone produced salivation. Whether classical conditioning contributes to a significant portion of learned behavior is still a controversial issue.

Finally, reflexes are often modified during voluntary movement or locomotion. Motion itself stimulates many sensory receptors and often elicits reflexes that oppose the intended movement. Such reflexes are thought to be overridden or suppressed by commands from the brain in order for the desired movements to be executed.

Early Reflex Studies

Seventeenth century French philosopher, mathematician, and scientist René Descartes (1596-1650) combined the physiological discoveries of Galen (a Greek physician of the second century C.E.) with a conception of the body as a machine to provide the first notion of reflex action. Descartes thought that within a nerve there were thin threads attached at one end to the sense organs. External stimuli pulled on the threads to open small gates to the ventricles, thereby allowing *pneuma* (the breath of life; soul or spirit) to flow back out of the ventricles (reflected) through the same hollow nerves. This activity then caused movement by the pineal gland (a small, cone-shaped gland in the brain of all vertebrates having a cranium), extending from the midline into the ventricles. He observed that in animals this process was strictly mechanical. In humans, who unlike animals have souls, however, the soul was thought to interact with the body at the pineal gland and thus could influence the flow of the pneuma to the muscles.

Thomas Willis (1621-1675), anatomist, physician, and Oxford professor, advanced Galen's idea one step further and related it to actual brain structures. His *Cerebri Anatome*, illustrated by Sir Christopher Wren, was the most complete description of the brain to date. Sense impressions, Willis speculated, were carried by *pneuma* within the nerves to the *sensus communis* in the corpus striatum (two striated ganglia in front of the thalamus in each half of the brain) and then on to the corpus callosum (a mass of white, transverse fibers connecting the cerebral hemispheres in higher mammals) and the cerebral cortex (a layer of gray matter over most of the brain), where they were perceived and remembered. Some were "reflected" back to the muscles via the cerebellum (the section of the brain behind and below the cerebrum, regarded as the coordinating center for muscular movement). Voluntary movement was thus controlled by the cerebrum (upper, main part of the brain of vertebrates, consisting of two equal hemispheres—the largest part of the human brain and believed to control both conscious and voluntary processes) and involuntary, or "reflex" movement, by the cerebellum.

The first actual experiments on neural mechanisms of reflexes were conducted by Robert Whytt (1714-1766) of Edinburgh. Using frogs, he demonstrated that only a segment of the spinal cord was necessary for reflex responses to skin stimulation. He also showed that the pupillary reflex was contingent upon the midbrain. More than Descartes, he stressed the protective function of reflexes. While movement was strictly mechanical for Descartes, Whytt believed that it was dependent on the "sentient principle," even when involuntary or reflex, an idea that persisted into the nineteenth century.

Modern Reflex Studies

The modern concept of a reflex largely began with the nineteenth century English physiologist and physician, Marshall Hall (1790-1857). Hall used Charles Bell and François Magendie's distinction of sensory and motor roots to develop the notion of the reflex arc. Reflexes were, by then, by definition dependent on the spinal cord, independent of the brain, and strictly unconscious and involuntary. Hall also described the excitation or inhibition of reflex movements by various drugs. Finally, he was the first to use reflexes in medical diagnosis and treatment.

The next significant development was advanced by Charles Scott Sherrington in approximately 1890. Sherrington's work on reflexes (which led to the concept of the synapse) was built upon two foundations: He conducted a meticulous anatomical analysis of the nerves to various muscles and then used this knowledge to analyze quantitatively the reflex properties of specific nerves and muscle groups. This painstaking work provided the means for obtaining the first clear conception of the reflex as a combined structural and functional unit, and it established the reflex arc as a subject for further anatomical and physiological analysis by many twentieth century scientists. In addition, Sherrington emphasized the importance of the reflex as an elementary unit of behavior and thus laid one of the cornerstones for the modern studies of animal behavior.

Sherrington's first studies involved a correlation of anatomical tracing of sensory and muscle nerves with careful observations of various reflex behaviors. He introduced methods for cutting across the brain stem of a cat at the level of the midbrain, which produced a great enhancement of tone in the extensor muscles of the limbs (those muscles responsible for keeping an animal in the standing position). In order to study the reflex basis of this activity, Sherrington and his collaborators, in 1924, began to analyze the responses to passive stretch of an extensor muscle. The results indicated that stretch of the muscle by only a few millimeters produces a large increase in tension, as measured by a strain gauge. If the muscle nerve is cut, the tension developed is low because it results only from the passive elastic properties inherent in the muscle and its tendon. Thus, the greater tension depends on a reflex pathway that passes through the spinal cord. The reflex activity produces contractions of the stretched muscle. Since the reflex feeds back specifically to the stretched muscle, it is called a "myotatic reflex" or "stretch reflex." This is the familiar knee-jerk reflex evoked by a tap on the tendon of the knee. While most muscles, invertebrate and vertebrate, demonstrate this type of reflex, working extensor muscles best demonstrate it. Although the feedback to the muscle stretched is excitatory, there is, in addition, an inhibitory effect on muscles with antagonistic actions at a joint; thus, when a knee flexor is stretched, some of the tension in the knee extensor dissipates. This action illustrates the principle of reciprocal innervation of the muscles to a joint.

Next, it was necessary to analyze the nervous pathways involved in these and other types of reflex activity. David Lloyd at Rockefeller University began these studies in about 1940. The experiments required laborious dissection of individual peripheral nerves as well as removal of the laminae (thin layer of tissue) of the vertebral bones to expose the spinal cord so that electrodes could be placed on the dorsal and ventral roots. A single burst could then be set up in a peripheral nerve, and the response of motor neurons could be recorded in terms of the compound action potential of their axons in the ventral root. He found that stimulation of a muscle nerve produces a short-latency, brief volley in the ventral root. The input from muscles is thus carried over large, rapidly conducting axons, and there is only one, or at most two or three, synaptic relays in the spinal cord. In contrast, the ventral root response to a volley in a skin nerve has a long latency and duration. This response suggests the involvement, in skin reflexes, of shower-conducting fibers, polysynaptic pathways, and prolonged activity in the neurons in these pathways.

Reflexes and Neurology

Since reflex responses are essentially invariant in healthy individuals, their examination can often provide valuable information about neurologic disorders. Relatively simple tests, such as pupillary responses or auditory perceptions, can reveal information about complex brain functions. Scratching the skin of the foot, an activity normally leading to flexion of the toes, can demonstrate the condition of the spinal circuits that control them. For example, if the toes extend and spread in response to scratching the sole of the foot (called the Babinski response), a spinal lesion in the pyramidal tracts descending from the motor centers of the cerebral cortex is indicated. When observations of these and many other reflexes are combined with data on paralyses, spasms, or losses of sensation, it is often possible to localize the site of the lesion.

In addition to the diagnostic functions of reflexes, the reflex concept has exerted a great influence on psychological thinking and initially led to premature attempts to develop a psychology based on reflexes. Pavlov's innovative work led to extensive research in the early twentieth century on the physiology of behavior; for some time, the conditioned reflex provided the best technique for enabling at least a part of the learning process to be investigated quantitatively and to be subjected to an exact analysis. The principles proposed by such behaviorists as Edwin Ray Guthrie, Clark Leonard Hull, and B. F. Skinner to explain psychological actions as conditioned or learned responses to external and internal stimuli were based in part on earlier reflex notions and upon the fundamental model of the conditioned reflex as demonstrated by Pavlov. It is now generally recognized, however, that the reflex relationship between stimulus and response is not nearly as simple as was previously thought. The use of the conditioned reflex as a model for learning in classical-conditioning experiments artificially isolates, to an extreme degree, part of the total learning process in higher animals and is by itself inadequate in attempting to analyze the complex physiological and mental interactions that ultimately determine the behavior of humans and other mammals.

—Genevieve Slomski

See also: Ethology; Habituation and sensitization; Nervous systems of vertebrates.

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REGENERATION

Type of animal science: Development
Fields of study: Cell biology, embryology, immunology

Regeneration is a phenomenon by which the cells surviving from damaged tissue grow to replace missing tissue. The process is common in tissues of lower animals (such as starfish and insects), but it is rare in mammals. Regeneration is important for replacing damaged organs and for understanding organismal development.

Principal Terms

- CHEMOTAXIS: a process by which cells are attracted to a chemical, moving from low to high concentrations of the chemical, until the cells cluster
- DETERMINATION: an event in organismal development during which a particular cell becomes committed to a specific developmental pathway
- DIFFERENTIATION: the process by which a determined cell specializes or assumes a specific function
- FATE MAP: a map of determined, but undifferentiated, tissue by which specific cell regions can be identified as giving rise to specific adult structures
- IMAGINAL DISK: a determined, undifferentiated tissue in fruit fly larvae that gives rise to a specific adult structure
- POSITIONAL INFORMATION: a concept by which differentiating cells organize themselves to produce a particular tissue type based upon cell-to-cell interactions
- STEM CELL: a determined, undifferentiated cell that is hormonally activated and changes into a specific cell type
- TRANSDETERMINATION: an event by which a determined, undifferentiated cell changes its determination, thereby giving rise to a different tissue type

Regeneration is a process by which some organisms replace damaged or missing tissue using living cells adjacent to the affected area. The phenomenon is not well understood, but several animal systems have enabled developmental geneticists to develop strong models describing the process.

The replacement of tissue is a common occurrence in fungi and plants. Regeneration can also occur in animals, although the capacity for regeneration progressively declines with increasing complexity in the animal species. Among primitive invertebrates (animal species lacking an internal skeleton), regeneration frequently occurs. A planarium can be split symmetrically into right and left halves. Each half will regenerate its missing mirror-image, resulting in two planaria, each a clone (exact genetic copy) of the other.

In higher invertebrates, regeneration occurs in echinoderms (such as starfish) and arthropods (such as insects and crustaceans). A radially symmetrical starfish can regenerate one or several of its five arms. Regeneration of appendages (limbs, wings, and antennae) occurs in insects such as cockroaches, fruit flies, and locusts. Similar processes operate in crustaceans such as lobsters, crabs, and crayfish. Limb regeneration extends even to lower vertebrate species (species having an internal skeleton) such as amphibians and reptiles, although on a very limited basis.

In amphibians, the newt can replace a lost leg. In reptiles, some lizards can lose their tails when captured by a predator, thus assisting their escape. If the lizard is young, the tail can regenerate.

The tail breaks because of a breakage plane in the tail which severs upon hormonal activation. The glass-snake lizard is such a species.

Principles of Regeneration

Regeneration in these organisms is based upon two principles: the symmetrical organization of cells in the organism, and the reversal of determination and differentiation in the surviving cells, termed blastema, adjacent to the missing tissue. These two factors are fundamental to the development of the organism.

In animal systems, two major body symmetries emerge—radial symmetry and bilateral symmetry. In radially symmetric organisms, including plants and primitive invertebrates such as hydra, jellyfish, and starfish, body tissues are arranged in a circular orientation about a central axis. Appendages may also be present that likewise orient in a circular pattern of cells. In bilaterally symmetrical organisms, including animal species such as planaria, arthropods, fish, amphibians, reptiles, birds, and mammals, the body is oriented into mirror-image halves about a central body plane, resulting in its having right and left equivalent structures along each half.

Body symmetry is critical for tissue regeneration because of positional information. The cells of an individual organize into a specific pattern during development. Cell-to-cell interactions and chemical messengers between cells provide the cells of a given tissue with information signals directing the cells to grow in a particular direction or pattern. The loss of a tissue portion may stimulate the remaining cells to carry out a programmed growth, that is, to complete a specified pattern.

Determination and differentiation both play an important role in the genetic basis for development. All cells of an organism contain the same genetic material; that is, they all contain the same deoxyribonucleic acid (DNA), the same genes. In a specialized organism (one having different tissue types—eyes, ears, skin, and nerves), these cells must behave differently, even though they contain the same genetic information. The process by which identical cells with the same genetic information give rise to different tissues is termed differentiation.

What causes similar cells to differentiate to form different tissues is a process called determination. Prior to differentiation, cells become determined, meaning that some genes in these cells are turned on, making certain proteins, while other genes are turned off, not making other proteins. All cells of a specific tissue have the same genes that are turned on or off and therefore make the same proteins (for example, all red blood cells manufacture hemoglobin). Cells of other tissue types have different genes that are turned on or off and make other proteins (for example, epidermis cells manufacture keratin, not hemoglobin). How cells determine and differentiate depends upon chemical signals (hormones). Hormones signal different cells that receive chemically coded information based upon their location in the organism, which is based upon the organism's symmetry.

Cockroaches, Newts, and Fruit Flies

Three principal animal regenerative systems have been studied: cockroach limb regeneration, newt limb regeneration, and fruit fly imaginal disk regeneration. In all animal systems, regeneration occurs primarily in younger individuals undergoing metamorphosis, which is a change in development involving considerable alterations in body size and physical appearance. Adult regeneration is incomplete or does not occur.

Severing a cockroach limb results in distal regeneration; the remaining leg part regenerates the lost portion. If the middle portion of a leg is removed and the remaining leg parts are grafted together, complete regeneration of the missing middle portion occurs precisely between the grafted parts, but grafting requires correct orientation of the body parts. If the leg parts are grafted backward, regeneration will be distorted, resulting in a malformed limb, sometimes with multiple leg structures sprouting from one limb. Virtually identical results have been obtained for newt limb regeneration. Furthermore, limb regeneration in the presence of certain chemicals such as retinol palmitate causes complete limb regeneration, including undamaged regions. The net result is a severely deformed limb.

For the fruit fly *Drosophila melanogaster*, the period from egg to adult is approximately ten days at 25 degrees Celsius. The period includes roughly seven days during which the organism proceeds through three larval (maggot) stages, followed by a three-day immobile pupal stage, during which metamorphosis occurs. Metamorphosis involves the replacement and modification of larval body structures with adult body structures (eyes, legs, and wings). The cells that are to become the adult structures are present, but dormant, in the larval stages. These special cells, called imaginal disks, are determined to become specific adult structures, but remain undifferentiated until activated by the hormone ecdysone during metamorphosis.

There is one imaginal disk for each future body structure (two eye imaginal disks, six leg imaginal disks, for example). Gerold Schubiger and other geneticists have determined "fate maps" for each imaginal disk. They have determined what each cell group on each disk will become in the adult. For example, the male genital disk has been mapped so that specific cell groups are associated with the formation of the specific adult structures of, for example, the heart, penis, and testes.

Experiments by Peter J. Bryant and Schubiger focused upon removing parts of leg and wing imaginal disks. The remaining surviving cells either regenerated the missing tissue or duplicated themselves. Whether regeneration or duplication occurred depended upon the amount of tissue lost and the position of the surviving imaginal disk tissue. If a small portion of a disk or a particular region of the disk was lost, then the remaining disk cells regenerated the missing part, thus producing a complete disk and ultimately a normal adult structure. If a large section of a disk or a sensitive region of it was lost, then the remaining cells du-

Starfish are capable of regenerating broken-off arms. (PhotoDisc) plicated a mirror-image of themselves, giving rise to a useless adult structure.

Models of Regeneration

These collective studies, especially those involving the *Drosophila* imaginal disks, have produced two comprehensive regeneration models: the gradient regeneration model and the polar coordinate model. The gradient regeneration model, proposed by Victor French, explains the regenerative capacity of a given tissue by arranging the cells of the tissue along a gradient of regenerative capacity. Cells are arranged in order of high regenerative capacity to low regenerative capacity. This high-to-low regenerative gradient is directly correlated to the positional information of each cell. Cells located proximal (near) to the main body axis have high regenerative capacity. Cells located distally (far) from the main body axis have progressively lower regenerative capacities. Removal of distal cells results in their replacement by regeneration of the proximal highly regenerative cells. The removed distal cells, which lack regenerative information because they are at the low end of the gradient, cannot regenerate the proximal cells.

The gradient regeneration model can best be visualized as a right triangle with its hypotenuse (longest side) being a downward slope. Highly regenerative cells (proximal to the main body axis) are at the top of the slope. They contain positional information for themselves plus information for all cells below them on the slope. Higher cells can replace lost lower cells (located distal to the main body axis). Distal cells low on the slope have considerably less positional information and therefore can only duplicate themselves.

The polar coordinate model, proposed by French with Peter J. Bryant and Susan V. Bryant, is a more elaborate version of the gradient model that explains not only the *Drosophila* imaginal-disk experiments but also the cockroach and newt regeneration experiments. This model is a three-dimensional gradient that covers regeneration not only in a proximate to distal direction but also from the exterior to interior. The polar coordinate model can best be visualized as a cone. The circular end of the cone represents proximal tissue, whereas the tapered tip represents distal tissue, thus simulating the proximal-to-distal regeneration gradient.

On the circular (proximal) base of the cone, imagine a bull's-eye. The outermost circle represents exterior tissue, whereas the circle center (bull's-eye) represents the most interior tissue. There is thus a three-dimensional regeneration gradient—proximal-to-distal and exterior-to-interior. The circle is furthermore subdivided clockwise into twelve regions, completing the polar coordinate model of tissue regeneration capacity.

The tissue pattern of regeneration will again favor those cells located at high gradient positions, namely proximal (cone base) and exterior (outside circle). These cells possess positional information for regeneration of lower gradient tissue. Lower gradient cells, located distally (cone tip) and interiorly (circle center), will have limited positional information and will be capable only of duplicating themselves.

For clockwise regeneration, the polar coordinate model operates by the shortest intercalation route; that is, if a small tissue section is lost, the remaining large section will regenerate the lost piece based upon positional information. If a large tissue section is lost, however, the remaining small section will lack sufficient regenerative information and will be capable only of duplicating a mirror image of itself.

The French, Bryant, and Bryant polar coordinate model is a three-dimensional regenerative capacity gradient intended to model a tissue based on cell position. The model really boils down to one principle: a large, proximal (or exterior) group of cells can regenerate missing tissue; a small, distal (or interior) group of cells cannot.

Studying Regeneration

Developmental geneticists have studied regeneration in a variety of ways. Among the principal experimental techniques have been fate map determination of imaginal disks and limb regeneration, already discussed above, transdetermination of imaginal disks, and studies of simple organismal development.

Geneticists have found that under special circumstances, an imaginal disk or a portion of an imaginal disk can change its pattern of determination, that is, it transdetermines. A wing occasionally grows from an eye, for example, or a leg from a wing. Cells that are programmed to follow one developmental route follow another route instead. The cause of transdetermination is unknown, but the process does follow specific patterns. For example, a genital imaginal disk can transdetermine to form an antenna or leg, but not vice versa. An antenna disk can transdetermine to produce an eye, wing, or leg, but the wing and leg disks cannot transdetermine to an antenna.

Further regenerative studies involve the model developmental systems, including the cellular slime mold *Dictyostelium discoideum*. In the presence of adequate food, this exists as single, amoeba-like cells. If the cells are starved, they release a chemical attractant (chemotaxic) substance, cyclic AMP, that attracts the cells to one another. The resulting cellular mass moves as a single unit until the organism finds a suitable food source, upon which the cells differentiate and specialize to produce and release spores, each of which subsequently gives rise to a new amoeba-like stage. Such studies are necessary because regeneration ultimately involves changes in the determination and differentiation of cells.

Future Prospects

Regeneration research presents two opportunities for further development: an understanding of higher cell differentiation and growth, and prospects for replacing lost or damaged human tissues and organs. The polar coordinate model for tissue regeneration indicates that tissue replacement depends upon blastemas at the damaged area replacing tissue using positional information. Future research includes genetic and molecular studies to identify intercellular chemotaxic molecules and other information molecules that mediate cell-to-cell communication and thereby control how cells develop and grow in specified patterns. Such research will unravel important clues to cellular development and regeneration.

Scientists' understanding of cellular differentiation and growth is currently limited to more primitive species (such as *Dictyostelium discoideum* and *Drosophila melanogaster*). The most effective breakthroughs have been with the *Drosophila* imaginal disk studies and cockroach and newt limb regeneration experiments. Much more work remains to be done, particularly with respect to genetic and molecular analysis. The action of specific steroid and protein hormones on cellular growth and differentiation is a further avenue of research.

While regeneration research has been pursued for many decades, it is still in its infancy. Further research will allow the understanding of organismal development.

—David Wason Hollar, Jr.

See also: Aging; Amphibians; Cleavage, gastrulation, and neurulation; Determination and differentiation; Development: Evolutionary perspective; Fertilization; Growth; Insects; Sexual development.

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REINDEER

Types of animal science: Anatomy, classification, ecology, reproduction
Fields of study: Anatomy, zoology

Reindeer are deer native to subarctic and arctic regions. Males and females have antlers. Reindeer migrate in herds of up to 200,000. Imported into Alaska and Canada, they are valuable resources.

Principal Terms

DOMESTICATED: trained and raised by humans for specific uses.
GESTATION: term of pregnancy
HERBIVORE: an animal that eats only plants
RUMINANT: a herbivore that chews and swallows plants, which enter its stomach for partial digestion, are regurgitated, chewed again, and reenter the stomach for more digestion

Reindeer are large deer, native to subarctic and arctic regions of northern Europe and Asia. They are related to North American caribou, as both are variants of the species *Rangifer tarandus*. Reindeer can be domesticated and have long been valuable possessions of humans in those regions of the world. They yield meat, cheese, butter, clothes, and draft animals able to carry heavy burdens.

Many Eurasian reindeer still run wild and are trapped for domestication. Whether wild or domesticated, reindeer are herbivores, eating only plants. Their diet is grass, moss, leaves, twigs, and lichens. They often obtain food by scraping snow cover with their antlers and hooves. Reindeer are diurnal, meaning that they are active only during the day. They spend most of their time seeking food. Their preferred habitats are barren, open plains (tundra), forests, grasslands, and mountains.

Physical Characteristics of Reindeer

Reindeer differ from most deer in having large, deeply cleft hooves, hairy muzzles to help to keep them warm, and antlers on both males and females. Reindeer have long bodies and legs. Their hooves are broad, to provide footing on snow and ice. Male reindeer are four feet tall at shoulder height and weigh up to six hundred pounds. Females are shorter but reach similar maximum weights. Both genders grow up to seven feet long. Their thick, waterproof fur is brown in summer and gray-brown in winter. White fur covers their rumps, tails, and the lower portions of their legs. Males have white neck manes during mating season. Reindeer do not see well, but they have an excellent sense of smell.

Reindeer antlers have pointed branches (points). In females, they grow to two-foot lengths, while males' antlers reach five-foot lengths. Very large male antlers have forty points. Those of females only have a few points. As in other deer, reindeer antlers are shed and regrown each year. Males lose their antlers in winter and females lose their antlers in late spring. The antlers that grow back are larger than those replaced. Antlers are important during mating season, when males fight for mates. Fights can damage antlers, so if they were not shed and regrown each year, many males would be unable to fight well, lose fights, and be unable to mate.

Reindeer are also ruminants, animals that chew and swallow their food more than once. After a little while, food that was swallowed reenters the ruminant mouth from the stomach. Reindeer and other ruminants chew the food, swallow it again, and the food enters a different stomach for additional digestion. The process, also called cud chewing, helps reindeer to get maximum

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amounts of nutrients and vitamins from their difficult-to-digest food.

Reindeer are social animals. They live in groups of about 20 most of the year. The groups consist of a male, his mates, and their young. Reindeer migrate great distances each fall and spring to feeding and mating grounds, travelling in herds of up to 100,000 and migrating about twenty miles per day.

Reindeer mate mostly in October. Gestation is about eight months long. The female leaves the herd to give birth to one calf, in May or June. The calf weighs up to twenty pounds. Mother and calf then rejoin the herd and the calf nurses for six months. A calf can mate when three years old. The life span of reindeer is up to fifteen years.

North American Reindeer Imports

Reindeer are excellent sources of food, clothes, and draft animals, as the Laplanders of Finland

Reindeer Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Artiodactyla
Family: Cervidae (deer)
Genus and species: Rangifer tarandus (reindeer and caribou)
Geographical location: Northern Europe, Asia, Canada, and Alaska
Habitat: Open plains (tundra), forests, grasslands, and mountainous areas
Gestational period: Eight months
Life span: Twelve to fifteen years
Special anatomy: Antlers, ruminant stomach

have long known. In order to provide a reliable food source for the Inuit of Alaska, who live in a comparable environment with a similar social structure, the U.S. Office of Education imported thirteen hundred reindeer from Siberia near the end of the nineteenth century. Several million reindeer are now found throughout Alaska. In 1935, the Canadian government set up a herd of reindeer in the Yukon Territory to benefit Native Americans and Inuit. This herd also flourished and Native Americans and Inuit now own all reindeer herds in North America. The deer satisfy many of their basic needs, becoming a valuable North American resource.

—Sanford S. Singer

See also: Cattle, buffalo, and bison; Deer; Domestication; Elk; Herbivores; Herds; Horns and antlers; Moose; Ruminants.

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REPRODUCTION

Type of animal science: Reproduction
Fields of study: Ethology, genetics, reproduction science

Reproduction is a prerequisite for life. Sexual organisms reproduce when the gametes of two adults unite. Similarities and differences in how these adults maximize their own lifetime offspring production influence the diversity of mating behaviors observed in nature.

Principal Terms

GAMETE: a sexual reproductive cell that must fuse with another cell to produce an offspring: a sperm or egg

MATE CHOICE: the tendency of members of one sex to mate with particular members of the other sex

MATE COMPETITION: competition among members of one sex for mating opportunities with members of the opposite sex

NATURAL SELECTION: the process that occurs when inherited physical or behavioral differences among individuals cause some individuals to leave more offspring than others

REPRODUCTIVE SUCCESS: the number of offspring produced by one individual relative to other individuals in the same population

SEXUAL DIMORPHISM: an observable difference between males and females in morphology, physiology, and behavior

SEXUAL SELECTION: the process that occurs when inherited physical or behavioral differences among individuals cause some individuals to obtain more matings than others

The ability to reproduce is central to the existence of any organism. Simple one-celled organisms reproduce asexually by duplicating their genetic material and dividing in half. For reproduction in sexual species the participation of two individuals is essential. Mating partners have a common interest: production of successful offspring. They also have conflicting interests. Appreciating the diversity of reproductive behaviors that occur in different organisms requires understanding of the reproductive conflicts that exist between mates even more than their mutual reproductive interests.

Early sexual species most likely consisted of individuals that produced gametes of similar size. Except that one set of individuals produced smaller gametes that would be called sperm and another set produced larger gametes called eggs, males and females did not exist. Yet, reproduction was sexual. Through time it is thought that distinct sexes evolved because some individuals obtained reproductive advantages by producing smaller than average gametes whose greater motility increased their likelihood of fertilizing other gametes, while other individuals obtained reproductive advantages by producing larger than average gametes whose greater stores of nutrients increased the survival prospects of their young. Such evolution of gamete dimorphism would then lead to the many specializations in appearance and behavior of present-day males and females.

Reproductive Success

For species whose parents do not provide care for their young, the maximum number of offspring that an individual female can produce is determined by the number of eggs that she can manufacture. For species in which parents do provide care, the number of young a female can produce might be limited more by the number of young she can raise than by the number of eggs she can make. For both these types of species, females that copulate with more than one male produce roughly the same number of young each season as females that mate with only one male. Thus, the quality of an individual mate, or the resources of paternal care that he can provide, should affect the reproductive success of females more than the number of mates they can obtain. As a result, females of most species are expected to be selective about which male fertilizes their eggs.

In contrast, the reproductive success of males of most species is not limited by the number of sperm they can produce. In species lacking parental care, males that mate with the most females usually leave the most offspring. In parental species, the reproductive consequences of mating with more than one female are slightly more complex. If one parent can provide sufficient care to raise young to independence, males that mate with multiple females usually leave more offspring than males that mate with only one female. If both parents are necessary to raise young, males that mate with only one female should leave more offspring than males with multiple mates. Given the reproductive advantages of mating with multiple females and a tendency for breeding males to outnumber breeding females, competition for mating opportunities is more pronounced in males than in females for many species. Furthermore, males should usually be less selective in mate choice than females.

Mate Competition and Mate Choice

Charles Darwin realized that the struggle to obtain mates could be an important process affecting the evolution of organisms. He deemed this process "sexual selection" to distinguish it from the struggle for existence, or "natural selection," and suggested two components of sexual selection: mate competition and mate choice. The importance of mate competition is rarely questioned by biologists because it often involves frequent and conspicuous aggressive interactions and distinctive weapons (for example, antlers of various ungulate species, horns of bovids, and enlarged canine teeth of primates). Mate choice is another matter. This exceedingly subtle behavior is difficult to document in any species. Although females of most species are demonstrably more reluctant to mate than males and are remarkably good at rejecting the mating attempts of males of other species as well as those of closely related males of their own species, few studies can convincingly show that females actively choose particular types of males as mates. The lack of direct evidence for the pervasiveness of mate choice in nature has caused many biologists to doubt its significance ever since Darwin first suggested it. Mate choice is also often misunderstood. The decision process it embodies is not thought to result from conscious deliberation; rather, individuals might simply react more favorably to some members of the opposite sex than to others.

Fighting for Mates

Similarities and differences in the details of mate competition and mate choice of different species can be exemplified by comparing three North American vertebrates: bullfrogs, sage grouse, and elephant seals. Male bullfrogs fight each other for small areas in ponds that females use as egg deposition sites. The wrestling matches that occur between males do not involve weapons as such, but being larger than an opponent almost always confers success. During nighttime choruses, females move among the territorial males, apparently assessing features of the male and his territory. Pairing begins when a female approaches a particular calling male and touches him. The male clasps the female, and within an hour, the female releases up to twenty thousand eggs, which the male fertilizes externally. Neither the male nor the female provides parental care for their young. Each year, roughly half of the males in a population obtain mates, and the most successful male may mate with six or seven different females.

Male elephant seals can weigh as much as three thousand kilograms and are highly aggressive.

Rather than fight for territories, they fight directly for groups of females, called harems, that haul out on land to give birth. Males that monopolize large groups of females might mate with ninety or more females each year. One study revealed that less than 10 percent of the males sire all the pups in a breeding colony. Success in male competition not only involves being large but also involves having formidable canine teeth to use as weapons. During a fight, males rear up to half their length, slam themselves against the opponent, and bite him on the neck. Skin on the chests of males is highly cornified; these "shields" provide some protection against such onslaughts, but injury is still common. Mate choice by females is limited to vocalizing before and during copulation. If the male attempting to mate with her is a subordinate individual, the dominant male quickly responds to the call and attacks the copulating male.

Male sage grouse often congregate, or "lek," in traditional areas where they display and fight to control small territories. The territories function as courtship sites and places to copulate. Males provide neither resources nor parental care for their young; yet, females initiate mating and appear to be highly selective in mate choice. Near unanimity in preferred mates by the females in the population results in only a few males obtaining all the matings.

In all three of these species, many males compete for mates by fighting for territories; however, some males employ different tactics to obtain mates. Small, young bullfrog males remain silent near large, calling males and attempt to intercept any female attracted by the calling male. Small, young elephant seal males lurk about on the surf and grab females as they leave land to feed in the ocean. These males force females to copulate. Some sage grouse males attempt copulation with females away from the display arena. In another lekking bird species, the ruff, two types of males exist: territorial males and satellite males. The latter males are nonaggressive and appear to capitalize on the ability of territorial males to attract females. Unlike the case of bullfrog males, however, genetic differences of male ruffs produce the striking differences in plumage and behavior, rather than their ages.

Mate choice by females is well developed in bullfrogs and sage grouse. The benefit that female bullfrogs obtain by choosing particular males is relatively straightforward: Chosen males tend to control superior egg deposition sites that increase offspring survival. Benefits that female sage grouse obtain from mate choice are unknown. Mate choice in such lekking species continues to pose a significant question for biologists.

Competition and Reproductive Success

Differential success of males in mate competition and mate attraction may translate to large differences in reproductive success. In contrast, variation in reproductive success among females is usually low because most females mate and produce at least some offspring. The relative amount of variation in reproductive success within each sex can influence the evolution of sexual traits. When only a few adults produce most of the offspring in a population, genes affecting the traits that underscore their success will be passed on to their offspring and quickly become the predominant characteristics of future generations. In contrast, if the most successful individual produces only slightly more offspring than other individuals, genes from all these parents will be present in roughly similar numbers in subsequent generations.

A consequence of greater variation in reproductive success of males relative to females is the evolution of elaborate sexual characteristics that are expressed only in males. These traits can be morphological, physiological, or behavioral. The extent of sexual dimorphism is predicted to be related to the relative variation in reproductive success in the sexes. Thus, species in which one or a few males sire most of the offspring produced in the population would tend to be species with considerable phenotypic differences between the sexes.

Field Research and Laboratory Studies

Studies of the reproductive behavior of organisms usually involve observation and experimentation of male and female interactions in nature or the laboratory. Early studies were mostly observational and cataloged the most typical behavior patterns observed in each sex. These studies ignored differences in behaviors among individuals. Because such differences can have significant consequences in terms of reproductive success, more recent studies usually involve marking males and females for individual recognition and recording various features of their morphology, behavior, and reproductive success.

Quantifying reproductive success in nature is a difficult task, and various methods have been used for different organisms. For all studies, the identity of each individual must be known. For some species, researchers can assess only the number of copulations that individuals obtain; for other species, they can count the number of young born; in yet others, they can determine the number of young that survive to independence or even sexual maturation.

Laboratory and field experimentation has been used to study a plethora of questions concerning the acquisition, function, and evolutionary significance of a variety of reproductive behaviors. Early studies of bird song investigated not only the role of song in attracting mates but also how individuals acquired their species-typical song. Choice experiments on female frogs using either naturally calling males or playbacks of recorded male calls revealed the call characteristics that females use in species and mate recognition. Crossing different species that varied in reproductive behaviors and noting the characteristics of their

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hybrid offspring provided some insights into the genetic basis of various behaviors. Staging aggressive interactions between males that differ physically in some regard demonstrated the significance of various male characteristics.

Researchers investigate general trends in reproductive behaviors by using the comparative method. This method usually works best when fairly closely related taxa (for example, species within the same genera or family) are considered. Using the comparative method, researchers can look for the relationships between the degree of sexual dimorphism in some characteristic and sex-specific differences in reproductive success variation, or the ecological and social conditions that affect male behaviors such as territoriality or female behaviors such as the amount of maternal care provided to young.

A thorough understanding of reproductive behaviors requires the creative use of all three methods of investigation: observations of individuals in nature to document normal behavioral patterns, precise experimentation on behaviors under controlled conditions to understand mechanisms of behavior and the stimuli that produce them, and comparison of trends in closely related species to gain insights into the evolutionary history of behavioral traits.

Reproduction is one of the defining attributes of life itself, and for most organisms, reproduction is sexual. Yet, despite the universality of sexual reproduction, the behavior patterns associated with it in different organisms are exceedingly diverse. For solitary organisms, sexual reproduction may be the only form of social behavior. For highly social species, individual interactions can be much more complex but still usually influenced by sex in some manner. Biologists seek to find some order to the variety of reproductive behaviors observed in different organisms. A unifying theme for this diversity is an evolutionary one: How do the sexes differ in maximizing the number of offspring they can produce? More specifically: How do males or females maximize the number of offspring they produce given the behavior patterns of the other sex and the various ecological factors that affect them? Thus, current research on reproductive behaviors has gone well beyond the point of merely describing what animals do to reproduce to determining why they do what they do.

—Richard D. Howard

See also: Adaptations and their mechanisms; Asexual reproduction; Birth; Copulation; Courtship; Embryology; Ethology; Evolution: Historical perspective; Fertilization; Hormones and behavior; Infanticide; Lactation; Marsupials; Monotremes; Parthenogenesis; Reproductive strategies; Reproductive systems of female mammals; Reproductive systems of male mammals; Sex differences: Evolutionary origin; Sex differences: Evolutionary origin; Sexual development.

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REPRODUCTIVE STRATEGIES

Types of animal science: Ecology, reproduction
Fields of study: Ethology, genetics, reproduction science

Reproductive strategies are a set of attributes involved in an organism's maximizing its reproductive success. Theoretical and experimental studies of reproductive strategies reveal why various reproductive patterns have evolved.

Principal Terms

- BET-HEDGING: a reproductive strategy in which an organism reproduces on several occasions rather than focusing efforts on a single or few reproductive events
- K STRATEGY: a reproductive strategy typified by low reproductive output; common in species living in areas having limited critical resources
- LITTER SIZE: the number of offspring produced per birth; also referred to as "clutch size"
- POPULATION DENSITY: number of individuals per unit of area, especially when it pertains to the group's reproductive potential
- R STRATEGY: a reproductive strategy involving high reproductive output; found often in unstable or previously unoccupied areas
- REPRODUCTIVE STRATEGY: a set of traits that characterizes the successful reproductive habits of a group of organisms

The term "reproductive strategies" is probably something of a misnomer. A strategy implies that an organism has had conscious forethought in determining how to proceed with its reproductive events, that some planning has occurred. With the exception of humans, who can plan aspects of their parenthood, this is virtually impossible. Having a reproductive strategy implies only that an organism has evolved a pattern that maximizes its success in the production of offspring.

The concept of reproductive strategies is closely related to that of natural selection. Natural selection results in the more fit individuals within a population, under a given set of environmental circumstances, being more likely to pass on their genes to future generations. By this process, the gene pool (genetic makeup) of the population is altered over time. An organism's fitness can be assessed by evaluating two key characteristics—survival and reproductive success. The organism's reproductive strategy, then, is that blend of traits enabling it to have the highest overall reproductive success. Application of the term "reproductive strategy" has also been extended to describe patterns beyond individual organisms: the population, species—even entire groups of similar species, such as carnivorous mammals.

Examination of reproductive strategies is part of the larger study of life-history evolution, which attempts to understand why a given set of basic traits has evolved. These traits include not only those pertaining to reproduction but also those such as body size and longevity. To consider a reproductive strategy appropriately, one must view it within the context of the organism's overall life history, precisely because these traits (particularly body size) often affect reproductive traits. One should also evaluate the role that the organism's ancestry plays in these processes. A species' evolutionary history can have a profound effect on its current attributes.

Traits and Behaviors

A reproductive strategy consists of a collection of basic reproductive traits, including litter, or "clutch," size (the number of offspring produced per birth), the number of litters per year, the number of litters in a lifetime, and the time between litters, gestation, or pregnancy length. The age of the mother's first pregnancy is also a consideration. Another trait is the degree of development of the young at birth. In different species, mothers put varying levels of time and energy into the production of either relatively immature, or altricial, offspring or offspring that are well developed, or precocial.

Reproductive strategies also consist of behavioral elements, such as the mating system and the amount of parental care. Mating systems include monogamy (in which one male is mated to one female) and polygamy (in which an individual of one sex is mated to more than one from the other). The type of polygamy when one male mates with several females is called polygyny; the reverse is known as polyandry.

Finally, physiological events such as those involved in ovulation (what happens when the egg or eggs are shed from the ovary) may also be used to characterize a reproductive strategy. Some mammals are spontaneous ovulators. Females shed their eggs during the reproductive cycle without any physical stimulation. Other mammalian species are induced ovulators—a female ovulates only after being physically stimulated by a male during copulation. These patterns, induced and spontaneous ovulation, may be regarded as alternate reproductive strategies, each enabling a type of species to reproduce successfully under certain conditions.

The overall effectiveness of a reproductive strategy is important to consider with respect to the relative success of the offspring (even those in future generations) in leaving their own descendants. A sound reproductive strategy results in increased fitness. An organism's fitness as it affects the population's gene pool may not be adequately assessed until several generations have passed.

The r and K Selection Model

The model of r and K selection is the most widely cited description of how certain reproductive traits are most effective under certain environmental conditions. To appreciate this model, an understanding of elementary population dynamics is needed. At the early stages of a population's growth, the rate of addition of new individuals (designated r) tends to be slow. After a sufficient number of individuals is reached, the growth rate can increase sharply, resulting in a boom phase. In most environments, however, unrestrained growth cannot continue indefinitely. Critical resources—food, water, and protective cover—become more scarce as the environment's carrying capacity (K) is approached. Carrying capacity is the maximal population size an area can support. When the population approaches this level, growth rate slows, as individuals now have fewer resources to convert into the production of new offspring.

This pattern is defined as density-dependent population growth—the density or number of individuals per area that influences its growth. This description of population dynamics is also referred to as logistic growth and was conceived by the Belgian mathematician Pierre-François Verhulst in the early nineteenth century. It has successfully described population growth in many species.

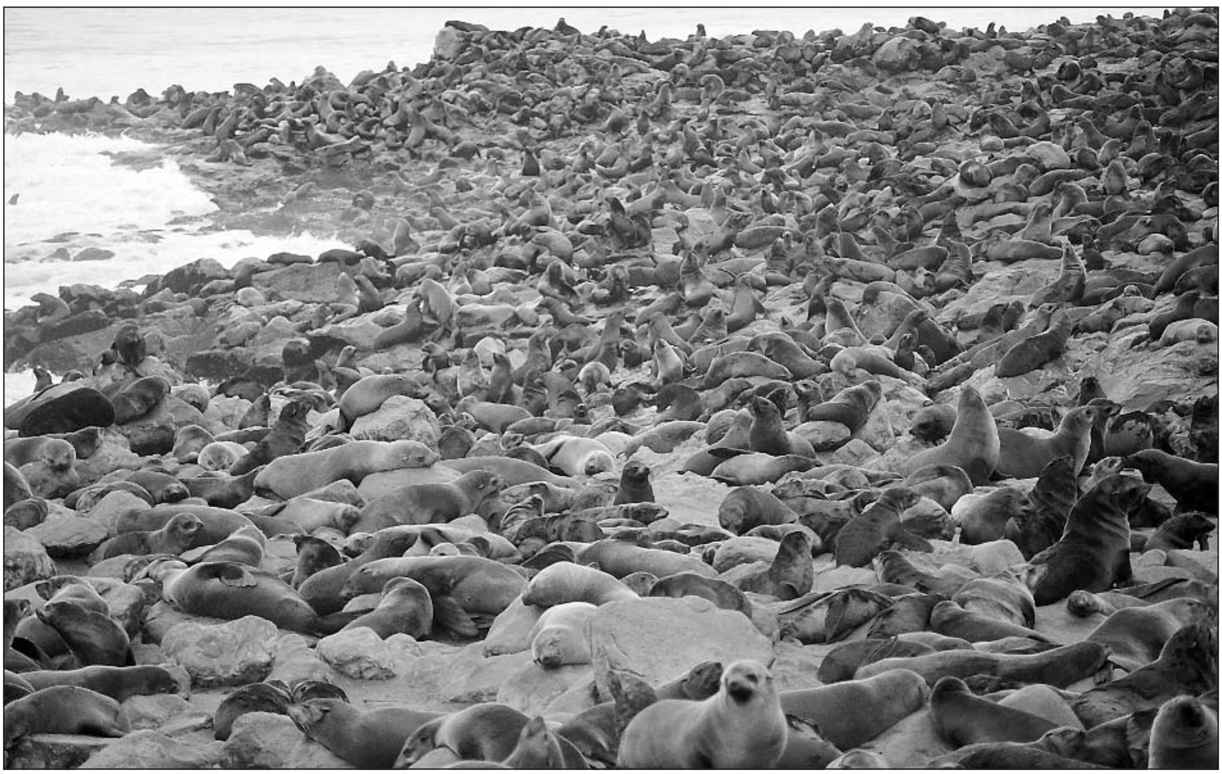
The r and K selection model was presented by Robert H. MacArthur and Edward O. Wilson in their influential book, *The Theory of Island Biogeography* (1967). They argued that in the early phase of a population's growth, individuals should evolve traits associated with high reproductive output. This enables them to take advantage of the relatively plentiful supply of food. The evolution of such traits is called r selection, after the high population growth rates occurring during this phase. They also suggested that, as the carrying capacity was approached, individuals would be selected that could adjust their lives to the now reduced circumstances. This process is called K selection. Such individuals should be more efficient in the conversion of food into offspring, producing fewer young than those living in the population's early phase. In a sense, a shift from productive to efficient individuals occurs as the population grows.

Other biologists, most notably Eric Pianka, have extended this concept of r and K selection to entire species rather than only to individuals at different stages of a population's growth. Highly variable or unpredictable climates commonly create situations in which population size is first diminished but then grows rapidly. Species commonly occurring in such environments are referred to as r strategists. Those living in more constant, relatively predictable climates are less likely to go through such an explosive growth phase. These species are considered to be K strategists. According to this scheme, an r strategist is characterized by small body size, rapid development, high rate of population increase, early age of first reproduction, a single or few reproductive events, and many small offspring. The K strategist has the opposite qualities—large size, slower development, delayed age of first reproduction, repeated reproduction, and fewer, larger offspring.

Various combinations of r and K traits may occur in a species, and few are entirely r- or K-selected. Populations of the same species commonly occupy different habitats during their lives or across their geographic ranges. An organism might thus shift strategies in response to environmental changes—it may, however, be constrained by its phylogeny or ancestry in the degree to which its strategies are flexible.

Criticism of the Model

Because the r and K model of reproductive strategies seems to explain patterns observed in nature, it has become widely accepted. It has also met with considerable criticism. Charges against it include arguments that the logistic population-growth model (on which the r and K strategies model is based) is too simplistic. Another is that



Seals congregate in huge numbers for mating. (PhotoDisc) cases of r and K selection have not been adequately tested. Mark Boyce, an ecologist, has persuasively argued that for the r and K model to be most useful it must be viewed as a model of how population density affects life-history traits. Within this framework, also called density-dependent natural selection, the concept of r and K selection remains true to the one that MacArthur and Wilson originally proposed. Boyce suggests that the ability of r and K selection to explain reproductive strategies will have the best chance of being realized when approached in this fashion.

In addition to the r and K model, there are many other ways of describing reproductive strategies. For example, some species, such as the Chinook salmon, are semelparous: They reproduce only once before dying. The alternate is to be iteroparous—having two or more reproductive events over the organism's life. If juvenile death rates are high, an individual might be better off reproducing on several occasions rather than only once. (This reproductive strategy is referred to as "bet-hedging.") Finally, it has also been useful to evaluate reproductive strategies based on the proportion of energy that goes into reproduction relative to that devoted to all other body functions. This mode of analysis addresses such considerations as reproductive effort and resource allocation.

Studying Reproductive Strategies

Initially, one who studies the reproductive strategy of an organism should attempt to characterize its reproduction fully. The sample examined must be representative of the population under consideration—it should account for the variability of the traits being measured. Studies can involve any of several approaches. Short-term laboratory studies can uncover some hard-to-observe features, but there is no substitute for long-term field research. By studying an organism's reproduction in nature, a biologist has the best chance of determining how its reproduction is shaped by an environment. If the research is performed over several seasons or years, patterns of variability can be better understood. This is important in determining how the physical environment influences reproductive traits.

After data have been systematically collected, it might then be possible to characterize a reproductive strategy. Imagine that a mouse population becomes established in a previously uninhabited area and that the population has a high reproductive rate (it produces large litters). The young develop quickly and produce many young themselves. Because of this combination of circumstances, one might consider the reproductive strategy to be r-selected since the population has a high reproductive output in an unexploited area. Though the concept of r and K strategies is problematic, it still is common to typify a strategy as r- or K-selected based upon this approach.

Because a reproductive strategy needs to be seen as part of an organism's overall life history, however, other things should be measured to understand it fully. These may include the life span and population attributes such as survival patterns. Values should be taken for different age groups to characterize the population's strategy. Correlational analysis is a statistical procedure that is used to evaluate reproductive strategies. Through such a methodology, one assesses the degree of association between two variables or factors. This may involve relationships between two reproductive variables or between a reproductive and an environmental variable—for example, to determine whether there is a significant correlation between litter size and decreasing body size in mammals. If one were found to occur, the conclusion that smaller species typically have larger litters might be drawn, which is, in fact, true. Such an analysis enables the characterization of a change in reproductive strategy based on body size. Simply establishing a correlation does not prove that causation has occurred—it does not automatically mean that one factor is responsible for the expression of the other.

Multivariate statistical procedures are also used to analyze reproductive strategies. These allow the determination of how groups of reproductive traits are associated and of how they can be explained by several factors. One might determine that a certain bird species produces its greatest number of young, and that the young grow most rapidly, at northern locations having high snow levels. Such an approach is often needed in dealing with reproductive strategies—a combination of traits typically requires explanation.

Reproduction and Survivial

The characterization of an organism's reproductive strategy involves more than an understanding of reproductive traits. There is a successful process by which offspring are produced, and reproductive success is one of the two principal measures of fitness—the other is survival. Because a successful reproductive strategy ultimately results in high fitness, any discussion of these strategies bears directly on issues of natural selection and evolution.

An organism's reproductive strategy represents perhaps the most significant way in which the organism adapts to its environment. A successful reproductive strategy represents a successful mode of passing genes on to the next generation, so traits associated with a reproductive strategy are under intense natural selection pressure. If environmental conditions change, the original strategy may no longer be as successful. To the extent that an organism can shift its reproductive strategy as circumstances change, its genes will persist.

The study of reproductive strategies has helped scientists understand why certain modes of reproduction occur, based upon observations of a species itself and of its environment. An understanding of reproductive strategies may also be of some practical use. An organism's reproduction directly influences its population dynamics.

If an animal has small litters and is at an early age at first reproduction, its population should grow at a concomitantly high rate. These and other components of reproduction may strongly affect a species' population growth. A knowledge of how reproduction influences population dynamics can be important in wildlife management activities, which can range from strict preservation efforts to overseeing trophy hunting.

—*Samuel I. Zeveloff*

See also: Adaptations and their mechanisms; Courtship; Displays; Evolution: Historical perspective; Mating; Population Growth; Reproduction; Reproductive systems of female mammals; Reproductive systems of male mammals; Sex differences: Evolutionary origin; Tool use.

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REPRODUCTIVE SYSTEM OF FEMALE MAMMALS

Type of animal science: Reproduction
Fields of study: Developmental biology, embryology, physiology

The mammalian female reproductive system is a complex system of organs and hormones that functions to produce offspring. The female also provides a protective environment in which the offspring develop until birth.

Principal Terms

ANTERIOR PITUITARY GLAND: the front portion of the pituitary gland, which is attached to the base of the brain; the source of luteinizing hormone (LH) and follicle-stimulating hormone (FSH)

ESTRUS CYCLE: hormonally controlled changes that make up the female reproductive cycle in most mammals; ovulation occurs during the estrus (heat) period

EXTERNAL GENITALS: the external reproductive parts of the female

GONAD: the primary reproductive organ (the ovary in females and the testes in males), which produces sex cells (gametes) and sex hormones

MENSTRUAL CYCLE: a series of regularly occurring changes in the uterine lining of a nonpregnant primate female that prepares the lining for pregnancy

OVARY: the female gonad, which produces ova and the hormones estrogen and progesterone

OVUM (pl. OVA): the female reproductive cell (gamete); a mature egg cell

UTERUS: the hollow, thick-walled organ in the pelvic region of females that is the site of menstruation, implantation, development of the fetus, and labor

The function of the mammalian female reproductive system, in cooperation with the male reproductive system, is to produce offspring. The role of the female is very complex: She must produce gametes (sex cells) called ova (singular, ovum) or eggs, provide the site for the combination of ova with sperm from the male (fertilization), and nourish and protect a developing fetus during pregnancy. She also must provide for the delivery of offspring from her body to the outside. These functions are carried out by a group of organs or structures and a number of chemicals called hormones. The major organs of the system include ovaries, which produce ova and hormones; uterine (Fallopian) tubes that transport the ovum and provide the site of fertilization; the uterus, which houses the developing offspring; the vagina, which receives the male penis and sperm during sexual intercourse and also functions as a birth canal; and the external genitals. Hormones important to the function of the female reproductive system include estrogen and progesterone from the ovaries, and follicle-stimulating hormone (FSH) and luteinizing hormone (LH) from the anterior pituitary gland. Release of FSH and LH is under control of chemicals called releasing factors, which are produced by a small region of the brain called the hypothalamus.

The Ovaries

The paired ovaries are the primary sex organ, or gonad, of the female. They are analogous to the testes in the male reproductive system and actually develop from the same tissue. The size and shape of the ovary depend on the age and size of the female and whether the female usually has a single offspring or several at one time. Before birth, small groups of cells called follicles are formed in each ovary. In the center of each follicle is a single large cell called an oocyte, which is able to mature into an ovum. In other words, all the oocytes a female will ever produce were already in place before she was born. The ova are special cells; they are formed by a process (meiosis) that results in a cell with only half of the chromosomes found in other body cells. The only other cells that divide by this process are those that form sperm in males. When an ovum and sperm unite, then, each cell contributes half the necessary chromosomes to make a new complete cell. This new cell, the first cell of an offspring, will have characteristics of each parent. The follicles develop in response to the hormone FSH from the anterior pituitary gland. A mature follicle releases its mature ovum through the wall of the ovary into the pelvic cavity. This process is called ovulation and is controlled by LH and FSH.

The ovary also produces the female sex hormones—estrogen and progesterone. Estrogen is produced by the maturing follicle cells. In addition to causing growth of the sex organs at puberty and stimulating growth of the uterine lining each month, estrogen is responsible for the appearance of female secondary sex characteristics. The follicle cells that are left behind following ovulation form a structure called the corpus luteum, which produces both estrogen and progesterone. The most important function of progesterone is to stimulate the lining of the uterus to complete its preparation for pregnancy.

The Accessory Organs

The rest of the internal structures of the reproductive system are called accessory organs. The first of these is a pair of uterine (Fallopian) tubes, or oviducts, which extend from each ovary into the uterus. They are frequently shaped like funnels, with fingerlike ends, called fimbria, that partially surround each ovary. Movements of the fimbria sweep the ovum and some attached cells into the uterine tube following ovulation. If fertilization is to take place, it will be in the uterine tube.

The uterus in most mammals consists of two horns and a body, although much variation occurs. Marsupials, mammals that have pouches, such as the opossum, have two completely separate uteri, each opening to the outside through a separate vagina. Rats, mice, and rabbits have uteri with two horns. Primates have simple uteri with no horns. The uterus has an amazing ability to expand during pregnancy. In all cases, the wall of the uterus is thick and muscular. This muscle layer, the myometrium, is able to contract rhythmically and powerfully to move the young down the birth canal and out of the mother's body during the birth process. The lining of the uterus is called the endometrium.

The uterus narrows down into a muscular, necklike region called the cervix. This structure acts like a valve to keep the opening into the uterus closed most of the time. This prevents bacteria and other harmful objects from entering. The final internal accessory structure is the vagina, a thin-walled muscular tube. The vagina surrounds the cervix of the uterus at its anterior end and extends to its opening to the outside of the body. It allows for childbirth, sexual intercourse, and, in primates, menstrual flow. The walls of the vagina normally touch one another and have deep folds that allow for stretching without damage. A thin fold of tissue called the hymen partially covers the external opening of the vagina. This structure has no function and varies considerably in different mammals.

The external structures of the female reproductive system are called the external genitals. These include the labia majora, labia minora, and clitoris. Two thick, hair-covered folds of skin, the labia majora, protect and enclose other structures. In some mammals, two smaller hair-free folds of skin are located within the labia majora. These folds, the labia minora, are very prominent in primates but small in most other mammals and completely lacking in some. They enclose a region called the vestibule. Within the vestibule are located the clitoris, the external opening from the urinary system (the urethra), and the external opening of the vagina. The clitoris is a small structure almost covered by the anterior ends of the labia minora. It is very sensitive, being richly supplied with nerve endings and blood vessels.

Sexual Maturity

Reproduction can occur only after females reach sexual maturity. In mammals, this requires the full development of the reproductive structures. The point at which maturity is attained is ultimately under the control of the hypothalamus, as it controls the release of FSH and LH. Many factors, such as attainment of a particular body weight, temperature, day length, and climate may influence the release of hormones.

After the female reaches maturity, reproductive activities are cyclic. In mammals, there are two different kinds of reproductive cycles. Most mammals have an estrus cycle in which females will mate with a male only if they are "in heat," which happens at certain restricted times. An estrus cycle is divided into stages: an inactive phase, called anestrus, which may last for days, weeks, months, or years; proestrus, during which the follicles are developing; estrus, when ovulation occurs; and metestrus, when the ova are moving into the oviduct. Females mate, and may become very aggressive about finding a mate, during estrus only. Usually ovulation is triggered by LH from the pituitary gland. In some mammals, including cats and rabbits, ovulation does not occur until the animal mates. Many females signal that they are in estrus. The signals may be chemical—a special scent which carries for a long distance, for example—or visual. Chimpanzees, for example, develop pink swollen skin on the external genitals during estrus.

The Menstrual Cycle

Primates have a menstrual cycle instead of an estrus cycle. The menstrual cycle is coordinated by estrogen and progesterone from the ovary. These hormones, in turn, are controlled by FSH and LH from the anterior pituitary gland, so all the functions of the reproductive structure are coordinated and synchronized. The three stages of the menstrual cycle are the menses, proliferation, and secretion stages.

In menses, the thick endometrium is sloughed off and flows out of the uterus and out of the body through the vagina. This is also called the menstrual flow or menstrual period. The menstrual fluid consists of roughly equal parts of blood and other accumulated bodily fluids. In the proliferation phase, the endometrium again grows thick. Ovulation occurs in the ovary at the end of this stage, following a sudden increase in the release of LH from the anterior pituitary gland. In the secretion stage, the endometrium becomes very thick and cushiony and prepared to nourish a developing embryo if fertilization has occurred. If fertilization did not occur, the endometrial cells die and the cycle begins again. These stages are controlled by estrogen and progesterone from the ovary. Female primates will mate throughout the entire menstrual cycle.

Studying the Female Reproductive System

Detailed examination of individual reproductive tissues is performed using a variety of very thin tissue slices, various dyes and stains, and microscopes. Frequently, preserved tissue is used. Electron microscopes have made it possible to magnify single cells, or parts of cells, several thousand times to observe minute details of structure. Fresh tissue is also examined. It is possible to freeze a small tissue sample quickly, slice it very thin, and then expose the tissue to chemicals, which can add to researchers' understanding of the function of particular cells.

The study of reproductive hormones and the understanding of their function demand the use of many different methods. Again, much information comes from nonhuman studies. The procedures vary widely but a typical laboratory experiment may involve removing the ovaries from a female rat and then injecting small amounts of estrogen or progesterone to observe the response of the endometrium. It is also possible to use chemicals that block, or inhibit, one or more specific hormones. By creating an abnormal, controlled situation and observing the results, an understanding about the role of individual hormones within a complex interrelated system can be obtained.

It is also frequently necessary to measure how much hormone is present in some bodily fluid, either for research to gain understanding of normal function or for medical diagnosis. This is very difficult, as most hormones occur in very minute concentrations. Procedures called radioimmunoassay (RIA) techniques, introduced during the late 1950's and early 1960's, represent a very important advance in the study of hormone concentrations. These procedures, which use special recognition molecules for each hormone, plus certain hormones that have been purified and made radioactive, make it possible to measure levels of hormones as low as one trillionth of a gram (a picogram).

In a system as complex in its function as the female reproductive system, it is not surprising that information is obtained from a variety of sources. Each technique has made a contribution to an understanding of the whole system.

Understanding the Female Reproductive System

The reproductive system is unique among all body systems. It is the only system not called upon to function continuously for the well-being of the individual. It is nonfunctional during the early part of the female's life, then is activated by chemical messages from the anterior pituitary gland. Its primary function is not, after all, the well-being of one individual but rather the continued existence of the species. It is also unique in that it must interact with another individual, a male, in order to fulfill this function. Throughout the reproductive years, all the functions of the female reproductive systems are directed toward pregnancy.

—*Frances C. Garb*

See also: Breeding programs; Cloning of extinct or endangered species; Copulation; Endocrine systems of vertebrates; Fertilization; Gametogenesis; Hormones in mammals; Lactation; Pregnancy and prenatal development; Reproductive systems of male mammals; Sex differences: Evolutionary origins; Sexual development; Wildlife management.

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REPRODUCTIVE SYSTEM OF MALE MAMMALS

Type of animal science: Reproduction
Field of study: Physiology

The male reproductive system is a group of organs that function together to produce sperm and carry them to the outside of the male body. Sperm carry the male's genetic information to his offspring. Continued survival of the species is assured by the proper functioning of the male and female reproductive systems.

Principal Terms

CHROMOSOME: a molecule of deoxyribonucleic acid (DNA) that contains a string of genes, which consist of coded information essential for all cell functions, including the creation of new life

EJACULATION: the process of expelling semen from the male body

ENDOCRINE GLANDS: glands that produce hormones and secrete them into the blood

ERECTION: the process of enlargement and stiffening of the penis because of increased blood volume within it

FERTILIZATION: the union of a sperm with an ovum; fertilization is the first step in the creation of a new individual

GAMETE: a reproductive cell—sperm in the male, ovum in the female; produced in the gonads, gametes contain a set of chromosomes from the adult male or female

GONAD: the organ responsible for production of gametes—the testis in the male, the ovary in the female

GONADOTROPIN: a hormone that stimulates the gonads to produce gametes and to secrete other hormones

SEMEN: the sperm-containing liquid that is expelled from the male body

The reproductive systems of all male mammals have the same basic design. The reproductive organs produce sperm and deliver it to the outside of the body. The sperm can be regarded as packages of chromosomes that the animal passes on to his offspring. Hormones and nerves control and coordinate the functions of the reproductive organs.

The Brain and Reproduction

Although the brain is not usually considered to be a component of the reproductive system, part of the brain is, in fact, essential to the function of the reproductive organs because of the hormones produced there. This part of the brain is the hypothalamus, a relatively small area that acts without conscious control. The hypothalamus is located in the lower middle of the brain; it contains centers that control eating, drinking, body temperature, and other essential functions.

Hypothalamic control over reproduction in the male is primarily by way of the hormone called gonadotropin-releasing hormone (GnRH). GnRH is released from the hypothalamus to enter blood vessels that carry it to the pituitary gland, a small gland suspended just below the hypothalamus. When GnRH arrives at the pituitary, it stimulates the pituitary to produce and release two more hormones, follicle-stimulating hormone (FSH) and luteinizing hormone (LH). FSH and LH in the male are identical to hormones of the same names in the female. The names of these hormones describe their functions in the female. Like other hormones, FSH and LH are released into the blood and circulate throughout the body. FSH and LH are called gonadotropin hormones: gonadotropin means "gonad stimulating." These are the hormones that stimulate the gonads (testes in the male, ovaries in the female) to produce sperm or eggs and to secrete gonadal hormones. In the male, the gonadal hormones are primarily testosterone and related hormones. There is a chain of hormonal commands, with GnRH from the hypothalamus at the top of the chain. GnRH stimulates the pituitary to secrete FSH and LH, which in turn stimulate the testes to produce sperm and testosterone.

In addition to the chain leading from the brain to the pituitary to the testes, information is sent back to the brain from the testes, a checks-and-balances system using principles of negative feedback to ensure that the hormones are produced in the appropriate quantities. If, for example, the hormone system gets slightly out of balance, leading to too much testosterone being produced, this excess of testosterone will be sensed by the hypothalamus. It will cause a temporary shutdown of GnRH production, leading to the system's correcting itself, because then a little less testosterone will be produced. If testosterone levels fall too low, the opposite will happen: GnRH, and then FSH and LH, and then finally testosterone, will all increase, again resulting in a correction of the original aberration. The hormonal system is a delicately balanced network that ensures the proper functioning of the testes.

The Testes

The testes are the sites of sperm production. Within the testes are hundreds of tiny tubes, the seminiferous tubules, that are responsible for sperm production. The sperm develop gradually from round cells called spermatogonia, which are located in the walls of the seminiferous tubules. As a sperm matures, it develops a long, whiplike tail attached to an oval head. The head of the sperm contains chromosomes, the genetic information of the male that will be passed on to his offspring. The sperm of some mammals can be distinguished under the microscope by characteristic differences in their appearance.

Between the seminiferous tubules are clusters of hormone-producing cells, the interstitial or Leydig cells. The Leydig cells produce testosterone and related hormones. Testosterone is essential for proper sperm development. In addition, testosterone is responsible for the development of male body features, including, in most species, a large muscle mass, and for the growth of the reproductive organs during puberty. In some animals, testosterone is also linked to aggressive and reproductive behaviors.

The testes of most mammals are located in the scrotum, a pouch of skin and muscle that is suspended outside the abdomen. In some animals, the testes may be withdrawn into the abdomen when the animal is startled or when it is not in the breeding condition.

The function of the scrotum is to maintain the temperature of the testes at a few degrees lower than average body temperature. The capability to maintain this temperature of the scrotum is rooted in the fact that the muscles within the scrotum are responsive to temperature. Under warm conditions, the scrotum relaxes, allowing the testes to move away from the body and lose heat. In cool temperatures, the opposite occurs: The scrotum wrinkles, pulling the testes closer to the body and allowing them to stay warmer. The reduced temperature maintained by the scrotum is mandatory for the production of normal fertile sperm. Fever or other situations that raise the temperature of the scrotum can interfere with sperm production, even resulting in temporary infertility. In a few large mammals (such as elephants, whales, and dolphins), the testes are not located within a scrotum, but instead occupy a position in the abdomen. It is not known why these species apparently do not require a temperature lower than that of the body for sperm production.

The Epididymus and Vas Deferens

Sperm are removed from the testes by a system of tubes that lead out of the body. Located next to each testis within the scrotum is the epididymis, a highly coiled tube that is directly connected to the seminiferous tubules of the testes. The epididymis serves two functions: sperm maturation and sperm storage. The epididymis is drained by a long, thin tube called the vas deferens, which carries sperm out of the scrotum through the inguinal canal into the abdomen. The inner end of the vas deferens is a widened area that may serve as a site of storage for mature sperm.

The vas deferens passes in a loop next to and under the bladder, the sac that stores urine until it can be removed from the body. Immediately beneath the bladder, the vas deferens is connected by a short tube, the ejaculatory duct, to the urethra. The urethra is the long, fairly straight tube that carries either urine from the bladder or sperm from the reproductive system. A valve located in the urethra below the bladder opens and closes to prevent sperm and urine from mixing, so that only one type of fluid is in the urethra at a time.

From their site of production in the testes, sperm pass through the epididymis, the vas deferens, the ejaculatory duct, then finally the urethra to the outside of the body. As sperm are expelled from the body along this route, they are mixed with seminal fluid to produce semen. Seminal fluid is secreted into the tubes by three sets of glands: the seminal vesicles, the prostate, and the bulbourethral (Cowper's) glands. The sperm never enter these glands; fluid is squeezed out of them into the tubes where the sperm are located.

The Penis

The penis is designed to deliver sperm to the female system. The penis consists of a long shaft with an enlarged head, the glans. The skin of the penis, especially the glans, is extremely sensitive to touch. In some species, the penis is withdrawn into a sheath of skin except during sexual arousal.

Internally, the penis contains the outer segment of the urethra, as well as erectile tissue. This erectile tissue is designed like a sponge. The many blood vessels in the erectile tissue are capable of greatly expanding and increasing the quantity of blood that they contain. When this happens, the erectile tissues swell, and the entire penis increases in length and width and becomes stiff. This process, called erection, is an involuntary reflex: It cannot be consciously prevented or caused. Erection can result from direct stimulation of the penis, as during sexual contact, or from erotic sights or sounds. In some animals, a bone within the penis, the baculum, assists in maintenance of the erection.

Continued sexual stimulation will eventually result in an ejaculation, with semen being forced out of the body by contractions of muscles in the fluid-producing glands and along the tube system. Ejaculation is coordinated by nerves that arise in the spinal cord. The normal volume of fluid ejaculated varies from species to species. In man, it is usually two to six milliliters; it may be up to one hundred milliliters in pigs. The ejaculate of most animals contains many millions of sperm per milliliter of fluid.

Studying Male Reproduction

The hormonal system that controls the male reproductive system is the subject of much research. The most straightforward type of hormonal research is simply descriptive: The scientist seeks to describe the levels of the reproductive hormones when the animal of interest is in different physiological states. The hormones can be measured in blood samples taken from the animals. Obtaining a blood sample from an experimental animal may pose difficulties: Some large animals may be difficult to restrain, and some small animals may not have veins large enough for an easy puncture. Another consideration is how often blood samples should be taken. Endocrinologists have become increasingly aware of the importance of the pattern of hormone release over time. In particular, it now appears that fluctuations in hormone levels within a time frame of minutes or hours may be critical in regulating the responses of hormone target sites. To obtain blood samples with such a high frequency, researchers usually implant a cannula into a vein of the animal; the cannula can be left in place for repeated blood sampling with very little stress to the animal.

Scientists interested in hormonal feedback may examine the roles of specific hormones by removing one of the endocrine glands from the system, and then examining the effects on the remaining hormones. For example, the testes (as the site of testosterone production) can be removed from an experimental animal. Blood samples after the surgery can then be assayed to determine the circulating levels of LH, FSH, and GnRH. The endocrine glands may be left in place, but the researcher may administer hormones either by injection or by implanting timed-release capsules containing the hormone under the skin. Then, blood samples taken from the animal will reveal how levels of hormones produced by the animal's own endocrine glands have changed as a result of the exposure to the added hormone.

A technique that is widely used to study males of seasonally breeding species is to subject the animals to carefully controlled environmental conditions. Length of exposure to light, temperature, rainfall, nutrients in the diet, and other factors can be controlled in the laboratory to determine which acts as the cue for seasonal reproduction. The status of the reproductive system can be determined by various methods. The testes can be measured: Inactive testes are usually smaller and lighter in weight. Hormone levels in the blood can be measured: Testosterone and other hormones may decrease when the animal is reproductively quiescent, or the male can be exposed to a female to determine whether he will show mating behavior.

For some types of research, the most revealing experiments may not use the entire animal (referred to as in vivo research), but will instead focus on specific organs. Living samples of organs can be maintained in the laboratory for such in vitro experimentation. For the in vitro approach, a small piece of living tissue can be removed from an animal and the cells suspended in a liquid that contains the nutrients necessary for their life. Under these isolated conditions, the scientists can investigate a number of areas such as which hormones tissues produce and the hormones that make the tissue itself respond. Organs respond optimally to a particular pattern of hormonal stimulation, and this is another important area of research. By combining the results of in vivo and in vitro experiments, scientists are able to piece together a complete picture of how the reproductive system functions.

Controlling Reproduction

Knowledge of how the male reproductive system functions has allowed scientists to develop technologies for controlling reproduction to enhance or curtail fertility in domestic animals. Knowledge of male reproductive physiology has been applied to the management of domestic breeding populations. Hormone measurements and sperm counts can be used to determine the optimum age at which to begin breeding young stock. Techniques for collecting and storing semen can be combined with artificial insemination of females to increase the number of offspring produced by valuable males, thus resulting in improvement of the population. These methods are particularly valuable to breeders of large animals because maintaining large numbers of males of these species (such as stallions and bulls) can be costly and difficult because of the aggressive behaviors that these males may exhibit.

The study of seasonal breeding has also been of value in agriculture. Scientists now know much about the environmental conditions that are responsible for promoting reproductive activity in many domestic species. Farmers can apply this knowledge to their breeding stock to increase production throughout the year. Another area in which reproductive studies are of vital importance is the enhancement of the breeding of captive animals that are endangered in the wild. Zoos, once considered merely spectacles for entertainment, are now seen by many as the last hope of saving many species on the verge of extinction. Knowledge of the conditions necessary for successful breeding of exotic animals will help to increase their numbers and, perhaps, to return them to the wild.

—Marcia Watson-Whitmyre

See also: Breeding programs; Cloning of extinct or endangered species; Copulation; Endocrine systems of vertebrates; Fertilization; Gametogenesis; Hormones in mammals; Hydrostatic skeletons; Lactation; Pregnancy and prenatal development; Reproductive systems of female mammals; Sex differences: Evolutionary origins; Sexual development; Wildlife management.

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REPTILES

Type of animal science: Classification
Fields of study: Herpetology, systematics (taxonomy), zoology

Living reptiles are vertebrates that lay eggs or bear live young. Included in this class are turtles, the tuatara, lizards and snakes, and crocodilians. The study of reptiles provides insight into a group of often very successful animals and into the characteristics of their ancestors, including groups that gave rise to birds and mammals.

Principal Terms

Anapsida: a group of reptiles in which the temporal region of the skull lacks openings

Chelonia (testudines): a living order of reptiles composed of turtles and tortoises

cleidoic egg: a shelled egg equipped with internal membranes that make terrestrial reproduction possible

Crocodylia: a living order of reptiles that includes crocodiles and alligators

Diapsida: a group of reptiles in which the temporal region of the skull is characterized by two openings

Euryapsida: an extinct group of reptiles in which the temporal region of the skull is characterized by a single opening situated high on the side of the skull

Rhynchocephalia: a living order of reptiles represented by a single species, the tuatara

Squamata: a living order of reptiles composed of lizards and snakes

Synapsida: an extinct group of reptiles in which the temporal region of the skull is characterized by a single opening; this group gave rise to mammals

venom: a toxic substance that must be injected in order to elicit damaging effects

Reptiles are a class of vertebrates characterized by their ability to produce cleidoic eggs (which are similar to bird eggs and were their evolutionary precursors). The development of this egg, protected by an impervious shell, was a historic step, as it allowed animals to exploit terrestrial habitats. The egg and the reptiles' dry, horny scales differentiate all living reptiles from amphibians. Skeletal features (single bones for sound conduction in the middle ear and jaws composed of several bones) and the lack of feathers and hair differentiate reptiles from birds and mammals, respectively. One must realize, however, that it is the combination of features that characterizes reptiles and that, since soft tissues such as reproductive tracts and skin do not fossilize well, distinguishing extinct forms from other closely related vertebrate groups is often dependent on a single characteristic and may not be precise. For example, *Archaeopteryx*, a primitive bird, would have been classified as a reptile had not feathers been adventitiously preserved.

Early Reptiles, Turtles, and Crocodiles

Reptiles arose from amphibians roughly 315 million years ago, during the Carboniferous period. These "stem-reptiles" gave rise to all other groups. The "cheek," or temporal region, is very important in reptilian classification. In early forms, the region was solid (lacked openings). These forms are placed in the subclass Anapsida (without recesses or openings). Along with some of these earliest reptilian fossils are some from a distinctly different group, with a single temporal opening. These animals are placed in the subclass Synapsida. Referred to as "mammal-like reptiles," they gave rise to mammals prior to their extinction. During the Permian period (280-215 million years ago), another reptilian group appeared. This group, characterized by two temporal recesses, is placed in the subclass Diapsida (two openings), to which the majority of reptiles, living and extinct, belong. Another subclass, the Euryapsida, with a single opening high on the side of the skull, became extinct near the end of the Mesozoic era (approximately 175 million years ago). It included large marine (sea-dwelling) forms, such as fishlike ichthyosaurs and flat-bodied, long-necked plesiosaurs.

Anapsids include not only the stem-reptiles, but also a surviving order, the Chelonia or Testudines, composed of turtles and tortoises. Primitive turtles appear almost fully formed in the fossil record, and their relationship to the first reptiles is uncertain. Their principal feature is a shell, composed of flattened ribs fused to layers of bony tissue, usually covered by large, flat scales called scutes. The upper portion, to which vertebrae are fused, is the carapace; the underside is the plastron. They are connected by bridges. Shoulders and hips have been modified and are located within the rib cage, a unique arrangement. All lay eggs on land. The order contains almost 250 species in 75 genera and 13 families. Although it is easy to fall into the trap of thinking that "if it has a shell, it is a turtle" and "a turtle is a turtle is a turtle," the group is quite diverse. The most common (and probably primitive) body plan is associated with marsh dwellers. Characterized by somewhat flattened shells (streamlined for locomotion through water) and webbed feet for propulsion, these surprisingly agile swimmers include the familiar sliders that drop into the water from logs or the bank when approached too closely. Though adept in water, they are no match for sea turtles; these animals have reduced, flattened shells to minimize resistance and limbs modified into paddles with which they fly through the water using movements almost identical to those of birds. Though they lay their eggs on land, they are practically helpless there. Graceful in the water, they often swim considerable distances, guided by a very effective navigational sense. Sea turtles include the largest living reptiles, the leatherbacks, which may exceed a ton in weight. Other turtles are bottom dwellers; ambush predators or scavengers, they lie in wait or slowly crawl along bottoms of ponds and streams. They possess webbed feet and flat, often rough shells. Algae growing on their shells serves as camouflage, hiding them from prey and predators. A final body plan characterizes land turtles, which include tortoises. A firm, generally high-domed shell minimizes surface area through which water might be lost (critical in terrestrial animals) and also resists attacks by predators to which a land dweller is exposed. Some very large forms are quite long-lived; one documented record exceeds 150 years.

The term "dinosaur" is often used to describe any large, extinct reptile, including mammal-like synapsids, marine euryapsids, and diapsids such as flying reptiles and some large lizards. Used properly, however, it refers to only one group of diapsids, the Archosauria, or "ruling reptiles," which gave rise to birds. Other close relatives are in the living order Crocodylia, which now contains only twenty-two species in eight genera and three families. These animals share some very advanced features that cause some authorities to place them in a distinct class, the Dinosauria. All have fully partitioned hearts, allowing separate circuits for oxygenated blood to be carried to the body and deoxygenated blood to the lungs. Recent evidence indicates that many dinosaurs may have possessed birdlike capabilities for temperature regulation, allowing levels of activity beyond that of other reptiles. Modern crocodilians, some exceeding 7.5 meters in length, are quite aquatic and feed principally on fish or animals ambushed as they drink. They are restricted to tropical and subtropical zones. All are egg-layers.

Lepidosauria and Squamata

All other living reptiles are in the diapsid group Lepidosauria (scaly reptiles). The tuatara, a lizardlike reptile up to sixty centimeters long, is the only surviving member of the order Rhynchocephalia, a diverse assembly that coexisted with dinosaurs. Restricted to roughly thirty small islands off the coast of New Zealand and well adapted to a cool climate, it demonstrates considerable longevity (approximately 120 years) but also has a low reproductive rate. It feeds primarily on insects and eggs and the young of sea birds or other tuataras, with which it shares burrows.

Arguably the most successful reptilian group, extinct or living, is the order Squamata. All are equipped with efficient vomeronasal organs with which they "smell" by sampling air or substrate with their tongues. They may lay eggs or give live birth. There are approximately 3,750 species of lizards, suborder Sauria or Lacertilia, in almost 400 genera and some 16 families. They are found from north of the Arctic Circle to the southern tip of South America; such range is perhaps attributable to their exceedingly efficient capacity for thermoregulation. Some lizards at below-freezing temperatures may maintain body temperatures near 20 degrees Celsius. It is difficult to characterize lizards because of their tremendous diversity. Some are legless—an adaptation for burrowing or living in dense grass. Others have the capacity for gliding. Feet may be modified for running (many run on their hind legs, in one instance so rapidly that the lizard can run on water for considerable distances) or climbing, with digits equipped with claws and/or adhesive pads. Teeth may be used for grasping, cutting, or crushing food. Tails may be prehensile (capable of grasping), may be used for balancing while climbing or running, may come equipped with spines or knobs for defense, may be capable of fat storage, and may even break off if grasped by a predator (often to regenerate rapidly). Some lizards are excellent swimmers; the marine iguana of the Galápagos Islands feeds primarily on seaweed. Two species are venomous. The smallest lizards are only a few centimeters long; the largest may exceed three meters.

Snakes

Snakes, suborder Serpentes or Ophidia, are distinct from lizards in that they lack external ears, eyelids, and limbs (at least one of which most lizards have—worm lizards lack these features and have been treated as snakes or even placed into a separate suborder). Despite these constraints, snakes are quite diverse: There are almost 2,400 species in more than 400 genera and 11 families, ranging from the Arctic Circle to the southern tip of South America. Leglessness was a primitive adaptation for burrowing, but modern snakes also swim, crawl, climb, and, in one case, even glide adeptly. The elongated body form that accompanies limblessness requires that paired internal organs be arranged longitudinally, with one often degenerating. Digestive tracts are short and straight, resulting in all snakes being carnivorous, as meat is more easily digested by snakes than plant material. Locomotion is surprisingly varied. The familiar serpentine movement works well either on land or in water, but heavy-bodied snakes often use rectilinear locomotion, pushing their bodies in straight lines by alternately raising and retracting their large belly scales. In tight quarters, snakes anchor their necks and pull their bodies forward or, alternately, push off using anchored tails (many are equipped with spines for this purpose). A few snakes, especially on loose substrates such as sand, sidewind, pushing down to prevent sliding while lifting loops of their bodies laterally.

Snakes swallow their prey whole. Jaws, which are loosely attached to the skull and to each other, alternately slide forward and pull back on food with recurved teeth. Prey may be swallowed alive, killed by constriction, or killed with venom. Venom injection may accompany a bite or may be facilitated by special fangs in the rear or front of each jaw. In vipers, the bones to which fangs are attached rotate, so that very long fangs can be folded back when not in use. Burrowing snakes tend to be slender and small, with smooth scales and rigid heads. Aquatic snakes are usually stout, with rough scales to prevent slipping through water. Arboreal snakes (climbers) are often extremely slender. Active hunters are usually more slender than ambush predators, which eat more rarely but can consume much larger items. Some snakes have temperature-sensitive pits with which they find prey in the dark. Sizes range from a few centimeters to almost ten meters.

The Komodo dragon is the largest living lizard species, with strong jaws that can sever the muscles of most vertebrates. (Corbis)

Studying Reptiles

Methods used to study reptiles are determined by the nature of the particular investigation. Historical studies rely on paleontological methods. The discovery of fossils, followed by recovery, preservation, reconstruction, and analysis, leads to an understanding of the structure and function of prehistoric animals and provides information about both how they lived and conditions in which they existed. Comparisons, especially of structures, with other fossils and with animals alive today constitute much of the field of comparative anatomy and lend insights into relationships between various living and extinct forms. These studies, in turn, lead into the discipline of systematics, which attempts to reconstruct relationships and build classification schemes accordingly. The actual naming of various groups is called taxonomy. Since fossil records are typically incomplete, however, other methods must be used to establish fully the nature of relationships.

Similarities and differences between living forms may be established on the basis of detailed anatomical studies or various biochemical techniques. In the latter case, the analysis of the molecular structure of the deoxyribonucleic acid (DNA) and proteins produced by different species (or even by different populations of the same species) allows determinations of how closely related certain forms may be. These studies also have considerable evolutionary implications, providing insights not only into methods that might have resulted in evolutionary changes among reptiles but also into the processes that were responsible for the origins of birds and mammals. One phenomenon that was first discovered in reptiles is parthenogenesis, the development of an individual from an unfertilized egg, a process that leads to all-female populations. In lizards these often result from hybridization between two species, the offspring of which are distinctive. Analysis of mitochondrial DNA, which is passed to descendants through the egg (never the sperm), allowed determination of which hybridizing parental species was maternal.

Another field of study that uses biochemical techniques and that focuses on reptiles concerns the venoms produced by some snakes and two lizard species. Knowing the composition of venoms is important in determining their effectiveness as devices to kill prey, but it is also significant in that some substances in these venoms have been shown to possess functional traits that have important medical implications.

Reptiles have also been used widely in ecological and behavioral studies. Methods include both field and laboratory techniques. Studies in natural situations often involve extensive observations and, as such, require organisms that are easily observed. Laboratory studies, in which environmental factors are often simulated and then modified, demand subjects that are small and readily maintained in captivity. Many of these studies also have physiological implications. Studies monitoring such factors as body temperatures, food intake, and foraging strategies often rely on reptiles, especially lizards, as they are ideally suited to these observational and experimental investigations. Considerable work in reproductive physiology also relies on reptiles; their eggs are accessible, and they demonstrate developmental patterns similar to those in birds and mammals. This aptitude as a subject for studies has also resulted in reptiles becoming the focus of many biogeographical studies, especially on islands, where (as in deserts) they often dominate the fauna. For many of the same reasons, environmental studies of endangered species or altered habitats frequently use reptiles as models.

Reptiles and Other Animals

The study of reptiles not only increases scientists' knowledge of this fascinating group of animals, but also has many other applications. Historically, reptiles were the first group of fully terrestrial vertebrates; they dominated the earth for many millions of years and gave rise to both birds and mammals. Thus, studies of fossil forms, with additional insights from investigations of living species, provide insights into the conditions that prevailed on the earth during prehistoric times. They also lead to theories regarding relationships between animal groups and lend understanding to the origins and nature of early birds and mammals. Studies of this type need not be restricted to arcane facts relevant only to times long past; they are also significant in understanding long-term biological processes, such as those that reflect climatic cycles and periods of mass extinction (both problems of considerable interest today). Also, since many reptilian groups are sufficiently old to predate the breakup of Pangaea (the single landmass that existed historically and which has since broken up into the continental areas of today), or at least its subsequent parts, applications can be made to the areas of biogeography and even geology.

Physiological investigations of reptiles have been invaluable in developmental and reproductive studies and in increasing knowledge of how animals interact with their environments. Lizards, especially, have been widely studied in regard to their ability to thermoregulate effectively using environmental sources of heat. These studies have numerous applications to broader investigations of homeostasis and adaptations to cold and hot environments by many animals (including man). Lizards also have been widely used as models in behavioral and ecological studies. Especially in the tropics, they are abundant, diverse, easily observed, and often remarkably well-adapted to their environment. Like birds, much of their behavior is quite stereotypical, that is, innate and consistent. As a result, the recognition of patterns is much easier than it is in secretive mammals, for example, where the problems are further magnified by frequent modifications of instinctive mechanisms by learned behaviors. This same visibility and ease of observation lends itself to ecological investigations. Lizards have been more widely utilized in niche partitioning studies than has any other animal. Niche partitioning studies seek to investigate how limited resources are used by animal communities. They often center on the hypothesis that food habits are critical, but microhabitat preferences, activity cycles, and other aspects of environmental impact are also involved.

—Robert Powell

See also: *Allosaurus*; *Apatosaurus*; *Archaeopteryx*; *Brachiosaurus*; Chameleons; Circulatory systems of vertebrates; Cold-blooded animals; Crocodiles; Dinosaurs; Evolution: Historical perspective; Extinction; Fish; Hadrosaurs; Ichthyosaurs; Lizards; Pterosaurs; Sauropods; Scales; Snakes; Systematics; Stegosaurs; *Triceratops*; Turtles and tortoises; *Tyrannosaurus*; Thermoregulation; Velociraptors.

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RESPIRATION AND LOW OXYGEN

Type of animal science: Physiology
Fields of study: Anatomy, biochemistry, physiology

Nearly all animals require free oxygen in order to convert food to living tissue and energy, yet many animals face periods when oxygen supply is diminished. Adaptation to low oxygen involves developing mechanisms to compensate for the reduced oxygen supply.

Principal Terms

HYPERVENTILATION: an increase in the flow of air or water past the site of gas exchange (lung, gill, or skin)

HYPOXIA: from two Latin words, *hypo* and *oxia*, meaning "low oxygen"

METABOLISM: the sum of all of the reactions that take place in an animal allowing it to move, grow, and carry out body functions

RESPIRATORY PIGMENT: a protein that "supercharges" the body fluid (blood) with oxygen; the oxygen can bind to the pigment and then be released

RESPIRATORY SURFACE: the gill, lung, or skin site at which oxygen is taken up from the air or water into the animal, with the release of carbon dioxide at the same time and site

SYSTEMIC: referring to a group of organs that function in a coordinated and controlled manner to accomplish some end, such as respiration

VENTILATION: the movement, often by pumping, of air or water to the site of gas exchange; commonly thought of as breathing

Adaptation to low oxygen refers to a number of different changes in metabolism or body function, or both, that animals use to survive low-oxygen conditions. Low-oxygen conditions mean a reduction in the amount of oxygen available in relation to the need or demand for oxygen by the cells, or tissues. Low oxygen, or hypoxia, therefore, can result from either a decrease in the supply at constant demand, or an increase in demand at a constant supply. The former, a reduction in oxygen supply, is the focus of the present discussion. Low oxygen resulting from increased oxygen demand usually is referred to as tissue hypoxia and is discussed only briefly here.

Oxygen is required by animal cells in order to produce energy used for growing, moving around, or simply maintaining normal body functions. At times when less oxygen is available, animals must either move to some place where there is sufficient oxygen, or change some internal function or process. A change in internal function or process is an adaptation that allows the animal to live with less oxygen or that will be a means of keeping the supply of oxygen to the tissues great enough to meet the needs of the cell.

External or environmental hypoxia results from one of two conditions: a greater utilization of oxygen by plants and animals than can be renewed by natural processes, or a lower density of air (at high elevations). It is necessary that animals cope with a decrease in oxygen in some way, in part because of the consequences of a decrease in internal oxygen supply. If oxygen supply to the tissues and cells falls, then the functions that require oxygen will fail or at least be reduced. The functions that fail include the "maintenance functions" of a cell, apart from growing or producing specialized chemicals. The types of low-oxygen conditions that have received the most attention from researchers are high altitude, diving by air breathers, and oxygen depletion in water. Some of these are temporary; others, such as high altitude, can last for a lifetime for animals that do not migrate.

Increase in Ventilation

One common adaptation to hypoxia is an increase in ventilation—the amount of air or water that the animal breathes. This increase is referred to as hyperventilation, and it makes up for the reduced amount of oxygen in the air or water by breathing a greater volume. This response is especially common in mammals that move to high altitude, fish and crabs, and some other water-breathing animals. A simple mathematical example will show how the response is effective. If an animal normally breathes one liter of air per minute and removes half the oxygen (air contains 209 milliliters of oxygen per liter), then it is taking in 104.5 milliliters of oxygen per minute. If the amount of oxygen in the air falls to only 104.5 milliliters per liter, and the animal still uses half of that (52.25 milliliters), then it must breathe two liters of air per minute to keep taking up 104.5 milliliters of oxygen per minute. Such an increase in ventilation can be accomplished by an increase in the frequency of the respiratory pump, or by increasing the volume of water or air that is moved with each "breath." For this response to occur, the nervous system must sense the reduction in oxygen and provide a nerve impulse to the brain, which then stimulates the ventilatory pump(s) to increase activity.

It may seem that this adaptation is all that would be needed for animals to survive hypoxia, but there are some limitations to this adaptation. First, hyperventilation causes increased muscular activity and an increase in oxygen used to move the respiratory muscles. The greater ventilation volume is a benefit, but the cost is a greater demand for oxygen. For animals that breathe air, the increase is rather small, but for animals that breathe water, the increase in the muscular activity causes a substantial increase in the oxygen used to pump the water, so that the "cost" may be greater than the "benefit" when the oxygen falls to low levels. Another problem exists for air breathers. Air breathers are in danger of losing water in the air that is exhaled (desert animals, such as camels, have elaborate mechanisms to conserve this respiratory water loss). Hyperventilation increases the water loss and requires the animal to drink more water. A final problem for both air and water breathers is that carbon dioxide is lost from the same respiratory surface where oxygen is taken up. Hyperventilation thus increases the loss of carbon dioxide, changing the chemical balance of the body as a whole.

Blood Flow and Oxygen Delivery

In response to an internal hypoxia, many animals also exhibit an increase in the flow of blood to the tissues. This response is similar to that described for the ventilation system. An increased rate of flow compensates for a smaller amount of oxygen delivered for a given volume of blood (or respiratory medium in the case of ventilation). As with ventilation, blood flow can be elevated by increasing heart rate or by increasing the volume of blood pumped with each beat. There are numerous limitations to the effectiveness of this response, and it is only short term. The limitations center on the critical role of blood flow and blood pressure in the function of other systemic body functions. An excellent example is how kidney filtration rate increases with blood pressure.

Long-term adaptations to low oxygen often increase the ability of systemic respiratory functions to maintain oxygen delivery to the tissues. In the case of internal oxygen transport, this can be accomplished by increasing the amount of oxygen carried by the blood. A higher concentration of respiratory pigment accomplishes this, increasing either the number of red blood cells or the concentration of respiratory pigment in the blood. This adaptation requires the synthesis of new proteins and possibly new cells. Not surprisingly, many days or even weeks may be needed to increase respiratory pigment levels. Another way in which oxygen transport by the respiratory pigment may be improved is by increasing the concentration of a chemical that affects oxygen binding. This adaptation requires a change in metabolism and is discussed below.

Metabolic Alteration

One final type of adaptation to low oxygen is an alteration in the basic metabolism of the animal. Metabolic changes can take one of several forms. First, a simple reduction in metabolism will lower the need and demand for oxygen by the cells. To be effective, this must occur before the oxygen has been exhausted, so as not to impair normal functions. A few animals show this type of adaptation, which is thought to result from the metabolic reactions being limited by the availability of oxygen. Second, the chemical reactions involved in metabolic pathways (a series of chemical reactions) may be altered in low-oxygen conditions so that different reactions take place to maintain energy production. The nature of these adaptations is that an alternative metabolic pathway requires different enzymes and perhaps different chemicals in the reactions. Last, a metabolic adaptation may yield a product that has an enhancing effect on oxygen transport. An enhancement of oxygen transport occurs when certain chemicals increase the ability of the respiratory pigment to bind oxygen or cause the respiratory pigment to bind oxygen at lower oxygen levels; this is called an increase in oxygen affinity. The change in metabolism at low oxygen thus results in an improvement in the supply of oxygen to the tissues. This response is seen in both vertebrates and invertebrates.

An excellent example of an animal that shows nearly all of the adaptations to low oxygen is the blue crab, the common commercial crab found throughout the Gulf Coast of North America and on the East Coast from Florida to New York. To compensate for low oxygen, the blue crab increases the flow of water over the gills, thereby keeping the amount of oxygen that actually passes over the gills nearly constant. Blue crabs also increase the heart rate, thereby increasing the rate of blood flow in the gills and to the muscles and organs of the body. This increase helps maintain the oxygen supply. If the period of hypoxia is brief, only a few hours, then these reactions may be all that is required for the animal to survive. If, however, the hypoxia continues for days or even weeks, then other responses come into play. There are changes in metabolism and in the way in which oxygen is transported in the body. Metabolism actually decreases so that less oxygen is needed by the animal. When that happens, then there must be some activity, such as swimming, that the animal gives up for lack of energy. The other change is an improvement in the way oxygen is transported to the tissues by the respiratory pigment, hemocyanin—a certain kind of protein, dissolved in the blood, that binds oxygen at the gills and can release the oxygen at the tissues where it is used by the cells. This improvement takes the form of increasing the level of a chemical in the blood that changes the binding of oxygen to hemocyanin. The hemocyanin then works as well when the animal is in hypoxic water. In addition, the crab can, and does, make the hemocyanin in a new form, so that it works better in the hypoxic conditions.

Understanding the Respiratory and Circulatory Systems

Adaptation to low oxygen (either high demand or reduced supply) has been studied with the idea of understanding the functional capabilities of the respiratory and circulatory systems that supply oxygen to the tissues. Many different experimental protocols and procedures are used to assess the balance between oxygen uptake and oxygen demand when the external supply of oxygen is limited and demand remains constant. One approach to the study of low-oxygen conditions has been to compare animals that live at sea level in high-oxygen habitats with those living in habitats in which oxygen levels are low. A comparison of water breathers and air breathers is, strictly speaking, within the realm of consideration. Water holds much less oxygen than air, and is therefore a low-oxygen condition. Freshwater at room temperature contains about 0.8 milliliter of oxygen per 100 milliliters of water; there are 20.9 milliliters of oxygen in the same volume of air. To obtain the same amount of oxygen, an animal must thus take all the oxygen from either 2,600 milliliters of water or 100 milliliters of air. Consequently, air breathers have much lower ventilation rates, at the same temperature, than do water breathers of the same size. The lower ventilation rate of air breathers is considered functional by reducing the loss of water from the respiratory surface.

Such adaptation is principally evolutionary and involves the transition from water breathing to air breathing in the evolutionary transition to land. There are a great many morphological as well as physiological consequences of this transition.

Adaptation to short-term hypoxia has been studied under controlled conditions in the laboratory in a variety of animals. Short-term conditions may mean anything from a few hours to weeks or even months. The length of the low-oxygen exposure generally depends on the animal used, its ability to withstand low oxygen, and the nature of the inquiry into the responses. Some clams, for example, are able to live in the absence of oxygen for several weeks. These experiments require careful monitoring of the animal and the conditions to ensure that oxygen neither rises nor falls too low and that the animals will survive.

A method that has been used to study adaptation to low oxygen in mammals is to conduct field studies in which the subjects are temporarily moved to high elevations. Mountain-climbing expeditions have been involved in some of these experiments in areas throughout the world. Additionally, experimental stations have been established at certain locations for the purpose of conducting these research projects. In this way, medical researchers are able to bring in appropriate equipment and supplies necessary to make complex and precise measurements.

All approaches to the study of low-oxygen adaptation require measurements of respiratory function or metabolic processes, or both. These measurements assess the uptake and transport of oxygen and the transport and excretion of carbon dioxide. The specific measurements are of the rate of oxygen uptake, ventilation volume and rate, blood flow, heart rate, oxygen transport properties of the blood, and oxygen uptake. In long-term monitoring studies of free-ranging animals, the animals are frequently fitted with implanted electrodes and blood sampling tubes. In this way, measurements can be made routinely over long periods without disturbing the animals.

A common measure of respiratory function is the total amount of oxygen used by an animal in a given period of time. The rate of excretion of carbon dioxide is another measure of overall function. The ratio of carbon dioxide loss to oxygen uptake is used to determine the nature of the metabolic pathways at a given time. Different metabolic pathways have characteristic oxygen uptake and carbon dioxide excretion ratios, and these are used in a predictive or diagnostic fashion. Some of the methods do not impair normal activity and can be used in low-oxygen experiments. The technique of placing small animals in respiratory chambers is used in these types of experimentation. Measurement of single organ function is used more often with larger animals, such as humans.

Evolution, Metabolism, and Ecology

Adaptation to low oxygen has been studied to understand three concepts better: evolutionary changes associated with oxygen availability, cell metabolism, and ecology of hypoxic habitats. Literally every aspect of oxygen uptake, transport, and utilization has received some attention.

Some of the evolutionary changes during the transition from water to land and from low to high altitudes have been studied as problems related to low oxygen. Results indicate that air breathers have lower ventilation rates than do water breathers of the same size. The lower ventilation rates are possible because of the higher oxygen levels, but they result in higher internal carbon dioxide levels. Animals such as insects, reptiles, and mammals have respiratory structures that are internalized and are inpocketings of the body wall. This arrangement aids in water conservation and helps keep the respiratory surfaces moist.

Just as important as research on the transition to land has been the information gained about the evolution of life in high-oxygen environments as compared to the low-oxygen conditions that are believed to have occurred in the ancient oceans. From this research, it is clear that the major advances in respiratory systems are present in invertebrates and probably evolved quite early in the history of life on earth. Marine worms possess closed circulatory systems, respiratory pigments, red blood cells, special gas exchange structures, gills, and alternate metabolic pathways.

Biologists interested in metabolism and the factors that cause metabolic rate to change have examined the relationship between metabolic rate and other physiological functions. Specifically, oxygen supply, carbon dioxide removal, and glucose supply have been examined because all three are directly involved in aerobic metabolism. Imposing a limitation on external oxygen supply has therefore been used as an experimental tool to probe the limits and capabilities of cellular metabolism.

One of the observations that biologists have made over the years is that animals tend to find a way to live in places that are in any way habitable, and they tend to adapt to occupy new habitats. Understanding the physiological mechanisms required or used in adaptations to low-oxygen habitats, such as stagnant pools of water, has allowed explanation of some evolutionary changes.

There are several habitat types that undergo hypoxia routinely, and the utilization of the natural resources of those habitats, as well as the effective preservation of the habitats, generally dictates that attention be paid to the effects on the animals. One of the bodies of water that undergoes low-oxygen conditions is the Chesapeake Bay, and the effects on the animals there have been studied.

—*Peter L. deFur*

See also: Circulatory systems of invertebrates; Circulatory systems of vertebrates; Gas exchange; Heart; Lungs, gills, and tracheas; Metabolic Rates; Mountains; Respiration; Respiration in birds.

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RESPIRATION IN BIRDS

Type of animal science: Physiology
Fields of study: Anatomy, biochemistry, evolutionary science, ornithology, physiology, zoology

Respiration in birds presents a physiological challenge that has been solved by the evolution of a unique and very efficient respiratory system.

Principal Terms

ADENOSINE TRIPHOSPHATE (ATP): the energy currency of cell metabolism in all organisms

AEROBIC: requiring free oxygen; any biological process that can occur in the presence of free oxygen

DIFFUSION: the net movement of molecules from an area of high concentration to one of lower concentration as a result of random molecular movements

HEMOGLOBIN: a protein in vertebrate red blood cells that carries oxygen and carbon dioxide

METABOLISM: the sum of all chemical processes occurring within a cell or living organism

RESPIRATION: the utilization of oxygen; in air-breathing vertebrates, the inhalation of oxygen and the exhalation of carbon dioxide

Flying is an activity that demands an extraordinary amount of metabolic energy. During flight, the active muscles of birds require and produce very large amounts of the cellular "energy currency" known as adenosine triphosphate (ATP) to power their contractions. To accomplish this, the flight muscles must be well supplied with oxygen extracted from the atmosphere. The flight muscles furthermore generate large amounts of carbon dioxide as a waste product of their metabolism, and this must be eliminated from the blood.

These facts make it tempting to propose that birds need a specially designed respiratory system because their need for oxygen must be greater than that of comparably sized mammals. Many textbooks say exactly this. Studies have shown that resting birds and comparably sized resting mammals both consume nearly identical amounts of oxygen. The argument says that flying birds must consume more oxygen than mammals exercising at high levels of performance. Further studies have shown that flying birds consume ten to fifteen times more oxygen than when at rest. This is no greater than the increase in oxygen consumption that any well-conditioned human athlete can attain.

The primary reasons that birds require a special respiratory system become clear when the structural limitations of size and weight imposed by flight and the extreme environments encountered during high-altitude flight (such as low oxygen availability) are taken into consideration. The respiratory system of a bird needs to be relatively light, compact, and efficient in order to maximize the animal's chances of survival. The avian respiratory system has evolved successfully, which is evident if one observes birds in steady flight at altitudes so high that the scarcity of oxygen would cause most mammals to become comatose even when totally inactive.

The Avian Respiratory System

This sort of respiratory performance has been achieved, within the imposed size and weight restrictions, through the evolution of the avian respiratory system into a unique and very efficient structure. Typical mammalian lungs expand and collapse inside the body with each breath (the lungs have a variable volume), and there is a bidirectional flow of gas into and then back out of them. In contrast, the bird's two lungs have a nearly constant volume through which most of the inhaled gas flows in one direction. This is possible because of the presence of several large, thin-walled air sacs that join the lungs and assist in their ventilation, much in the manner of a system of bellows to push air through the lungs.

The inhaled air initially follows an anatomic pathway in birds that resembles that of mammals—through a trachea (windpipe) that then divides into two tubes called the primary bronchi, each of which enters a lung. At this point, the anatomy of the bird becomes different as the primary bronchi actually pass completely through the avian lung to terminate in paired abdominal air sacs. These air sacs also have connections to several hollow bones in the bird's legs. Near the posterior end of the primary bronchi, furthermore, there is a pair of posterior thoracic air sacs that are connected to the primary bronchi via laterobronchi. Joined to the primary bronchi via one of several secondary tubes called the ventrobronchi are paired anterior thoracic air sacs and, depending upon the bird species, usually several other anteriorly located air sacs.

Very soon after entering the lung, four ventrobronchi branch from a primary bronchus. Farther along the primary bronchus, there are as many as ten additional secondary bronchi, called the dorsobronchi, which also leave the primary bronchus. The dorsobronchi and ventrobronchi both divide many times as they penetrate the lung tissue. Eventually the dorsobronchi become connected with the ventrobronchi by thousands of tiny parabronchi, each of which is only about one millimeter in diameter.

The parabronchial walls are like a lattice, perforated extensively with pockets called atria, which themselves have indentations known as infundibula. Interconnecting the infundibula are numerous tiny air capillaries approximately five micrometers in diameter. The lattice itself is made up of the capillary blood vessels into which the oxygen and out of which the carbon dioxide diffuse during the exchange of these gases between the air and the blood. This region of parabronchi and the many tiny air passages extending from them, all of which are enmeshed by the very dense network of blood capillaries, make up the gas exchange area of the avian lung.

Inhalation and Exhalation

The bronchi, primary and secondary, and the air sacs do exchange gas with the blood during avian respiration. Their only function is to help move the air through the actual gas exchange organs, the lungs. To achieve the unidirectional flow of air through the lungs, the inhaled, oxygen-rich air passes through the primary bronchi directly into the posterior air sacs, which are being expanded as a result of the movements of inhalation. While this is happening, the air that is already in the gas exchange areas of the lungs is being pulled out of them and into the anterior air sacs, which are also experiencing expansion during inhalation. Replacing this air in the lungs is a portion of the oxygen-rich air from the primary bronchi that does not enter the posterior air sacs, but flows into the posterior lung regions and is directed forward to the anterior areas.

During exhalation, both the posterior and anterior air sacs are compressed and their contents emptied. The air from the posterior air sacs enters the gas exchange areas of the lungs, not yet having lost any of its oxygen, and flows in a posterior to anterior direction. The air from the anterior air sacs, loaded with the carbon dioxide which had diffused out of the blood capillaries, enters the primary bronchi and is exhaled by the animal. The cycle then repeats itself with the next inhalation.

During the cycles of inhalation and exhalation, the air is always passing through the gas exchange areas of the avian lungs in a single posterior to anterior direction. The air passing through the gas exchange areas of the lung also always contains a relatively constant and high percentage of oxygen that can diffuse into the blood inside the lung's blood capillaries. The blood entering these capil-

The structural limitations of size and weight as well as the low oxygen conditions encountered at high altitudes have caused birds to evolve exceptionally efficient respiratory systems. (Corbis)

laries is rich in carbon dioxide, which diffuses out of the blood and into the air as it passes through the lung on its way to the anterior air sacs, and eventually out of the animal.

Blood and Oxygen

It is necessary here to address the possibility that avian blood might have some special properties that allow it to extract and transport oxygen much better than mammalian blood. The blood of birds, however, is actually not significantly better in this respect. The primary oxygen transporter is the avian hemoglobin molecule, and it does not perform significantly better than the hemoglobin found in mammals, nor is there any real difference in the amount of hemoglobin contained in avian blood. Avian blood has no special properties that would contribute to the remarkable performance of the avian respiratory system.

The flow of the blood with respect to the gas flow through the gas exchange regions is a crucial factor. The flow of blood through the pulmonary (lung) blood capillaries is in a direction that permits the efficient extraction of the air's oxygen. While it was previously believed that there was a countercurrent flow of air and blood, with the air moving through the lung in a posterior to anterior direction and the blood flowing through the lung in an anterior to posterior direction, it is now known to be a crosscurrent system. This crosscurrent system has the air still passing in a posterior to anterior direction, but the blood flows in a combination of the opposite direction and at a right angle to the air flow. This critical design feature, combined with those mentioned in the next paragraph, permits the avian lung to be the most efficient of any known gas exchange organ for an air breathing animal.

To comprehend the compact and efficient design of the avian lung, it is necessary only to measure the ratio of the surface area it uses for gas exchange to the lung volume. This value is approximately ten times greater than the ratio found in mammals, allowing more blood per unit of volume of lung to be present at any time. This is really of importance only when it is noted that avian lungs have more blood in their capillaries per unit of volume of lung than do mammalian lungs. Since only the blood in the capillaries can pick up oxygen and get rid of carbon dioxide, the value of such features is obvious: small and very efficient lungs.

Avian Anatomy and Physiology

The primary techniques utilized in the study of the avian respiratory system come from the fields of anatomy and physiology. Modern work involves the use of electron microscopes, miniature gas flow meters, and even tiny radio transmitters that can send signals from sensors implanted in a freely moving animal.

The connection of the airways with the large air sacs was first reported in the seventeenth century. In the eighteenth century, pioneering studies were performed which showed the interesting fact that some hollow bones of the bird were connected to the respiratory system. It is, in fact, possible for a bird to breathe through one of these bones if its normal airway is blocked and the hollow center of the bone is opened to the atmosphere.

The rate at which birds consume oxygen can be measured in much the same way as it is in other animals. This can involve the use of a respirometer, a device to record the volumes of air inhaled and exhaled during breathing. It can also indicate how much oxygen is retained by the animal for its survival. Other methods are also used if the experimental demands preclude the use of such a device.

Scientists have even sampled the air at different places in the respiratory system of birds. To do this, it is necessary to insert small tubes into the regions of interest (for example, into the different air sacs) and to withdraw small samples of the gas found within these structures at different times during the breathing cycle. The samples are then tested for their oxygen and carbon dioxide content. The results can reveal whether the gas has already experienced exchanges of oxygen and carbon dioxide with the blood, and whether the gas is being replaced at regular intervals or is only being stored there. The latter question involves using a marker gas mixture that the animal first inhales for one or more breaths and that is then replaced by normal air for inhalation. The rate of disappearance of the marker gas indicates how quickly the gas content of the region being studied is replaced.

Similarly, miniature gas flow meters have been developed for investigating the direction of the gas flow within the various regions of the respiratory system. Inserting these into the airways of larger birds shows clearly that gas flows through the bird lung in a unidirectional way. The results of such investigations have allowed scientists to discard incorrect hypotheses about the manner in which the inhaled air is distributed throughout the bird's respiratory system and about the functions of various respiratory structures.

Biochemical studies of avian blood measure the same factors as are measured in other animal blood tests. The quantities of interest are the hemoglobin content of the blood (important because it carries essentially all the oxygen transported by the blood), the ability of avian hemoglobin to carry oxygen, the effects of various factors on the hemoglobin-oxygen interactions (such as the normally occurring acids of the blood, carbon dioxide, and temperature), and the ability of the hemoglobin to transport carbon dioxide. It is important to learn about these factors because of the intimate relationships between the respiratory organs and the blood (as transporter of the oxygen and carbon dioxide between the lungs and the other tissues of the body). These studies have revealed no dramatic differences between avian and mammalian blood with respect to the blood's respiratory functions.

These and many other methods are used to investigate avian respiratory systems. As a result of these studies, scientists know that a bird's ability to maintain sustained flight at high altitudes results not from any special properties of its blood, but is based on the very special design of its respiratory organs.

Altitude and Oxygen Demand

Regardless of the animal, there is one common need for survival—oxygen. Oxygen must be delivered at a rate high enough to permit the organism's cellular functions to take place, most of which require a continuous and large supply of adenosine triphosphate (ATP). The energy-rich ATP molecules are made in large quantity by the processes of aerobic cellular respiration (oxygen-dependent cellular respiration). Without sufficient oxygen, rates of aerobic cellular respiration sufficient for maintaining life are impossible. Correctly interpreting the value of the avian respiratory system requires an understanding of the characteristics and demands of avian life. Because of the high activity levels of flying birds, but especially because of the elevations at which this activity occurs and the consequent reduction of oxygen availability, birds require very efficient respiratory systems. To provide them with the required oxygen within the context and demands of their lifestyle, they have evolved a distinctive respiratory system. The anatomical, physiological, behavioral, and chemical components of the bird are all exquisitely adapted to these demands, not as independent entities but as an integrated system.

The unique structure of the avian respiratory system endows it with the distinction of being the most efficient air breathing organ among the vertebrates. It is able to extract oxygen from the air so efficiently that prolonged flight is possible at altitudes where the low availability of oxygen is disabling to most vertebrates even at rest.

Knowledge of how this is accomplished may eventually prove useful to engineers in the design and development of high-efficiency oxygen extraction devices. Large-scale applications of this sort of device could serve to enrich the atmosphere with oxygen for the survival of animals in hostile environments. Regardless of the possible practical applications of the knowledge of the structure and function of avian respiratory systems, they have provided a remarkable example of a creative solution to environmental demands which resulted from the process of natural selection.

—John V. Urbas

See also: Adaptations and their mechanisms; Birds; Circulatory systems of vertebrates; Flight; Gas exchange; Lungs, gills, and tracheas; Respiration; Respiratory system; Wings.

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ANIMAL LIFE

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ANIMAL LIFE

Volume 4

Respiratory System–Zoos
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RESPIRATORY SYSTEM

Types of animal science: Anatomy, geography, physiology
Fields of study: Anatomy, biochemistry, cell biology, environmental science, histology, immunology, pathology, physiology

The respiratory system maintains a constant flow of oxygen into the blood while removing carbon dioxide. Other functions of the respiratory system include maintaining blood acid-base balance, reducing body temperature, communicating by means of sounds, and removing inhaled microbes.

Principal Terms

ALVEOLUS: the thin-walled, saclike lung structure where gas exchange takes place

CHEMORECEPTOR: specialized nervous tissue that senses changes in pH (hydrogen ions) and oxygen

COUNTERCURRENT EXCHANGER: the process where a medium (air or water) flowing in one direction over a tissue surface encounters blood flowing through the tissue in the opposite direction; this improves the gas diffusion by maintaining a concentration gradient

DIFFUSION: the process by which gas molecules move from a higher to a lower concentration through a medium or across a permeable barrier; the rate at which gases cross a barrier is increased by the surface area, and gas concentration gradient is decreased by the thickness of the barrier; gas solubility determines the amount that crosses the barrier

GILL: an evaginated organ structure where the membrane wall turns out and forms an elevated, protruding structure; typically used for water respiration

LUNG: an invaginated organ structure where the membrane wall turns in and forms a pouch or saclike structure

Animals generally meet their energy needs by oxidation of food, and the respiratory system supplies the oxygen necessary for cell metabolism while removing its waste product, carbon dioxide. Oxygen is available either dissolved in water or as a component of the air, and animals have evolved special organ structures to effectively obtain oxygen from their environment.

Organs of Gas Exchange

Single-cell and simple organisms, such as flatworms and protozoa, can obtain sufficient oxygen to meet their energy demands by simple diffusion through their body surface. Some amphibians utilize gas exchange through their skin to supplement their lung respiration, but generally, larger, more complex animals require specialized organ systems with a large surface area for gas exchange and a circulatory system for distribution of oxygen to each cell. The basic mechanism, however, for gas exchange between the environment and the blood and between the blood and cells is by diffusion. The three major types of gas exchange organs are the gill for water respiration, the lung for air and in some special cases water respiration, and the tracheas system of tubules for air respiration in insects.

Gills consist of several gill arches located in the operculum or gill cover on each side of the fish's head. A gill arch contains two rows of gill filaments, and each filament has a row of parallel platelike structures on its surface called lamellae. The lamellae are everted structures that rise up

Respiratory Pigments

The amount of oxygen dissolved into circulatory fluids is insufficient to meet the oxygen requirements for almost all vertebrate animals. Respiratory pigments, colored proteins that contain a metal (usually iron or copper) have evolved to increase the amount of oxygen carried by the blood one hundredfold (20 milliliters of oxygen per 100 milliliters of blood, compared to 0.2 milliliters of oxygen per 100 milliliters of blood). These pigments have the unique property of binding oxygen at the gas exchange surface of the gill or lung, transporting the oxygen in circulation, and then releasing the oxygen to the cells, where it can be utilized for energy metabolism.

The most common respiratory pigment is hemoglobin, which has a positively charged iron atom (divalent) attached to a circular protein ring (porphyrin ring). Oxygen is negatively charged and binds to the positive charge of the iron. This bond is easily broken at the tissue level, where oxygen is released. Copper-containing respiratory pigments are called hemocyanins and are found in mollusks and arthropods. Next to hemoglobin, they are the most widely used respiratory pigment.

Hemoglobin is bright red when it carries oxygen and turns a purple-blue color when it has released some or all of its oxygen molecules. Hemoglobin can be found either circulating free in the plasma, typically in insects called hemolymph, or contained in red bloods cells called erthyrocytes, circulating in the plasma.

from the filament surface and are only a fraction of a millimeter apart. Water flows between the lamellae, and oxygen diffuses from the water into the lamellar capillary blood. The lamellar blood flows in the opposite direction of the water flow and creates a countercurrent exchanger. The countercurrent maximizes the diffusion of oxygen into the lamellar capillary blood by maintaining a diffusion gradient over its entire length.

Lungs, in contrast to gills, are invaginations, where the surface turns in and forms a hollow or saclike structure. Lungs typically are divided into two functional areas: the conducting zone and the respiratory zone. The conducting zone branches from the trachea to the bronchioles and distributes air to the respiratory zone but is not involved in gas exchange. The respiratory zone comprises the majority of the lung and contains small respiratory bronchioles and ducts that lead to the primary gas exchange area, the alveolus. The alveoli vary from simple saclike structures in a pulmonate land snail to the complex alveolar wall structure of mammals. The alveolar wall is fifty micrometers thick, or about one fiftieth the thickness of a sheet of paper, and is composed of epithelial cells covering the alveolar surface, an interstitial space, and the endothelial cells that make up the capillaries. This thin-wall structure allows for the diffusion of oxygen and carbon dioxide between the air and blood.

The insect tracheas respiratory system is unique because it is both the gas exchange and distribution system. Pairs of openings on the insect's thorax and abdomen called spiracles regulate the movement of air in and out of a tubule system. The spiracles open and close in a pattern that allows unidirectional flow of air through the tubule system. The tubules branch and extend throughout the insect's body and deliver oxygen to the cells independent of the circulatory system.

Air and Water Environments

Important aspects of the atmosphere for respiration are the barometric pressure and concentration of gases, temperature, and humidity. The atmospheric gases important to animals are oxygen, carbon dioxide, and nitrogen, and the atmosphere is a constant 20.95 percent oxygen, 0.03 percent carbon dioxide, and 79 percent nitrogen (plus other inert gases). The rate of diffusion of oxygen from the inspired air into the circulation depends on the partial pressure of the oxygen. The barometric pressure, however, decreases with increasing altitude, and this decreases the partial pressure of oxygen, which decreases the diffusion of oxygen into the blood. Thus an animal's difficulty in obtaining adequate oxygen at higher altitudes is related to the reduction in atmospheric pressure and not to a change in the percentage of oxygen in the atmosphere.

The temperature and amount of water vapor or humidity in the atmosphere are variable, and during inspiration, the inspired air is warmed to body temperature and saturated with water vapor (100 percent humidity). The heat and moisture come from the airways and can potentially cool and dehydrate an animal. Therefore, a minimal amount of air is inspired to prevent excess heat and water loss. However, heat-stressed animals will use this respiratory heat loss or panting to cool their bodies.

Water poses several challenges for respiration compared to air: a lower oxygen content, slower gas diffusion rate, higher viscosity, and greater weight. The amount of oxygen available in the water is thirty times less than that found in air. Thus, more water has to flow over the gill surface for adequate oxygen delivery. The speed at which oxygen moves through the water is ten thousand times slower than oxygen moving through the air. Thus, the distance between the water and the gill surfaces can only be a fraction of a millimeter apart. In contrast, the lung gas exchange surfaces are a few millimeters apart.

Water's greater viscosity and weight compared to air require more energy to move water over the gill surface. Water-breathing animals compensate for this by having a unidirectional flow through the gill. This avoids water being moved, stopped, and then moved again in the opposite direction, which works well for air, but would be very energy costly for the heavier, more viscous water.

The gill structure depends on water to support and separate the rows of lamellar structures. Thus, when a fish is exposed to air, the gill structure collapses on itself and greatly reduces the surface area available for oxygen diffusion. Thus, the fish will suffocate if not returned to the water.

Breathing Water and Breathing Air

Water can be moved through the gill lamellae by either opercular pumping or ram ventilation. Opercular pumping involves the movement of the mouth and opercular covering to create pressure gradients for unidirectional flow of water through the mouth, across the gill surface, and out the opercular covering (unidirectional flow). Ram ventilation takes advantage of the fish's forward speed to flow water through the mouth and gill. Opercular pumping is used from rest to slow swimming speeds, and a fish switches over to ram ventilation when swimming at faster speeds.

For air breathers, inspiration (inflating the lungs) can be accomplished by either positive-pressure or negative-pressure breathing. Positive-pressure breathing requires air pressure to inflate the lungs, which is similar to inflating a balloon or tire with a compressed air. The pressure is considered positive because it is greater than atmospheric pressure. For example, frogs use positive-pressure breathing by closing their mouths and then elevating the floor of the mouth. This compresses and pressurizes the air and forces it into the lung. The elastic lung tissue is stretched like an inflated balloon by the increased volume. The process of the air moving out of the lung is called expiration. When the frog relaxes and opens its mouth the lung elastic recoil forces the air out similar to a balloon deflating.

With negative-pressure breathing, the lung is pulled open by contraction of the diaphragm. The pressure becomes negative (below atmospheric pressure), and air flows into the lung until it equalizes with the atmospheric pressure. If additional inflation is required, such as during exercise, accessory inspiratory muscles lift the ribs to inflate the lungs further. Expiration is accomplished by the relaxation of the inspiratory muscles, and the lung elastic recoil increases airway pressure and air flows out of the lung.

Inspiration is always an active process, whereas expiration results from the passive elastic recoil of the lung tissue. However, active expiration is possible by contracting muscles that pull the ribs down and by using abdominal muscles to push the diaphragm farther into the thoracic (chest) cavity.

August Krogh

Born: November 15, 1874; Grenå, Jutland, Denmark
Died: September 13, 1949; Copenhagen, Denmark
Fields of study: Anatomy, environmental science, invertebrate biology, physiology, zoology
Contribution: Krogh originally described how animals exchange oxygen and carbon dioxide by diffusion and invented many instruments needed to conduct experiments that led to his conclusions. He received the Nobel Prize in Physiology or Medicine in 1920 for his studies on capillary function and muscle metabolism. In this work, Krogh published the first account of regulation of blood perfusion in muscle and other organs.

August Krogh's work focused on gas exchange in mammalian respiratory systems. (Nobel Foundation)

In 1897, Schack August Steenberg Krogh began working in the lab of the famous physiology professor, Christian Bohr. Dr. Bohr had studied the solubility of oxygen in different tissues and fluids, as well as the mechanisms of muscle contraction. These experiments greatly influenced Krogh's early studies of gas exchange in snails, frogs, and fishes. In 1899, Krogh published the equivalent of a master's thesis, demonstrating that, in birds, oxygen moved by diffusion through the thin lung membranes into the blood. His dissertation, in 1903, studied gas exchange in the frog and showed that skin respiration remains fairly constant, whereas large variability occurs in lung respiration. Krogh reasoned this was an example of the oxygen secretion hypothesis proposed by Bohr. However, later he would doubt his conclusion and demonstrate that oxygen moves solely by diffusion through tissues.

Krogh participated in an expedition in 1902 to Disko, North Greenland, where he investigated the carbon dioxide and oxygen content in springwater, streams, and the sea. From these studies, Krogh described the important role of the oceans in regulation of atmospheric carbon dioxide. He applied these techniques of measuring dissolved gases in animal physiological studies in 1904.

Krogh won the prestigious Seegen Prize, awarded by the Austrian Academy of Sciences, in 1906 for investigating whether free nitrogen or nitrogenous gases were released as a normal by-product of metabolism. He showed that gaseous nitrogen remained constant by using his unique respiratory gas quantification methods. Krogh determined nitrogen dynamics with gas measurements instead of using the traditional German method of Liebig and Rubner, who measured nitrogen content in ingested food and liquids and excreted nitrogen in feces and urine.

Marie Jörgensen, a medical student and scientist, married August Krogh in 1905. Together they published seven papers on the quantification and diffusion of gases in the blood. This overturned the view held by Dr. Bohr and the scientific establishment that stated that oxygen and carbon dioxide were "secreted" by a glandlike structure in the lung.

In 1908, a special position as Associate Professor in Zoo-Physiology was created for Krogh at the University of Copenhagen, and in 1910 Krogh founded a zoo-physiology (animal) laboratory at the University of Copenhagen. The laboratory was moved and enlarged in 1928 with financing from the Rockefeller Foundation. Eight years later, Krogh was promoted to a chair, which he held until his retirement in 1945. The Krogh Institute is still active today.

—Robert C. Tyler

Setting Breathing Rate

In water-breathing animals, such as fish and lobsters, the level of oxygen sets the ventilation rate (volume of water moved through the gill per minute) such that as oxygen content in the water decreases, the frequency of breathing movements increases. During fast swimming, fish using ram ventilation regulate the mouth opening so that the amount of water flowing over the gills just meets tissue oxygen demand. A wider mouth opening than is necessary increases the fish's frictional drag through the water and thus decreases the energy efficiency. Carbon dioxide is highly soluble in water and easily diffuses from water-breathing animals. Thus, blood carbon dioxide levels in water-breathing animals are very low and not used to regulate respiration rate.

In air-breathing animals, the blood levels of carbon dioxide and oxygen regulate the ventilation rate (air volume moved in and out of the lungs per minute). Carbon dioxide quickly diffuses from the small capillaries in the brain circulation into the fluid surrounding the brain cells (cerebral spinal fluid). Here the carbon dioxide reacts with water and forms carbonic acid. The hydrogen ions released from the carbonic acid stimulate chemoreceptor cells that in turn stimulate the respiratory center in the medulla, located in the brain stem. Higher concentrations of carbon dioxide increase the hydrogen ion concentration and thus increase ventilation rate. Air-breathing animals primarily regulate ventilation rate by carbon dioxide produced from metabolism and not low blood oxygen levels.

However, oxygen can regulate ventilation in animals at high altitudes. Oxygen partial pressure is sensed by chemoreceptors in the aorta and the carotid artery. These peripheral chemoreceptors sense the partial pressure of oxygen in the blood plasma, and as the partial pressure of oxygen in the air decreases, such as with altitude, the partial pressure of oxygen in blood also decreases. This increases ventilation, which then compensates for the lower oxygen partial pressure. In addition to low oxygen partial pressure, the peripheral chemoreceptors are stimulated by blood acidosis. For example, lactic acid released from skeletal muscles during strenuous exercise stimulates the ventilation rate in animals and humans.

—Robert C. Tyler

See also: Anatomy; Beaks and bills; Bone and cartilage; Brain; Circulatory systems of invertebrates; Circulatory systems of vertebrates; Claws, nails, and hooves; Digestive tract; Ears; Endoskeletons; Exoskeletons; Eyes; Fins and flippers; Immune system; Kidneys and other excretory structures; Lungs, gills, and tracheas; Muscles in invertebrates; Muscles in vertebrates; Nervous systems of vertebrates; Noses; Physiology; Reproductive system of female mammals; Reproductive system of male mammals; Respiration and low oxygen; Respiration in birds; Sense organs; Skin; Tails; Teeth, fangs, and tusks; Tentacles; Wings.

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RHINOCEROSES

Types of animal science: Anatomy, classification
Fields of study: Anatomy, zoology

The five rhinoceros species, in the ungulate family Rhinocerotidae, are among the world's largest land animals.

Principal Terms

DIURNAL: active during the day
KERATIN: a tough, fibrous substance plentiful in hair and horns
NOCTURNAL: active at night
PERISSODACTYL: ungulates having an odd number of toes
PREHENSILE: able to grip things
RUMINANT: a herbivore that chews and swallows plants, which enter its stomach for partial digestion, are regurgitated, chewed again, and reenter the stomach for more digestion
UNGULATE: a hoofed mammal

Rhinoceroses (rhinos), which are among the world's largest land animals, belong to the ungulate family Rhinocerotidae. There are three Asian and two African species existing today; the fossil record shows several dozen extinct species as well. The name of the animal comes from Greek *rhino + ceros*, meaning "nose-horned."

Physical Characteristics of Rhinoceroses

Rhinos weigh up to four tons and have short, thick, supportive legs. Rhino skin is thick, gray to brown in color, hangs loosely on the body, and is almost hairless. In the Asian species, skin folds at the junctures of the neck and limbs make them look armored. The Asian species also have have incisors and canine teeth, which are missing in the African species. Rhinos have long, prehensile upper lips, for grasping branches and removing leaves, which they eat.

Depending on the species, rhinos have one or two nose horns. In two-horned species, the horn closest to the end of the snout is longer. The horns are made of keratin, a fibrous substance that also composes hair. The horns are used for digging food, for defense, and in mating combats.

Rhinos are ungulates with three toes per foot, each of which ends in hooflike nails. Each front foot has a vestigial fourth toe. Rhinos, which are ruminants related to horses, eat grass, bulbs, leafy twigs, and shrubs. Although they look clumsy, rhinos can run as fast as horses. They have sharp vision, very good smell, and excellent hearing. Their keen hearing is due in part to their funnel-shaped ears, that swivel in different directions.

Rhino Life Cycles

Most rhinos are both diurnal and nocturnal, active in daylight hours as well as after dark. They eat during the cool mornings and evenings, staying in mud wallows during hot afternoons. Rhinos have few enemies because of their size and their dangerous horns—an angry rhino charges its attackers. Humans are rhinos' great enemies, killing them for their horns, which are used in jewelry or medicinally.

Most rhinos, especially males, live alone except during mating. There are some exceptions to solitary living: mothers live with their offspring, and young males or females may form same-sex groups. Males have territories, which are marked and defended. They fight each other for mates. While rhinos may not live with others of their own species, they almost always have symbiotic birds, called oxpeckers, living on and around them. The birds eat insects from the rhinos' skins. This gives the bird food, and frees the rhino from the insects.

Mating takes place year round, and gestation lasts up to fifteen months. The female gives birth to a baby that weighs between 100 and 150 pounds. The young rhino stays with mother for 2.5 years, though it can feed itself in 2.5 months. Rhinos mate at seven to ten years of age. Females wait for approximately three years between gestations, only becoming pregnant after the previous offspring has left them. Rhinos live for up to forty-five years.

Rhinoceros Species

There are five rhino species: three in Asia and Malaya, and two in Africa. African rhinos are two-horned and classified as "black" or "white," though all are bluish-gray. Black rhinos live in habitats from mountain forests to scrub lands. Their maximum body length is 10 feet, their height is 5 feet at the shoulder, and they weigh 1.75 tons. Each has a front horn up to 3.5 feet long. The rear horn is shorter.

Rhinoceros Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Perissodactyla
Family: Rhinocerotidae (rhinoceroses)
Genus and species: Ceratotherium simum (white rhino); *Diceros bicornis* (black rhino); *Rhinoceros unicornis* (Indian rhino), *R. sondaicus* (Javan rhino); *Dicerorhinus sumatrensis* (Sumatran rhino)
Geographical location: Africa and Asia
Habitat: Forests, grasslands, and scrub lands
Gestational period: Eight to seventeen months
Life span: Twenty to forty-five years
Special anatomy: Incisors and canine teeth in Asian species; very thick skin; one or two horns; three-toed feet

Despite their size and awkward-looking bodies, rhinoceroses can run as fast as horses. (Corbis)

Black rhinos are mostly nocturnal, eating in the cool morning and evening hours and wallowing in river mud during the hot daylight hours. They eat grass, leaves, herbs, fruit, branches, and twigs. In the wild, a male has a marked territory, which he defends. When the territories of several males overlap, they form groups that share resources and defend the combined territory from strangers.

White rhinos, similar to black rhinos, are the largest land mammals except elephants. Their maximum length is 13 feet, shoulder height is 6.75 feet, and they weigh 4 tons. Females use their horns for digging, defense, and guiding their offspring. Nearly extinct, white rhinos exist only in preserves.

Indian rhinos—the largest Asian rhino species—average 10 feet in length and 5.5 feet in shoulder height, and weigh 2.75 tons. They have one thick, foot-long horn; their skin is sprinkled with knobs, and folds at the limb joints make them look as though they have armor. Females, although 75 percent the weight of males, have similar body heights and lengths. These rhinos live in marshy jungles and eat reeds, grass, twigs, and plant shoots. There are 1,500 Indian rhinos, all living in preserves and protected by legislation. Javan rhinos are similar to the Indian species, but smaller. They occur only in Western Java, though they once lived in forests of Bengal, Burma, Borneo, Java, and Sumatra.

Sumatran rhinos, the smallest rhinos, have two horns. They are approximately 4 feet tall, and weigh about 1 ton. Unlike the smooth-skinned African rhinos, they are hairy, especially on the tail and ears. The few living Sumatran rhinos are in Sumatra's forested hills.

Rhinoceroses are reputedly dangerous. However, they are usually peaceful and timid, except when threatened. Legally protected rhinos suffer from the market for rhino horn, reputed to be a medicine and aphrodisiac in traditional Asian medicinal practice. This market has been a major factor in driving four of the five rhino species into endangerment.

—Sanford S. Singer

See also: Fauna: Africa; Horns and antlers; Horses; Ruminants; Ungulates

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RHYTHMS AND BEHAVIOR

Type of animal science: Ethology
Field of study: Neurobiology

Biological rhythms are cyclical variations in biological functions that schedule and time countless physiological processes, including those necessary for behavior. Rhythms and behavior are closely associated; rhythms in hormonal and neural activity often bring about the expression of the specific behavior.

Principal Terms

BIOLOGICAL RHYTHM: a cyclical variation in a biological process or behavior, often with a duration that is approximately daily, tidal, monthly, or yearly

CIRCADIAN RHYTHM: a cyclical variation in a biological process or behavior that has a duration of about a day—from twenty to twenty-eight hours

ENDOGENOUS: refers to rhythms that are expressions of only internal processes within the cell or organism

ENTRAINMENT: the synchronization of one biological rhythm to another rhythm, such as the twenty-four-hour rhythm of a light-dark cycle

EXOGENOUS: refers to rhythms that originate outside the organism in the environment

FREE-RUNNING: denotes a rhythm that is not entrained to an environmental signal such as a light-dark cycle

FREQUENCY: the number of repetitions of a rhythm per unit of time, such as a heart rate of seventy beats per minute

PERIOD: the length of one complete cycle of a rhythm

PHOTOPERIODISM: the responses of an organism to seasonally changing day length, that cause altered physiological states

ZEITGEBER: "time giver" in German, it is also referred to as a synchronizer or entraining agent

Circadian and other biological rhythms have been observed and described in so many processes and behaviors in so many diverse organisms that their presence in higher plants and animals is considered a basic characteristic of life. The term "circadian" (from the Latin *circa*, meaning "about," and *diem*, "day") was coined by Franz Halberg to describe these approximately twenty-four-hour rhythms, which in time were found to exist not only in plants but also in animals and in human beings. The "circa" prefix is used also with words denoting other time periods (such as "circannual").

Circadian and Circannual Rhythms

Circadian rhythms enable animals to time precisely their daily activities. Animals are broadly classified as diurnal if they are active by day, nocturnal if they are active at night, and crepuscular if they are active at both dawn and dusk. Many species schedule their activity to start within minutes of the same time each day. Thus, the Swiss psychiatrist Auguste Henri Forel, in 1906, noticed that bees adapted to his schedule of eating breakfast on the terrace: The bees came each morning at breakfast time to feed on the jam. One of Karl von Frisch's coworkers, Ingeborg Beling, found that she could train bees to visit a feeding station every twenty-four hours but that the bees could not be trained to come every nineteen hours. Individual species of flowers produce nectar only at certain times of the day, and bees have been observed to plan their visits according to the time of nectar flow.

The activity rhythms of caged flying squirrels have been studied in detail by Patricia DeCoursey. She found that the time of the onset of activity in this nocturnal rodent was very uniform from day to day but that the time gradually drifted during the year from about 4:30 P.M. in January to 7:30 P.M. in July and then back to 4:30 P.M. by the following January. Such a pattern is called a circannual rhythm. Circannual rhythms are particularly evident in migratory birds, which show seasonal changes in both their physiology and their behavior. Many mammals have distinct reproductive seasons. Mammals that hibernate, such as ground squirrels and woodchucks, gain fat in the fall, enter hibernation, and then wake up in the spring according to a circannual rhythm.

Although the annual changes in temperature might be expected to be the environmental factor that would signal a change in season to a plant or animal, it is now known that many plants and animals respond to changes in the length of the photoperiod. This response is called photoperiodism. Photoperiodism was found first in plants in 1920, in insects in 1923, in birds in 1926, and in mammals in 1932. In a typical experiment, light was artificially added to the short days of late fall to create a longer photoperiod—similar to that characteristic of spring. As a result, the organisms came into reproductive development months early.

Circadian rhythms have been found to play an essential role in photoperiodism. What later became known as the Bünning hypothesis postulated that a circadian rhythm was involved in the organism's mechanism which measures the length of the photoperiod. It was hypothesized that the first twelve hours of the circadian rhythm was a light-requiring phase and the last twelve hours was a dark-requiring phase. Short-day effects occurred when the light was limited to the light-requiring phase, but long-day effects occurred when light was present during the dark-requiring phase.

In this scheme light plays two roles: It is a zeitgeber to synchronize rhythms and an inducer to stimulate reproductive responses. Later experiments demonstrated that short photoperiods followed by a brief flash of light in the middle of the dark were interpreted by the organism as long photoperiods, and the organisms became reproductively developed months early. Thus, the important thing is really not how long the photoperiod is, but rather when light is present with respect to a circadian rhythm of sensitivity to light.

Marine Rhythms

Some of the most dramatic examples of biological rhythms are found in marine organisms. The periods or lengths of the rhythms are rather diverse and include circadian, circatidal, circalunar, and circannual rhythms, and various combinations of them. Perhaps most famous is the rhythm of reproductive activity of the South Pacific marine worm referred to as the palolo worm. This species spawns at the last quarter of the moon in October and November (spring in the Southern Hemisphere). The worm lives buried in coral reefs and, at spawning, the last twenty-five to forty centimeters of the worm, which bears the gametes, breaks off and rises to the surface of the sea. The gametes are released into the seawater, where fertilization takes place. The spawning always occurs at daybreak. The exact timing of the spawning is an adaption that increases the chances for successful reproduction in this species.

Similarly, the California grunion, a small smelt about fifteen centimeters long, spawns in the spring at about fifteen minutes after the time of the high tide each month. During the spawnings, or "grunion runs," the fish ride the waves onto the sandy beaches, where the females burrow the posterior end of their bodies into the sand. The male curls around the female's body and releases sperm as the female lays her eggs. The fish return to the sea and the eggs continue to develop until approximately fifteen days later, when the high tide returns and uncovers the hatching young. During the grunion runs, the adult fish are caught by fishermen (legally only by hand) and are eaten. Neither the palolo worm nor the grunion has been sufficiently studied to determine what environmental factor—moonlight, gravity, magnetism, or another factor—synchronizes their rhythms so precisely.

Chronobiology

The broad field of the study of biological rhythms is called chronobiology. A rhythm is the cyclical repetition of a property or behavior, whether it concerns the level of body temperature, enzyme activity, or hormone level in the blood, or describes an activity of the whole animal, such as feeding patterns, daily or seasonal migrations, or seasons of reproduction. The period of the rhythm is the time it takes to complete one full cycle. This could be measured from crest to crest or trough to trough. The frequency of the rhythm refers to how many cycles occur per unit of time (such as a heart rate of seventy beats per minute). The amplitude refers to the strength of the rhythm (for example, one-half of the height of the rhythm when shown on a graph).

The properties of biological rhythms are fascinating. They are ubiquitous, innate, probably endogenous, free-running, self-sustaining, entrainable, relatively temperature-independent, and relatively unsusceptible to chemical perturbations. Biological rhythms are said to be ubiquitous because they are found everywhere—at all levels of life from cell organelles to cells, tissues, organs, whole organisms, and populations. They are found in all kinds of living things, with the possible exception of the prokaryocytes. They are said to be innate because the rhythms are not learned and are largely programmed by the genetic makeup of the organism. Biological rhythms are probably endogenous, with an oscillator inside the cells of the organism, but it should be noted that Frank A. Brown has published extensive evidence that the timing information may be exogenously derived from geophysical fluctuations. Biological rhythms are entrainable, which means that they usually are kept in synchrony with day/night or other environmental schedules. Entrainment is maintained by an organism's responses to environmental factors called synchronizers, zeitgebers, entraining agents, or time cues. Light, temperature, noise, and feeding are some of the zeitgebers that have been identified. The rhythms are called self-sustaining because they continue in the absence of any obvious zeitgebers. Biological rhythms have been found to be relatively temperature-independent, which is important because they often function as clocks. Biological rhythms can free-run when isolated from zeitgebers. When a rhythm free-runs, its period is found to be slightly different from the entrained period.

Despite years of investigation, biological rhythms are poorly understood. The search continues to find biological bases for the rhythmic processes so commonly seen. The innermost rhythmic process is sometimes referred to as the "biological clock," since it represents the seat of the cell's or organism's timekeeping mechanism.

Studying Biological Rhythms

One of the earliest scientific observations of a biological rhythm was reported in 1729 by Jean Jacques d'Ortous de Mairan, a French astronomer. He made detailed observations of the reactions to constant darkness of a so-called sensitive plant that normally has its leaves unfolded during the daylight hours and folded during the night. De Mairan wondered whether the leaves respond directly to the presence of the sunlight and therefore open at dawn and close at dusk. Placing the plant in constant darkness to see how it responded, de Mairan found that the plant continued to show the rhythmic folding and unfolding of its leaves. The curious results were published in a brief report in the Proceedings of the Royal Academy of Paris.

Several years later, in 1758, Henri-Louis Duhamel repeated de Mairan's experiment and further observed that warm temperatures failed to alter the pattern of the rhythmic opening and closing of the leaves of the sensitive plant. Later studies, in the nineteenth century, revealed that in the sensitive plant *Mimosa pudica* the rhythmic opening and closing of leaves in constant dark completed a full cycle in 22 to 22.5 hours. It was found that plants supplied with lamps during the night and kept in darkness during the day adapted to the new schedule within a few days and unfolded their leaves only during the artificial day. Charles Darwin did experiments that convinced him that plants survived frosts more successfully when they could fold their leaves at night.

The extent to which circadian or other biological rhythms are endogenous (originate inside the organism) has been a subject of debate. Frank A. Brown spent most of his research career trying to resolve this question. Brown found that even when organisms were placed in heavy metal chambers that were airtight, it was virtually impossible to isolate an organism from its rhythmic, geophysical environment. Normally, circadian rhythms keep in synchrony with the day/night cycle (supposedly they are reset slightly each day, since they are not exactly twenty-four hours long). Brown studied in detail free-running rhythms—that is, rhythms that are found in organisms in a seemingly constant environment. When he averaged oxygen uptake data over many months, he found exact geophysical rhythms of twenty-four hours as well as exact lunar and annual rhythms in the metabolism of many different organisms, such as potatoes, carrots, hamsters, and rats. Furthermore, he showed that many animals, such as snails and flatworms, are influenced by subtle changes in the earth's magnetic field. Therefore, he concluded that the actual timing information that underlies circadian and other biological rhythms may well be exogenous and derived from the rhythmic, geophysical environment that pervades the organisms' everyday surroundings. Despite such evidence for exogenous influences, most biologists today regard biological rhythms as the product of essentially endogenous processes.

Endocrine and Nervous System Rhythms

When looking for some basis for endogenous rhythms, researchers often investigate the endocrine and nervous systems because of their large roles in integrating and controlling biological functions. An especially interesting study has been made by Albert H. Meier. He has found that endocrine rhythms play a role in regulating the seasonal changes of physiology and behavior in the migratory white-throated sparrow and other vertebrates. By injecting birds with the hormones corticosterone and prolactin in different time relationships, he was able to induce seasonal changes. In early studies, he found that injections of prolactin either caused fat gain or fat loss, depending simply on whether the injections were given in the morning or in the afternoon. Migratory birds gain fat before they migrate and use this fat as an energy source for their flights. If the birds are given daily injections of corticosterone and prolactin four hours apart, the birds gain fat, try to fly from the south side of their cages, and do not have well-developed gonads—all characteristics of the normal fall bird. If the birds are given daily injections of corticosterone and prolactin eight hours apart, they remain lean, do not show any directed flight, and do not have well-developed gonads—traits characteristic of the normal summer bird. On the other hand, if the birds are given daily injections of cortiscosterone and prolactin twelve hours apart, the birds gain weight, try to fly out the north sides of their cages, and have gonads that will grow in response to a lengthening photoperiod—traits characteristic of the normal spring bird. Some assays, using radioactive isotopes of corticosterone and prolactin, have been made in wild populations of white-throated sparrows, and the results show that the timing of the peaks of the hormones is roughly similar to the time relationships just discussed. Further research by this group centered on the modification of brain chemistry to bring about the seasonal changes in vertebrates.

The methods used to study biological rhythms range from the simple methods used by pioneers in the field to the latest innovations in molecular biology. The field is attracting many new researchers; new discoveries are being published almost daily. Yet much remains to be done before the essential nature of biological rhythms can be understood.

Implications of Biological Rhythms

There are many implications to the fact that plants and animals possess circadian and other biological rhythms. Some scientists have speculated about whether man can survive living in space vehicles that leave the geophysical environment of the earth-moon complex. Will it be necessary, they ask, to try to duplicate parts of the terrestrial geophysical environment—by, for example, installing a rhythmic magnetic field in the space vehicles?

More mundane applications of a better knowledge of rhythms are to be found in animal husbandry. The annual rhythm of the reproduction of farm animals can be manipulated to result in higher productivity. It is a standard practice to lengthen the photoperiod in the henhouse to increase egg production and minimize the winter decrease in production. Sheep are treated with the hormone melatonin, naturally produced in more abundance in the winter months, in the early fall to hasten the reproductive season. Many more benefits of a better understanding of biological rhythms await discovery.

—John T. Burns

See also: Ethology; Hormones and behavior; Instincts; Mating; Migration; Reproduction.

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RODENTS

Type of animal science: Classification
Fields of study: Anatomy, vertebrate biology, physiology

About two thousand species of rodents, the gnawing mammals, are classified in the order Rodentia. They are found worldwide, in trees, on the ground, underground, and in partly aquatic environments. Rodents are fur sources, pets, laboratory animals, and pests.

Principal Terms

CUSPID: a tearing tooth found in the mouth of a carnivorous animal

HERBIVORE: any animal that subsists entirely on plant foods

INCISOR: a cutting tooth which acts like scissors or a chisel

MOLAR: a flat tooth found at the back of the jaw and used to grind food

OMNIVORE: an animal which eats both plants and other animals

Rodents, comprising about two thousand species, form the largest, most abundant mammal order. They are found almost everywhere on the earth. Most are ground dwellers and many rodent species dwell underground in burrows or tunnel networks of varying complexity and size. However, rodents also dwell in tree nests (squirrels) or lodges in ponds and streams (beavers), or simply run in herds (capybaras). Judging from fossil remains, rodents were widespread and plentiful fifty million years ago. It is believed that they evolved from small, insect-eating mammals, and did not develop into large species until a million years ago. The largest ancient rodents were giant, bear-sized beavers. Contemporary rodents are usually small. However, the largest modern rodents are herbivorous capybaras, which grow to approximately 100 pounds as adults.

Rodents also show remarkable diversity in their diets. These range from the vegetarian capybaras to the all-encompassing diet of omnivorous rats, which will eat meat. Rodents have many roles relative to humans. Hamsters and other small rodents are pets, capybaras are eaten as food, chinchillas are fur sources, and a few, such as rats and mice, are pests that compete with humans for their food crop supplies. The tremendous adaptability of rodents, especially rats, explains their wide geographical distribution in areas differing hugely in climate.

Physical Characteristics of Rodents

Among the two thousand known rodent species, size varies widely. Some small adult mouse species weigh about a fifteenth of a pound. At the other extreme, capybaras, largest of contemporary rodents, are the size of pigs.

Regardless of size, all rodents possess pairs of large, chisel-like front teeth in both the upper and lower jaws. The roots of these incisor teeth are located far back in rodent jawbones and grow continuously. Rodents lack the tearing teeth (cuspids) of carnivores as well as several premolars. Therefore, a large space exists between their incisors and molars. This allows the incisors to operate well in gnawing. The design of rodent dentition also allows the gnawed food to be transferred easily to the molars for efficient grinding. In addition, the muscles of the rodent lower jaw are arranged so as to enable its easy movement backward, forward, and laterally. This optimizes grinding of gnawed food.

Rodent incisors are different from those in other animals. Their continued growth from the

Groundhogs, like many rodents, live in underground dens where they hibernate through the winter. (Corbis)

root is valuable, especially because only the front surfaces of these teeth are protected by enamel, the hardest material in teeth. Thus, gnawing food causes the rear surfaces of the teeth to wear down faster than their front surfaces. This wear pattern is the basis for development of the chisel-like incisor edges. It continues as long as a rodent eats regularly, keeping the incisors sharp. Another interesting aspect of rodent mouths is that cheek fur grows inside the mouth and fills up the space between incisors and molars. This hair acts as padding and filters out food chunks too large to be swallowed comfortably.

Other than the special development of "gnawing machinery" of the mouth and teeth, rodents are anatomically unspecialized, with no other ubiquitous anatomic features. Where any special characteristic has developed in some rodents, it appears to be due to environmental need. For example, claws and front paws of burrowing rodents, such as woodchucks and moles, make them efficient diggers. In addition, gliding adaptations in some squirrels allow them to "fly" (or actually glide) from tree to tree. Furthermore, leaping rodents such as the kangaroo rat use both hind feet together to enhance leaping capability. Yet another such adaptation is the webbed feet seen in beavers.

The Lives of Rodents

Rodents, like all other mammals, are warm-blooded. They carry offspring to term in a uterus where each fetus is connected to the mother via the placenta, give birth to them, and nurse them. Depending on the rodent, the sequence of events between fertilization and the end of the nursing period takes between 5.5 weeks for a small mouse, to well over a year for large rodents. The process is easiest to describe for rats, although it is quite similar for mice and hamsters.

After fertilization, rat eggs make their way into a complex uterus which can hold eight to sixteen fetuses. There, each attaches to the uterine wall and develops, over three weeks, into a rat pup. The pups are born pink, hairless, blind, and incompletely developed. They are then nurtured by their mothers, who have the instinct of all mammals to care for their offspring. Rats breast-feed their pups for three weeks. At the end of this time, they are fully covered in hair, have full vision, and have begun to eat foods other than milk.

In another month the pups are sexually mature and can breed. This makes it clear why omnivorous wild rats pose a threat to humans. Any pair of rats can produce up to eighty offspring per year. Furthermore, within six weeks after birth, any two offspring can, and do, reproduce.

Inbred laboratory rats live for two to three years, depending on the strain. Males are much larger than females (often twice their size) and may attain body weights up to two pounds. In the wild the life expectancy of rats varies greatly. However, reports of animals living for over five years occur. Some males have been reported to be as large as small cats or dogs. Wild rats live in complex tunnels as colonies of a hundred or more animals.

Other rodents live different versions of the life of rats. Litter size, gestation time, group organization all vary. For example, the larger rodents have only a few offspring per litter, and some rodents live in tree nests (squirrels) or lodges in ponds (beavers). Life expectancies may be ten years or more, assuming death by natural causes.

Destructive and Beneficial Rodents

Rats and mice interact extensively with humans in a destructive fashion. The problems involved are

Rodent Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Rodentia (rodents)
Suborders: Sciurognathi (squirrel-like rodents), Myomorpha (mouselike rodents), Caviomorpha (cavy-like rodents)
Families: Castoridae (beavers, 1 genus, 2 species); Aplodontidae (mountain beaver); Sciuridae (squirrels, 49 genera, 267 species); Geomyidae (pocket gophers, 5 genera, 34 species); Anomaluridae (scaly-tailed squirrels, 3 genera, 7 species); Heteromyidae (pocket mice, 5 genera, 65 species); Pedetidae (springhares); Muridae (rats and mice, fifteen subfamilies, 241 genera, 1,082 species); Gliridae and Selevinidae (dormice, 8 genera, 11 species); Zapodidae (jumping mice and birchmice, 4 genera, 14 species); Dipodidae (jereboas, 11 genera, 31 species); Erethizontidae (northwestern porcupines, 4 genera, 10 species); Caviidae (cavies, 5 genera, 14 species); Hydrochoeridae (capybaras); Myocastoridae (coypus); Capromyidae (hutias, 4 genera, 13 species); Dinomyidae (pacaranas); Agoutidae (pacas, 1 genus, 2 species); Dasyproctidae (agoutis and acouchis, 2 genera, 13 species); Abrocomidae (chinchilla rats, 1 genus, 2 species); Echimyidae (spiny rats, 15 genera, 55 species); Chinchillidae (chinchillas and vicuñas, 3 genera, 6 species); Octodontidae (degus, 5 genera, 8 species); Ctenomyidae (tuco-tucos, 1 genus, 33 species); Thryonomyidae (cane rats, 1 genus, 2 species); Petromyidae (African rock rat species); Hystricidae (Old World porcupines, 4 genera, 11 species); Ctenodactylidae (gundis, 4 genera, 5 species); Bathyergidae (African mole rats, 5 genera, 9 species)

Geographical location: Every continent except Antarctica

Habitat: Mostly on land or underground, in forests, plains, and deserts; some live in a partly freshwater environment, using ponds or streams

Gestational period: Varies greatly, though generally two weeks in a mouse and about a month in a rat

Life span: Most smaller species live for one to three years, while large rodents survive for over ten years

Special anatomy: All rodents possess incisor teeth designed for gnawing, which grow continuously from the roots and wear away at their tips, giving them chisel-like edges that can gnaw through very hard materials; however, they lack cuspids (tearing teeth) seen in carnivores

Several Kinds of Rodents

BEAVERS, the largest Northern Hemisphere rodents, may weigh over fifty pounds. They live in dammed streams and in ponds, in lodges made of logs, rocks, and mud. Prized for their fur, beavers are vegetarians that eat tree bark and the roots, stems, and twigs of aquatic plants.

CAPYBARAS, the largest rodents, weigh about one hundred pounds. Found in Central and South America, they are land animals, travel in herds, and eat grass.

CHINCHILLAS, originally South American burrowers, are the source of valuable, silky fur. In the wild, they are colonial and venture above ground only at night to forage for vegetable foods.

CHIPMUNKS are small ground squirrels about ten inches in length. They are most often brown, with characteristic black and white stripes along their backs, and short tails.

GERBILS are desert rodents which dig extensive burrows. These gray, brown, or black rodents are related to rats but are more streamlined, and have prominent ears and furred tails.

MUSKRATS are semiaquatic rodents, named for musk glands in their hindquarters. Their luxuriant fur is used in fur garments.

PORCUPINES are arboreal or ground-living rodents with fur modified into defensive quills. When endangered, they backpedal at high speeds to impale predators with sharp quills that inflict painful wounds.

TREE SQUIRRELS are arboreal climbers and leapers. They are from four inches to several feet long and feed mostly on nuts.

RATS and MICE belong to the largest rodent family, which also includes hamsters. "Rat" denotes the large species, while smaller species are "mice." Often, they are crop-eating pests. Rats and mice are often used as lab animals.

competition for food, and disease transmission from rodents to humans. Rats and mice, viewed as pests, are known to eat 10 to 25 percent of grain crops grown, harvested, and stored worldwide. This percentage varies depending upon the extent of use of rodenticides, such as warfarin, in various nations and the extent of agricultural technology. Very careful use of rodenticides is important because they are quite toxic to humans.

Rodents are disease vectors, historically causing outbreaks of serious epidemics of the bubonic plague and tularemia. This was especially serious during the Middle Ages, when rats were responsible for the transmission of the Black Death. Currently, most sporadic outbreaks of rodent-derived infectious disease are handled by use of rodenticides to kill carriers and antibiotics to destroy rodent-borne microorganisms that infect humans. Most often it is not the rodents themselves that cause disease outbreaks. Rather, infection occurs as contaminated fleas and ticks move from rodents to humans. Rats are seen as the main disease vectors because they abound near and in human habitations. However, mice and any other infected rodents can be disease vectors.

Concerning beneficial use of rodents, one can point to the myriad rats, mice, hamsters, and guinea pigs utilized as laboratory animals in testing and developing pharmaceuticals, the identification of toxic cosmetic, paint, and food components, isolation of disease cures, and so on. This aspect of research is likely to become less common because a large segment of the population deems it morally inappropriate to submit animals to these testing procedures.

Another benefit of rodents that is becoming morally unacceptable is harvesting rodent fur. Beaver fur was once hugely important to the world fur trade. Presently, as beaver are nearly extinct, the use of rodents to provide fur for human use has shifted to muskrats, nutria, and chinchillas, which are valued for their attractive, luxuriant coats.

—Sanford S. Singer

See also: Beavers; Diseases; Gophers; Home building; Mice and rats; Porcupines; Squirrels.

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ROUNDWORMS

Type of animal science: Classification
Fields of study: Invertebrate biology, genetics, physiology

The phylum Nematoda consists of the roundworms. Nematodes are thought to be the most abundant organisms on earth, with some scientists estimating that nearly one million separate species of roundworms exist. Nematodes occupy a variety of habitats including soil, water, and even vinegar malts, and several species are significant animal and plant parasites.

Principal Terms

CUTICLE: the outer, noncellular covering of the nematode

PHARYNX: a muscular organ that is used to pump food into the digestive system of the nematode

PHASMID: sense organs located in the tail region of roundworms that are important for detecting chemical signals in the environment

PSEUDOCOEL: the unlined body cavity of the roundworm

Roundworms, also called threadworms, constitute the phylum Nematoda. Eighty thousand species of nematodes have been described, and four out of every five animals on earth are roundworms. Nematodes occupy almost every environment imaginable, ranging from soil to fresh and salt water and even vinegar and beer malts. One handful of soil generally contains thousands of free-living nematodes.

Nematodes are most notable for the huge economic impact they have as crop and animal pests. Plant parasitic nematodes cause billions of dollars in agricultural losses annually. Several species of nematodes are also human parasites. Nematode parasites and their hosts may have simple associations, in which the nematode uses the host as a means of transport from one food source to another, or more complex associations, in which the nematode is essentially a predator devouring the host from the inside.

Anatomy

Nematodes are unsegmented worms with a pseudocoelom and are round in cross section (hence the common name roundworms). The worms range in length from 0.1 millimeter to 9 meters, and most roundworms are transparent. All nematodes share a basic body plan of two concentric tubes separated by a fluid-filled space called a pseudocoelom. The outer tube is covered by a noncellular cuticle composed of the protein collagen, which is secreted by the cells immediately underneath. The inner tube is composed of the pharynx and digestive canal and includes the nervous system.

Most of the cells of the nervous system have their cell bodies clustered in a nerve ring that surrounds the pharynx. The pharynx is a muscular structure that pumps food into the worm's intestine. Roundworms have no specialized organs for circulation or excretion. Exchange of oxygen and carbon dioxide occurs across the body wall.

Roundworms move using a wavelike motion that relies on the contraction of the four sets of muscles that run the length of worm. The worms have no circular muscles, so they cannot expand and contract like segmented worms.

Reproduction

Reproduction of nematodes is sexual by internal fertilization. Most nematode species are dioecious (having both males and females), with the notable exception of the genetic model system, *Caenorhabditis elegans*. Males have specialized organs in the tail, copulatory spicules, which aid in depositing sperm into the vulva of a female. Nematode sperm do not swim using a flagellum, but instead are amoeboid and move by a crawling motion using a pseudopod.

Nematodes reproduce in massive quantities. Scientists have documented the production by the females of some species of up to twenty-seven million eggs and the laying of as many as one million fertilized eggs per day. Some parasitic species, such as the plant-root parasite, *Meloidogyne incognita*, can reproduce via parthenogenesis. Sex determination can be influenced by environmental factors in some species.

Roundworms hatch directly from eggs and undergo four molts before they become adults capable of reproducing. The life span and generation time varies; however the well-studied, free-living species, *C. elegans*, has a normal life span of two weeks and a generation time of three days.

Roundworm Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Nematoda
Classes: Adenophorea (having no phasmids, mostly aquatic, free-living species, some plant and animal parasites); Secernentea (having phasmids, mostly terrestrial, free-living species, some plant and animal parasites)
Orders: Adenophorea—Araeolaimida, Monohysterida, Desmosdorida, Chromadorida, Desmoscolecida, Enoplida, Dorylaimida; Secernentea—Rhabditida (mostly terrestrial, free-living worms), Tylenchida (plant and invertebrate parasites), Aphelenchia (plant and insect parasites), Strongylida (vertebrate parasites), Ascaridida (mostly vertebrate parasites), Oxyurida (vertebrate and invertebrate parasites), Spirurida (vertebrate and invertebrate parasites)
Geographical location: Found worldwide
Habitat: Soil, freshwater, and salt water; extreme habitats such as decaying cacti and vinegar malts; several species are plant or animal parasites
Gestational period: Varies with species
Life span: Varies with species; specialized dauer larvae are dormant stages resistant to drying and can survive for months under adverse environmental conditions
Special anatomy: External cuticle made of collagen; cylindrical bilaterally symmetrical organisms with a pseudocoelom; exchange of oxygen and carbon dioxide occurs across the body wall

Parasitic Nematodes

In tropical areas, nematodes infect humans, causing filarial diseases that affect 120 million people. With the disease elephantiasis, failure of the lymphatic system results in gross swelling of the limbs and genitals. *Trichinella spiralis* is the causative agent of trichinosis, a disease acquired by eating undercooked, infected pork or other meat. The worms encyst in the meat, hatch in the gut of the consumer, and migrate to the skeletal muscle of the infected individual, resulting in muscle pain and an itching sensation for the infected person.

Nematodes are also important parasites of domestic animals. Dog and cat heartworm is caused by *Dirofilaria immitis*. Pigs are often infected by *Ascaris* species. *Haemonchus contortus* is a gut parasite of sheep that can result in anemia, weight loss, and even death of the host.

In addition to animal parasites, plant parasitic nematodes pose a serious agricultural problem. The root-knot nematodes, *Meloidogyne* species, are the most serious plant pests, infecting more than two thousand plant species. These worms hatch in soil as second stage larvae; from the soil, they invade the root tip of the host plant and feed directly from the cells of the plant.

Caenorhabditis elegans

In spite of the diverse parasites of this phylum, most roundworms are beneficial, aerating the soil and breaking down decaying matter. One free-living soil nematode that has provided much information about development and genetics is *Caenorhabditis elegans*. This millimeter-long worm is the subject of intense investigation on a cellular and molecular level. Studies in *C. elegans* have led to a greater understanding of genes mutated in Alzheimer's disease, an understanding of programmed cell death as a normal part of development in multicellular organisms, and to the development of the technologies used to sequence the human genome.

—Michele Arduengo

See also: Flatworms; Genetics; Regeneration; Reproduction; Reproductive strategies; Worms, segmented.

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RUMINANTS

Types of animal science: Anatomy, classification
Fields of study: Anatomy, zoology

Ruminant herbivores regurgitate and chew food a second time, after swallowing it. This maximizes nutrient intake.

Principal Terms

ARTIODACTYL: a herbivore that walks on two toes, which have evolved into hoofs
CARNIVORE: an animal that eats only animal flesh
ESOPHAGUS: the tube through which food passes from mouth to stomach
GESTATION: the term of pregnancy
HERBIVORE: an animal that eats only plants
NUTRIENT: a nourishing food ingredient
OMNIVORE: an animal that eats both plants and animals

Ruminants are herbivorous animals that store their food in the first chamber of the stomach, called the rumen, when it is first swallowed, then after some digestion has taken place, regurgitate it as "cud," which is chewed again and reswallowed into another chamber of the stomach for further digestion. This maximizes the amount of nutrition the animal is able to derive from hard-to-digest plant food. Wild ruminants tend to eat very quickly, getting as much food mass into their rumens as possible, then retiring to places of safety where they can digest at their leisure. Ruminants include sheep, cows, camels, pronghorns, deer, goats, and antelope. They eat lichens, grass, leaves, and twigs.

The main ruminant suborders are the Tylopoda and Pecora. Tylopods have three-chambered stomachs. Examples are camels and llamas. Pecora are sheep, goats, antelope, deer, and cattle. Most pecorids have horns or antlers. These true ruminants have four-chambered stomachs, whose compartments are called the rumen, reticulum, psalterium, and abomasum. The abomasum is most similar to the stomachs of nonruminant mammals, while the other three compartments are developments peculiar to ruminants.

Ruminants chew or grind food between their lower molars and a hard pad in the gums of the upper jaw. The rumen collects partly chewed food when it is first swallowed. The food undergoes digestion in the rumen and passes into the reticulum. There, it is softened by further digestion intocud. Then the reticulum returns the cud to the mouth for rechewing, so that it is mixed with more saliva. Swallowing the chewed cud next sends food to the third compartment, the psalterium, for more digestion. The psalterium empties into the abomasum, where food mixes with gastric juices and digestion continues. Finally, the food enters the intestine, which absorbs nutrients that are then carried through the body by means of blood.

The stomachs of ruminants also contain numerous microorganisms. These help to break down the cellulose in plants, and also protect the ruminant from the effects of any toxins used as defense mechanisms by the plants.

Domesticated Ruminants

Cattle, sheep, goats, and reindeer are all domesticated ruminants, although there are still wild species of each. The world population of these ruminants exceeds four billion. Ruminants are useful food sources for humans because they are large mammals, providing a lot of meat, as well as milk, wool, hide, and fuel. Yet, because they eat plants, they are low on the food chain; since 90 percent of the energy from any food source is lost in digestion, domesticated ruminants are relatively efficient transmitters of food energy from plants to humans. The large size of these ruminants, however, means that their metabolisms are relatively slow, and thus they can afford the time it takes to digest grasses, leaves, and twigs through rumination, whereas smaller herbivores with higher metabolisms, such as rodents, must digest food more quickly and thus eat more nutrient-rich plant food, such as seeds.

Some Wild Ruminant Species

Wild ruminants are important to food chains because they eat plants, thereby preventing plant overgrowth. They also are eaten by carnivores and omnivores. Bactrian camels, with three-chambered, tylopod stomachs, inhabit the steppes and mountains of the Gobi Desert. These two-humped camels are domesticated as food and draft animals in Afghanistan, Iran, and China. Bactrian camels subsist on a diet of grass, leaves, herbs, twigs, and other plant parts. Their humps contain stored fat. Given the extreme aridity of their native environment, ruminant digestion allows them to derive the maximum nutrition from scarce food supplies.

Ruminant Methane Emissions

Ruminant digestion is essentially a process of fermentation, and one of its side products is huge quantities of methane gas. In fact, it is now estimated that livestock account for 15 percent of the methane in the atmosphere, actually contributing to the greenhouse effect on global warming. An adult cow will produce between thirty and fifty liters of methane per hour, while a sheep or goat will produce around five liters. This gas is released by almost continuous belching, with the gas traveling up the esophagus at the rate of 160 to 225 centimeters per second. Anything that prevents a ruminant from belching is life-threatening—the rumen blows up like a gas-filled balloon to the point that the animal asphyxiates.

—Leslie Ellen Jones

Chamois goats live in the mountains of Europe and southwestern Asia. Their diet consists of grass and lichens in the summer, while in winter they eat pine needles and bark. Pronghorns live in the open plains and semideserts of the North American West. They are the only living Antilocapridae, relatives of antelope. These true ruminants eat herbs, sagebrush, and grasses in the summer, and dig under the snow for grass and twigs in the winter. The large reindeer of northern Europe and Asia inhabit forests, grasslands, and mountains. Reindeer eat grass, moss, leaves, twigs, and lichens. Sable antelope live in southeastern African woodlands and grasslands, where they eat grass and shrub leaves and twigs.

—Sanford S. Singer

Ruminants, such as cows, have four-part stomachs where food is digested into cud, returned to the mouth for further chewing, and digested again to obtain maximum nutrition. (PhotoDisc)

See also: American pronghorns; Antelope; Camels; Cattle, buffalo, and bison; Deer; Digestion; Digestive tract; Food chains and food webs; Goats; Ingestion; Reindeer; Sheep.

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SALAMANDERS AND NEWTS

Types of animal science: Anatomy, classification
Fields of study: Anatomy, conservation biology, herpetology, systematics (taxonomy)

Nearly four hundred species of salamanders and newts are classified in the order Caudata. The two areas of greatest diversity of species in the world are in the southeastern United States and in Mexico and Central America.

Principal Terms

CLOACA: the common opening through which the products of the urinary, intestinal, and reproductive systems are expelled from the body

COSTAL GROOVES: parallel grooves or folds on the side of a salamander's body

EXTERNAL FERTILIZATION: the union of eggs and sperm in the environment, rather than in the female's body

GRANULAR GLANDS: one of many kinds of glands in the skin of salamanders and newts that secrete toxins for defense from predators

METAMORPHOSIS: in salamanders, the transformation of a larval salamander with gills into a juvenile salamander without gills

SPERMATOPHORE: a tiny, mushroomlike structure deposited by a male salamander for transferring sperm to a female during courtship

Salamanders and newts comprise one of three groups of amphibians living today. The other two, the caecilians (Gymnophiona) and the frogs and toads (Anura) can be readily distinguished by their body forms. Like other amphibians, salamanders and newts have glandular skin that lacks scales, feathers, or hair. Considering only species living today, salamanders and newts are a small group compared to the number of species of frogs and toads. Whereas frogs and toads are represented by about four thousand species, only about four hundred species of salamanders and newts are living today.

Systematists, biologists who study the classification of plants and animals, recognize ten families of salamanders. Newts are simply salamanders that are classified in the family Salamandridae; they can be distinguished from other salamanders by many osteological (bony) features and by their generally rough skin, compared to the smooth skin of other salamanders.

Anatomy of Salamanders and Newts

Salamanders have long, lizardlike bodies with long tails and four small legs. Many species have costal grooves along the sides of the body; the number of these grooves varies among species and can help with identification. Olfaction (sense of smell) is used during courtship, and males of many species have specialized glands on the body. Males of many species of lungless salamanders have a gland on the chin that is used to deliver hormones to the female during courtship.

Salamanders have a larval stage, but unlike frogs and toads, in which the tadpole is very different from the adult frog, larval salamanders are similar in body form to adults. Larval forms are frequently found in water and retain external gills, which are lost at metamorphosis (transformation to the adult stage). Species that breed in ponds, where oxygen levels are low, have large, bushy gills for added surface area to increase the intake of oxygen. In contrast, species that breed in streams, which have high oxygen levels, have larvae with short gills.

One of the most successful groups of salamanders are the Plethodontidae, the lungless salamanders. Most species of these salamanders live and breed on land, never entering water. They have no lungs, and oxygen uptake occurs primarily through the thin, porous skin. One requirement for this gaseous exchange is moisture, and these salamanders live primarily in damp, cool forests.

Life History of Salamanders and Newts

Primitive families of salamanders deposit eggs in water and have aquatic larvae. Other families of salamanders are unique among amphibians in producing a spermatophore for the transfer of sperm from the male to the female. The spermatophore is a gelatinous structure with a sperm cap resembling a tiny mushroom. The spermatophore is transferred from the male to the female in an elaborate courtship ritual. In some species, the male rubs secretions from a gland under his chin over the body of the female and entices her to follow him about. He then deposits a spermatophore on the substrate of the pond, which the female straddles and picks up with her cloaca. Fertilization is therefore internal in those species that produce a spermatophore.

Lungless salamanders are active on the forest floor during moist or humid periods. Males are antagonistic to one another and appear to establish small territories that they defend from other males. The territorial encounters include biting and chasing and can result in injuries, including loss of part of the tail.

Defense Against Predators

Like other amphibians, salamanders and newts have toxic skin secretions produced by skin glands that are used in various ways as defense mechanisms to repel predators. In some species of newts, glands are concentrated on the dorsum, and when disturbed by a predator, the salamander displays an "unken reflex." This display includes bending the body in a U-shape and showing bright coloration of the underbelly. At the same time, the animal becomes immobile, thus decreasing the chance that a predator will attack. Other species have glands concentrated on the tail and engage in tail lashing or tail undulation. In tail lashing, the salamander violently whips its tail toward the predator, which attacks the tail and tastes the noxious secretions. In tail undulation, the body of the salamander remains immobile while the tail is waved in a sinuous fashion above the body. The tail in these species can be autotomized, or broken from the

Salamander and Newt Facts

Classification:
Kingdom: Animalia
Phylum: Vertebrata
Class: Amphibia
Order: Caudata
Families: Ten families, including Ambystomatidae (mole salamanders), Amphiumidae (amphiumas), Cryptobranchidae (hellbender and giant salamanders), Dicamptodontidae (Pacific giant salamanders), Plethodontidae (lungless salamanders), Proteidae (waterdogs and mudpuppies), Rhyacotritonidae (torrent salamanders), Salamandridae (newts), Sirenidae (sirens)

Geographical location: Eurasia and North America, with one family extending into South America

Habitat: Many habitats, including forests, savannas, prairies, freshwater ponds and streams, and ephemeral pools

Gestational period: Varies among species; species that breed in ponds have larval stages that last two to six months, whereas the larval stage of stream-breeding species may last several years

Life span: Varies among species; larger species tend to live longer than smaller ones; large aquatic salamanders have lived for fifty to fifty-five years in captivity

Special anatomy: Long body with long tail and four legs; some species are legless

Image Not Available

body by the salamander. Thus, if a predator attacks the waving tail, the salamander loses the tail but escapes with its life.

Other species actively defend themselves if attacked by a predator. Amphiumas are large, powerful salamanders that live in ponds, swamps, or marshes in the southeast United States. Adults reach one meter in length and can inflict a painful bite with their sharp teeth. In a unique manner of defense, slender salamanders can secrete copious amounts of an adhesive substance from their glands. When attacked by a garter snake, the salamander's secretions glue the snake's body to itself, and it is unable to swallow the salamander.

—Janalee P. Caldwell

See also: Amphibians; Defense mechanisms; Frogs and toads; Gas exchange; Regenerations; Skin; Tails.

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SALMON AND TROUT

Type of animal science: Classification
Fields of study: Anatomy, ecology, marine biology, reproduction science

Salmon and trout are salmonid food and game fishes of the Northern Hemisphere.

Principal Terms

ANADROMOUS: ocean-dwelling fish that migrate to freshwater to breed

MILT: semen that holds sperms from male fishes

SEINE: a net hanging vertically with floats at its top and weights at its bottom

TROLL: fish by dragging a baited hook through the water.

Salmon, of the family Salmonidae, are valuable Northern Hemisphere food and game fish. Most belong to five species that live in rivers and off coasts of the North Pacific, from California to Alaska and Siberia. A sixth species inhabits the North Atlantic. Salmonids also include trout, graylings, and whitefish. They eat small fish, insects, and crustaceans. Salmon and some trout are anadromous, living in oceans and migrating to freshwater to breed. The five Pacific salmon species belong to the genus *Oncorhynchus*. Different species spawn in the rivers and streams of western North America during the spring (spring run), summer (summer run), and fall (fall run).

Physical Characteristics and Habitats

Salmonids have elongated bodies, small, round, smooth-edged scales, well-developed swimming fins, and a fleshy fin between the dorsal and tail fins. There are five Pacific salmon species: chinook (king), sockeye (red), humpbacked (pink), dog (calico), and coho salmon.

Spring-run chinook salmon swim upstream to spawn. The species has red, oily flesh, and average weights of twenty-three pounds. They live from California to the Bering Strait. Sockeye (red) salmon, also spring run, weigh five to eight pounds, have deep red flesh, and their fins redden during breeding. Like chinooks, they run up to one thousand miles to spawn. Prior to spawning runs, sockeye and chinook salmon store huge quantities of oil for energy to swim upstream. During migration, nest-building, and mating they do not eat.

The other Pacific species are fall run. Spawning closer to the ocean, they do not require a huge oil energy reserve. Pink salmon weigh three to six pounds and are most abundant in Alaska. Dog salmon are not eaten much because their flesh is not tasty. Coho salmon, six to nine pounds, have pink flesh and live from San Francisco to the Puget Sound.

Atlantic (true) salmon, the largest salmonids, have orange-red flesh. Most other fish of their genus (*Salmo*) are trout. Atlantic salmon weights average twenty pounds. They migrate from ocean to freshwater to spawn in spring or summer. Nonmigrant Atlantic salmon subspecies inhabit lakes in the northern United States. These "landlocked" salmon are smaller than salmon that migrate.

Trout are also salmonids. Sea trout are anadromous, but most species inhabit only freshwater lakes and streams. They eat smaller fishes, crustaceans, and insects. The most important true trout (genus *Salmo*) is the rainbow trout of the western United States. Chars, of the trout genus *Salvelinus*, have smaller scales than true trout and inhabit colder North American, Asian, and European waters. The largest char species, lake trout, often weigh twenty-five pounds and have dark gray

Salmon and Trout Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Osteichthyes
Order: Saliminiformes (salmonlike fishes)
Family: Salmonidae (salmon)
Genus and species: Includes *Oncorhynchus kisutch* (coho salmon), *O. gorbuscha* (pink salmon), *O. nerka* (sockeye salmon), *O. tschawytscha* (chinook salmon); *Salmo gairdneri* (brook trout), *S. salar* (Atlantic salmon), *S. trutta* (brown trout); *Salvelinus fontinalis* (speckled trout), *S. namaycush* (lake trout)
Geographical location: United States, Canada, Europe, and Asia
Habitat: Freshwater lakes, streams and rivers; oceans of the Northern Hemisphere
Gestational period: Two weeks to two months
Life span: Six to fifteen years, depending on species
Special anatomy: Bony skeletons; toothed mouths; caudal, dorsal, pectoral, and ventral fins developed for long swims; a fleshy fin midway between dorsal and tail fins

bodies with yellow-red spots. They inhabit the Great Lakes, Alaska, Labrador, New Brunswick, Vermont, and Maine.

Lives of Salmonids

Chinook salmon are typical anadromous salmonids. In autumn, adults spawn in Pacific Northwest streams, a few feet deep, where females place eggs in nests where fast-running water is rich in oxygen. Then the males squirt milt on them, and the females stir up the stream bottom so that earth and stones cover and protect the eggs, which hatch in two weeks to two months. This start of a new generation precedes the death of the adults by only a few days. After spawning, the dull-colored adults have slimy bodies and ragged fins from their treks to spawning grounds. For a few days they float downstream, tail-first and torpid, until they die. Their bodies wash ashore and become scavenger feed.

Yolk sacs nourish hatchlings for three months and they then become free-swimming. In one or two years, when they are three to five inches long, they swim to the ocean. Predators kill myriad migrants over the six-month trip, but some make it. In the ocean, salmon spend four years eating and growing. Then they swim back to their hatch sites. During salmonid runs, large numbers are caught for canning, but enough get through to restart the cycle. During their runs they leap rapids, waterfalls, and, increasingly, dams. Atlantic salmon survive spawning, return to the ocean, and later reuse the same spawning site several times.

The most widely distributed North American trout species is the brook (speckled) trout, found from Georgia to the Arctic Ocean. They spawn from September to December in holes that females scrape in gravel. Trout eggs take two to three months to hatch, and young develop as do salmon.

Catching and Disseminating Salmonids

In the United States, 4,500,000 pounds of salmon are caught yearly with nets and traps. Fishermen sell them to companies that supply consumers with fresh, frozen, smoked, or canned salmon. When salmon are caught before spawning, their eggs and milt can be removed. To maintain salmon numbers, the U.S. Fish and Wildlife Service yearly collects billions of eggs, fertilizes them and puts the eggs and young in breeding grounds. Trout caught by game and commercial fishermen are sold as food less often than salmon, though they are frequently eaten by their catchers. Their eggs are collected, fertilized, and disseminated by the Fish and Wildlife Service, too. Freshwater and ocean fish farms also produce salmonids.

—*Sanford S. Singer*

See also: Breeding programs; Eels; Fins and flippers; Fish; Lakes and streams; Lampreys and hagfish; Lungfish; Marine biology; Migration; Reproductive strategies; Sharks and rays; Whale sharks; White sharks.

A common danger for salmon is being caught by bears while swimming upstream to spawn. (Adobe)

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SAUROPODS

Types of animal science: Classification, evolution
Fields of study: Anatomy, evolutionary science, paleontology, systematics (taxonomy)

Sauropods are a group of dinosaurs that include the largest land animals that ever existed. Together with the theropods, or carnivorous dinosaurs, they form a group known as the Saurischia.

Principal Terms

CRETACEOUS: a period of time that lasted from about 146 to 65 million years ago
GASTROLITHS: polished pebbles that may have facilitated dinosaur digestion
GIGANTOTHERMY: a form of metabolism in which internal temperature is maintained by the large mass of the animal
JURASSIC: a period of geological time that lasted from about 208 to 146 million years ago
THEROPODS: the carnivorous dinosaurs and the closest relatives of the sauropods
TRIASSIC: a period of geological time that lasted from about 245 to 208 million years ago

Sauropods are a suborder of the Dinosauria, a vast group of reptiles that dominated terrestrial environments during the Mesozoic (245 to 66 million years ago). Dinosaurs ("terrible reptiles") are characterized by erect limbs and a pelvis that incorporates at least five vertebrae, characteristics that are related to their active lifestyle. Dinosaurs are divided into two major groups based on the structure of the pelvis. In the Saurischia ("lizard-hipped"), the pubis points forward, while in the Ornithischia ("bird-hipped"), the pubis has swung backward to lie parallel to the ischium. The Saurischia includes the carnivorous dinosaurs, or theropods, as well as the herbivorous sauropods ("lizard-foot"), the largest land animals that have ever existed.

Systematics and Anatomy

The earliest dinosaurs are known from the late Middle Triassic (220 million years ago) of South America, but the earliest sauropods do not appear until somewhat later, in the Early Jurassic. Sauropods are most closely related to the prosauropods, a group that originated in the Late Triassic and consisted of large, heavily built herbivores that reverted to the quarupedal locomotion of their dinosaur ancestors. Although it has been suggested that prosauropods were carnivores or omnivores, their teeth are coarsely serrate and numerous and were clearly adapted for shredding coarse vegetation. They were probably adapted as the first high browsers, capable of reaching up to high foliage to feed.

The earliest sauropods occur in the Early Jurassic of Africa and Asia, and from then on are a feature of dinosaurian faunas worldwide until the end of the Cretaceous, when the dinosaurs became extinct. All sauropods were quadrupedal and most were very large. The head was small and lightly built and contained peglike or spoon-shaped teeth that were confined to the front of the mouth, and nostrils that were placed on the top of the head. The neck was long and consisted of up to fifteen vertebrae, which although large were penetrated by many openings, so that they were constructed of struts and laminae providing maximum strength for minimum weight. The tail is also very long, perhaps up to seventy feet in *Seismosaurus*, and contained up to eighty vertebrae, of which the last forty were reduced to simple rods of bone that formed a whiplash. The limbs and girdles were massively constructed to support the enormous weight of these animals and the feet were broad and elephant-like, with the animal standing on the tips of its toes like all dinosaurs.

Several main groups are recognized—the diplodocids, the camarasaurids, and the brachiosaurids—but there are other, more poorly known sauropods, particularly at the beginning of sauropod evolution, that do not fit into these groups. The earliest sauropods come from Zimbabwe and are very similar to the prosauropods. Following these are Chinese forms from the Early Jurassic, in which weight-bearing features, such as shortening of the fingers and toes, become more apparent. In addition, teeth become restricted to the front portion of the jaws only. Sauropods had become diverse and widespread by the Middle Jurassic, but it is not until the Late Jurassic that they became common in North America. At this point, the three main groups are well represented and they remain abundant into the early part of the Cretaceous.

One of the best known diplodocids is *Diplodocus*, which is represented by a number of skeletons collected from the western United States. A related form is *Apatosaurus*, which for a long time was incorrectly known as *Brontosaurus* due to confusion caused by initial descriptions based on incomplete material. These animals were characterized by a protruding muzzle and small, pencil-like teeth restricted to the front of the jaws. The tail was very long, with more than eighty vertebrae present in some species. The fore limbs are considerably shorter than the hind limbs, so that the hip was high compared to the shoulder. Brachiosaurs and camarosaurs were contemporaries of the diplodocids. *Brachiosaurus* ("arm-lizard") is particularly well known from material collected from Tendaguru in Tanzania by German expeditions between 1908 and 1912. The very fine articulated skeleton mounted in the Humboldt Museum in Berlin stands 12 meters tall and is almost 22.5 meters long, and shows the relatively short tail and very long front limbs that are characteristic of this group. In addition, the head of brachiosaurs is more compact than that of diplodocids and the jaws are lined with large, chisel-shaped teeth. The camarosaurs, such as *Camarosaurus* ("chambered reptile"), were similar in many ways to the brachiosaurs, and like them had compact skulls, with large, chisel-shaped teeth in the jaws, although the muzzle was shorter. *Camarosaurus* had a much shorter neck, however, and the front limbs were shorter than the hind limbs, as in the diplodocids, so that the hips and shoulders were at about the same level.

For unknown reasons the sauropods almost perished at the end of the Jurassic, and there are only a few species known from the Cretaceous, although they were present throughout the period. The last survivors are members of a group known as the titanosaurids, which are widespread but known only from incomplete material. One of the interesting features of this group is that they bore bony armor that consisted of large bony plates scattered across the back with masses of small nodules in the hide between them. No other sauropods are known to have possessed armor.

Sauropod Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Reptilia
Order: Saurischia
Suborder: Sauropoda
Geographical location: Every continent except Antarctica
Habitat: Terrestrial habitats
Gestational period: Unknown
Life span: Estimated at fifty years
Special anatomy: Very large quadrupedal dinosaurs in which the head was small, the neck and tail long

Lifestyle

Sauropods were originally thought to have been aquatic animals, as it was considered that their large size would have precluded a terrestrial existence and that the long neck and nostrils on top of the head would have enabled them to reach the surface to breathe. However, it is now considered that sauropods lived a terrestrial lifestyle similar to that of modern elephants. Several features of the skeleton support this view. In particular, weight-reducing features, such as the openings developed in the vertebrae of the neck and tail, are adaptations associated with living on land where bodily support under the effects of gravity is critical in large animals. In addition, the presence of clefts in the top of neural spines on the neck vertebrae provides evidence of the presence of thick, ropelike ligaments that ran from the shoulders along the neck and allowed it to be held clear of the ground effortlessly. A similar feature is seen in the tail, indicating that it also was held horizontally, and this is supported by the evidence of tracks which only rarely show a tail-drag mark.

Trackways provide evidence that sauropods probably moved around in small groups, possibly up to twenty individuals. Although adults were probably big enough to have been immune to attack by large theropods, juveniles might have needed the protection that herding behavior would have given them. Studies of trackways have also shown that they would have moved slowly, perhaps at no more than four miles per hour, and that it would not have been possible for them to run. In all probability, they moved slowly from one stand of conifers to another, browsing high up in the trees.

As they had only small, weak teeth at the front of the mouth and no chewing teeth, it was originally thought that they fed on soft aquatic vegetation. However, stomach contents show that they fed on resistant conifers, and it is now thought that they stripped vegetation from branches and then passed it down to a gizzard, probably lined with stones, that would have processed the vegetation. The dwindling of conifers through the Cretaceous has been suggested as a cause of the decline of the sauropods during the same period.

The Size of Sauropods

Although sauropods were clearly the largest land animals that ever existed, it has been difficult to estimate the length and mass of particular species because this has to be based on reconstructions of skeletons and soft tissue estimates. The tallest sauropod seems to have been *Brachiosaurus*, as the head of the Berlin specimen is twelve meters above ground level. Other sauropods have a different build, and the neck was probably oriented more horizontally. Calculations of masses of sauropods are particularly difficult, as the amount of soft tissue probably varied for individuals depending on age, health, and even from season to season. *Apatosaurus* may have weighed between thirty and forty tons and *Brachiosaurus* thirty to ninety tons; however, some poorly known sauro-

Gastroliths

Collections of rounded pebbles are found in the rib cage of some sauropod skeletons and these have been named gastroliths, or "stomach stones." The best-documented case is the sauropod *Seismosaurus*, in which more than 240 stones were found in two groups, one in the pelvic region and another near the base of the neck. It is clear that these stones were held within the animal during life, as they are unknown in the surrounding sediment. A number of modern animals swallow stones and grit; it seems that crocodiles and turtles do this for buoyancy control, but in birds it is done to aid digestion. By analogy with birds, it has been proposed that in sauropods the gastroliths were held in a crop and a gizzard and were involved in the pulping of vegetation during digestion. In this scenario, the pencil-like teeth at the front of the mouth would have been used to strip vegetation, which would then have been passed down to the crop for initial processing before being passed on to the stomach for chemical digestion, and then to the gizzard for more mechanical breakdown before moving on to the intestine. However, a rival hypothesis is that the gastroliths were there to stir the digestive juices rather than mechanically abrade the food.

pods, such as *Supersaurus* and *Ultrasaurus*, may have been heavier. The record for the longest sauropod was long held by a specimen of *Diplodocus*, at 87 feet, but extrapolations of length from partial material suggest that *Seismosaurus* may have been as much as 150 feet long. Great size may have been a metabolic advantage for sauropods. As very large animals lose heat slowly, due to their relatively small surface area, they probably operated as gigantotherms, requiring only a small food intake to maintain their internal temperature.

—David K. Elliott

See also: *Allosaurus*; *Apatosaurus*; *Archaeopteryx*; Dinosaurs; Evolution: Animal life; Extinction; Fossils; Hadrosaurs; Ichthyosaurs; Paleoecology; Paleontology; Prehistoric animals; Pterosaurs; Stegosaurs; *Triceratops*; *Tyrannosaurus*; Velociraptors.

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SAVANNAS

Types of animal science: Ecology, geography
Fields of study: Ecology, environmental science, ethology, wildlife ecology, zoology

Savannas are grasslands in tropical regions near the equator that support a larger number of plant-eating animals than any other area in the world.

Principal Terms

CARNIVORES: flesh-eating animals
HERBIVORES: plant-eating animals
MARSUPIALS: animals having a pouch on the abdomen for carrying their young
RUMINANTS: grass-eating animals that chew again food that has been swallowed
UNGULATES: hoofed animals

Savannas, or tropical grasslands, are vast open spaces on which grow a large variety of plant life. Savannas usually endure long periods of drought that are punctuated by one or two rainy seasons. When the rains come, large herds of animals, mostly ungulates, make their annual journey along centuries-old migration routes from the river valleys where they have spent the dry season, to the fresh grass on the savanna. Although the principal vegetation is grass, trees or tall bushes appear occasionally on the landscape or along streams.

The huge African savanna is ancient, having probably evolved about sixty-five million years ago. Other areas are newer, some having been created by humans when forests were cleared to accommodate farming. Savannas also exist in South America, largely in Venezuela, and in northern Australia.

Plant-Eating Animals

The African savanna varies from very dry regions to areas of swamp, lake, and woodland, and can support the largest variety of herbivores in the world. Many animals are capable of living together because most of them have their own specific feeding habits. The hippopotamus, reedbuck, and waterbuck remain near the water, while various gazelles prefer dry areas, receiving moisture from plants. While the zebra chooses open grassland, the wildebeest (gnu), giraffe, and antelope are equipped to forage in the bush and also the woodland by virtue of their long snouts for gathering leaves and stems. All parts of trees and shrubs provide food; while some animals feed on the tough outer parts of grass, others eat the tender, fresh foliage or leaves of wild flowers.

The herbivores found on the African savanna are also the world's largest land animals. African elephants live in grassland, bush, and forest, in mountainous country and near lakes. Every day, elephants eat vast quantities of grass, leaves, twigs and bark, sometimes destroying trees and helping to create savannas. Elephant herds incorporate smaller groups of four to twenty elephants, led by the older females.

The white rhinoceros, weighing more than three tons, is one of Africa's rarest animals. The herds are composed of small family groups of one male, one or two females, and several young. Its smaller relative, the black rhinoceros, exists more abundantly. Browsing on leaves and branches, the black rhinos are protected by their size and horns and tusks. Humans are their only real enemies. Many of the grass eaters on the African savanna are antelope, which belong to a suborder of animals called ruminants. Equipped with complex stomachs, ruminants eat food which passes from the mouth, through the several chambers of the stomach, and back again to the mouth. The slow process of rumination, or chewing the cud, provides the animal with more safety from predators as chewing can be accomplished later in a less dangerous place than grazing.

In the savanna of northern Australia are found marsupials—kangaroos, koalas, and wombats. Marsupials also live on the South American savanna, along with the armadillo. Other particular species found in these geographically isolated areas are long-legged, flightless birds—the ostrich, rhea, and the emu.

Predators and Scavengers

When the sun's energy is converted by plants into food for herbivores, or primary consumers, then the predators and scavengers, or animals who live by preying upon other animals, become secondary consumers in the food chain. Big cats, such as the lion, cheetah, and leopard, are powerful animals who stalk and run down their prey. Lions function in teams, with females assuming most of the work.

African wild dogs are smaller animals that have strong jaws, sharp teeth, and a keen sense of smell. They live and hunt in packs made up of six to twenty members. Other predators, such as the hyena and the jackal, kill their prey and feed at night off the carcass of the animal; powerful, far-sighted vultures and marabou stork feed by day, each eating a different part of the carcass. Smaller scavengers—crows, ravens, rats, and insects—move in, helping to dispose of dead bodies that might carry disease organisms. Smaller predators of the African savanna include the desert lynx, which pursues the smaller antelope, and the black spotted serval, which hunts ground squirrels, large rats, and guinea fowl. Other predators are the genet and the fox. Puff adders and cobras poison their victims and are themselves attacked by the mongoose and the secretary bird. The aardvark hunts ants and termites at night.

The open savannas of Africa are home to many grazing species, such as elephants, giraffes, and zebras. (PhotoDisc)

Various species of monkeys, baboons, and vervets have adapted to living on the savanna by living mostly on the ground, trying to avoid predators. In the Australian savanna, the kangaroos are preyed upon by the dingoes, or wild dogs.

—Mary Hurd

See also: Chaparral; Ecosystems; Fauna: Africa; Fauna: Australia; Fauna: South America; Food chains and food webs; Forests, coniferous; Forests, deciduous; Grasslands and prairies; Habitats and biomes; Tundra.

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SCALES

Type of animal science: Anatomy
Fields of study: Anatomy, physiology

The skin of animals serves as a barrier between the exterior environment and the internal environment of the animal's body. It is, however, a barrier that is in many cases permeable and vulnerable to damage and so scales have evolved in most vertebrate groups as a protective element for the skin. Scales have the advantage of being considerably lighter than armor plating of the body with dermal bone and confer much more flexibility upon the body. Scales have evolved a number of different times in vertebrates, and variations in their form and structure reflect these separate developments of scale armor.

Principal Terms

CTENOID SCALES: scales with comblike serrations on rear edge, found on many bony fishes

DENTINE: the ivory portion of a tooth or scale; dentine or dentinelike substances such as cosmine are found in the scales of most fishes

GANOID SCALES: heavy, dense scales containing ganoine found in primitive bony fishes

KERATIN: a dense and rigid protein that makes up the scales of reptiles, birds and some mammals

PLACODERMI: extinct class of fishes characterized by dense armor plating made of dermal bone

PLACOID DENTICLES: toothlike scales found in sharks and rays

Scales have evolved in most vertebrate groups to provide a layer of protection for the integument, the outer layers of tissue that protect the internal environment of the animal from the external world. Scales are hardened plates that are made either of bonelike substance or the protein collagen, both of which are formed in the dermis (the dense, connective tissue layer of the skin) or from other rigid proteins such as keratin, which are secreted by epithelial cells in the outer layer of the skin. The protection afforded by scales does not come at the expense of flexibility, however, for most scales are attached only at one edge to folds in the skin and thus form overlapping plates which can slide over each other as the animal moves. As such, scales provide a protective armor that is lighter and more flexible than the armor formed by large plates of dermal bone such as those seen in extinct fishes such as the Placodermi.

Fish Scales

Sharks and rays possess a distinctive type of scales known as placoid denticles. These scales bear a strong resemblance to teeth; indeed, in sharks the teeth are enlarged and exaggerated placoid denticles that are replaced when lost. Each placoid denticle consists of a flat basal plate that is embedded in the dermis and a prominent, curved midline spine with a hollow interior pulp cavity. Both the basal plate and the spine are composed of dentine, the dense ivory material of teeth. The outer layer of the spine consists of a layer of vitrodentine, which is secreted by special cells (ameloblasts) in the epidermis. Within the central pulp cavity are blood vessels and nerve fibers, and fine canals (canaliculi) extend from the cavity to all parts of the dentine.

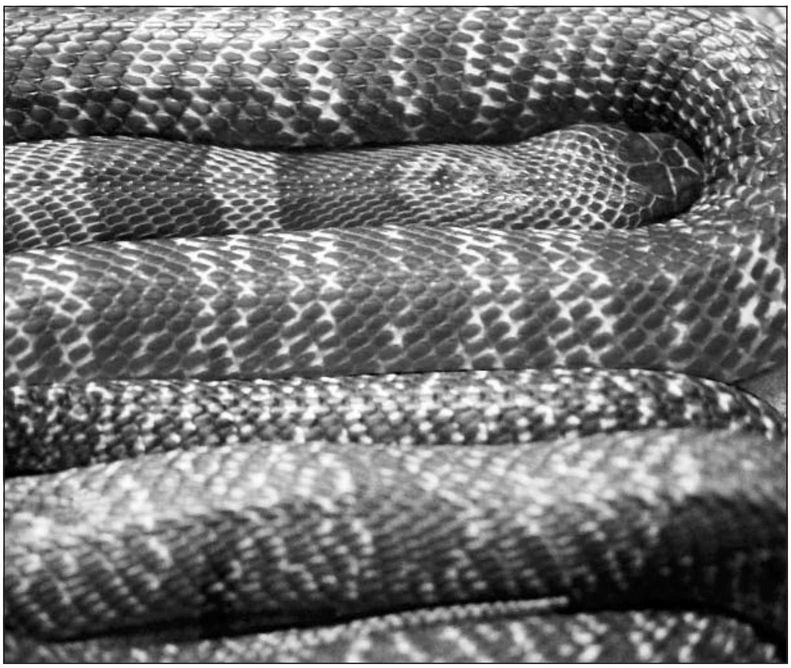
Some primitive bony fishes, such as gars and the African bichirs, possess ganoid scales. These heavy and dense scales are roughly diamond-shaped and consist principally of a dentinelike substance called cosmine. The outer surface of the cosmine layer is coated with many layers of a dense, silvery material called ganoine, which provides a lustrous, metallic sheen.

Modern bony fish, which comprise the vast majority of familiar fish species, have abandoned the heavy ganoid scales in favor of greater mobility and other protective devices. Their thinner and lighter scales contain neither cosmine nor ganoine, but rather consist of an osteoid layer (bonelike, but containing no bone cells) and an inner fibrous layer. There are two principal forms of these scales, cycloid scales, which are smoothly rounded in shape, and ctenoid scales, in which the free rear surface has comblike teeth (ctenii). Both types are fully embedded in the dermis and arranged in an overlapping fashion similar to roof shingles. The scales are covered with a thin layer of epidermis that contains single-celled mucous glands. Like the trunks of trees, these scales also exhibit "growth rings" (lamellae), the shape of which are uniquely characteristic to an individual species.

Amphibian and Reptile Scales

When amphibians became the first vertebrates to move from an aquatic to a terrestrial habitat, the weight of their scales may have become a liability in their less physically supportive environment. The earliest amphibians possessed dense and bony scales of cosmine, but these have been lost in most amphibian groups. Some of the legless modern amphibians (the caecilians) have very small dermal scales, but modern frogs, toads and salamanders lack them completely.

Scales have reappeared in reptiles; however, these scales lack any of the enamel-like dentine or cosmine components observed in aquatic vertebrates. Reptilian scales are composed primarily of a hard structural protein called keratin, which has two molecular forms, α-keratin and β-keratin. Many modifications of these scales are seen in reptiles. In turtles, the scales rest upon a layer of dermal bones (bones that arise from the layer of dermis). In snakes and lizards, the entire epidermis, including the scales, is shed periodically during growth and a new epidermis, with scales, replaces it.


Scales offer protection for an animal's skin while still allowing a great deal of flexibility. (Corbis)

Bird and Mammal Scales

Birds and mammals evolved independently from separate reptilian lineages, and birds typically retain scales on their feet, lower legs, and the base of the beak. These scales are very similar to those observed in reptiles and are also made of keratin. Most mammals have no scales whatever. However, some mammals, particularly rodents, possess scales of keratin on the epidermis of the tail. More dramatic are the epidermal scales of mammals like the armadillo, which are greatly enlarged and form an effective armor plating for these animals.

—*John G. New*

See also: Anatomy; Beaks and bills; Bone and cartilage; Brain;

Circulatory systems of invertebrates; Circulatory systems of vertebrates; Claws, nails, and hooves; Digestive tract; Ears; Endoskeletons; Exoskeletons; Eyes; Fins and flippers; Immune system; Kidneys and other excretory structures; Lungs, gills, and tracheas; Muscles in invertebrates; Muscles in vertebrates; Nervous systems of vertebrates; Noses; Physiology; Reproductive system of female mammals; Reproductive system of male mammals; Respiratory system; Sense organs; Skin; Tails; Teeth, fangs, and tusks; Tentacles; Wings.

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SCAVENGERS

Types of animal science: Anatomy, ecology, reproduction
Fields of study: Anatomy, ecology, zoology

Scavengers live partly or entirely on carrion. They are ecologically important because they assure that carrion does not become breeding places for disease organisms. Also, they help natural selection to enhance survival abilities of species they consume.

Principal Terms

CARRION: the corpses of dead animals
CARTILAGE: the wing case of a beetle
CHITINOUS: made of fibrous chitin
ELYTRA: the wing case of a beetle

Carnivorous worms, bears, beetles, kites, vultures, gulls, and hyenas do not live only by killing prey. To varying extents they eat scraps from other predator kills and the corpses of animals that died of old age, injury, or illness. Many scavengers are poorly designed for hunting. Some have short talons, lack optimum teeth, or are awkward. Regardless, they are ecologically important. They assure that carrion does not become breeding places for disease organisms.

All scavengers have a keen sense of smell to help them to find decaying flesh. They need not worry about corpses fighting back, although they do risk dangerous diseases. However, scavengers rarely die from eating carrion, because natural selection has given them tolerance of foods that kill other animals.

Scavenger Worms and Beetles

The sea mouse is a segmented worm, related to earthworms. An undersea scavenger, it lives in shallow coastal waters worldwide. In a sea mouse, each body segment is separated from the others by chitinous tissues. On the sides of the segments are muscular protrusions having bristly hairs, used in locomotion. Finer hairs growing from the segments allow the worm to sense its surroundings. As a sea mouse crawls through the seabed, it eats carrion. The worm has a flat, three-inch wide, nine-inch long body. Scales and bristles, like gray fur, cover it and lead to the name sea mouse.

Scarab beetles are one of the twelve thousand species of colorful beetles, which grow up to six inches long. They have horns on their heads or thoraxes. Males use the horns in combat during mating. Many beetles eat carrion. Dung beetles are most often called scarabs. Some scarabs (tumble bugs) form dung into balls and roll it into their burrows. There it becomes food for them or for their larvae, hatched from eggs deposited on the pellets. Ancient Egyptians worshiped tumble bugs, viewing the dung pellets as symbolizing the world and the scarab horns as symbolizing the sun's rays. Thinking that scarabs caused good fortune and immortality, they used scarab carvings as charms and replaced the hearts of the embalmed dead with carved scarabs.

Bears, Jackals, Raccoons, and Hyenas

Many mammals, such as bears, jackals, hyenas, and raccoons, are scavengers only when the need arises. Among bears, the best known scavenger is the American black bear. It averages six feet long, approximately three feet tall at the shoulder, and weighs three hundred pounds, which is small and light for a bear. This small size may make it unable to compete for choice bear fare and explain why black bears eat carrion. Given the option, black bears prefer twigs, leaves, fruit, nuts, corn, berries, fish, insects, beehives, and honey.

Raccoons, nocturnal animals, inhabit swamps or woods near water. They eat frogs, crayfish, fish, birds, eggs, fruits, nuts, rodents, insects, and carrion. Raccoons have stout, catlike bodies, masked faces, coarse yellow-gray to brown fur, body lengths up to two feet, and ringed, bushy tails, and weigh up to fifteen pounds. They are solitary, except for mating in January and February. After two-month pregnancies, females give birth to three to seven babies, which remain with them for a year. Wild raccoons live for up to seven years.

Jackals are Old World wild dog scavengers that live on plains, deserts, and prairies. Golden jackals live from North Africa to southeast Europe and India. Black-backed jackals inhabit East and South Africa. Jackals have foxlike heads, but otherwise resemble wolves. They are nocturnal creatures, holing up in dens during the day. They eat carrion and small birds and mammals, hunting in packs. Jackals live for up to fifteen years.

African and Asian hyenas are also built something like wolves. The two main species, spotted (laughing) hyenas and striped hyenas, were once thought to eat only carrion. This notion arose from observations of their carrion eating and because hyena hind legs, shorter than their front legs, make them look awkward.

African laughing hyenas have brown fur liberally sprinkled with spots, large heads, and jaws and teeth that are able to crush bones. These hyenas, six feet long and three feet tall at the shoulder, are less clumsy than they look. It is now thought that they are the greatest killers of zebras. Nocturnal hyena packs kill prey or eat carrion. Hyenas live in groups of about sixty members. Females have one or two cubs, after four-month pregnancies. Little is known about striped hyenas, which are smaller and less aggressive. They are tan, with dark, vertical stripes and live from East Africa to Asia. Hyenas live for up to twenty-five years.

Carrion Beetles

Carrion beetles of North American forests grow 2.5 inches long. Each of their bodies, as in other beetles, has a head, thorax (midsection), and abdomen (hind section). Abdomens are covered by hard wing cases (elytra), formed from front wings. Elytra protect flying wings from harm. Beetles smell with antennae, and the smell carrion beetles seek is that of carrion from small rodents, amphibians, birds, and reptiles.

Carrion beetles eat carrion and use it in reproduction. Prior to mating, males bury carrion in holes dug in the ground. Then, after battling others for the carrion, a pair of beetles wins and mates near it. After mating, the female digs an egg chamber above the carrion, lays her eggs, climbs onto the carrion, and digs a nest in it. When her eggs hatch, young are attracted to the carrion and enter the nest. The female feeds them until they can feed themselves. Then the larvae bore chambers in the earth, spin cocoons in the chambers, and mature into adults.

Scavenger Birds

Kites, one bird scavenger group, are hawks found in warm parts of all continents. Their legs and feet are small and weak, so they eat carrion and small animals. Swallow-tailed kites are two feet long, with beautiful white bodies and black wings and tails. They inhabit the southern United States. The smaller, white-tailed kite inhabits the Americas, Europe, and Asia. Kites often hover in the air, searching for insects and small mammal carrion.

Vultures are larger carrion eaters. New World vultures are related to storks and live in the temperate and tropical regions of the Americas. The Old World vultures of Europe and Asia resemble New World vultures in eating habits, but are related to hawks and eagles. Unlike kites, vultures look like carrion eaters. Most are ugly and dark feathered. They lack plumage on their heads and necks, minimizing messiness from blood and gore. Vultures are predisposed to carrion eating because they have blunt claws, which are poor weapons for hunting. They are suited to finding carrion by their ability to sustain long flights and their sharp eyes. Vultures fly in flocks, except during mating, when pairs nest on cliffs or in caves.

Most vultures lay three eggs among bare rocks. Parents incubate the eggs and feed their young, which can fly when six months old.

There are six New World vulture species. Turkey vultures (buzzards) live in the southern United States and northern Mexico. The largest North American land bird is a vulture, the California condor, which is up to six feet long, with a wingspan up to eleven feet. Andean condors are the largest South American vultures. Condors have black body plumage. The naked heads and necks of vultures and condors vary in color and in the presence or absence of feather ruffs and wattles.

There are fourteen Old World vulture species. Most interesting are the bearded vultures called lammergeiers, four feet long and weighing up to fifteen pounds. They inhabit mountains up to fifteen thousand feet high in Europe, Africa, and Asia. Lammergeiers build nests on ledges or in mountain caves. They have tan chest and stomach plumage, white faces, and dark brown wings and tails. Masklike black feather "beards" surround their eyes and beaks. Also of interest are Egyptian vultures, two feet long, with naked yellow heads, white body feathers, and black wings. They live in Mediterranean areas and as far east as India. Many Old World vultures are not as funereal-looking as the New World breeds.

Gulls, also scavenger birds, are pigeon-sized and long-winged. Most live on the oceans and large, inland lakes. Adults have gray plumage on their wings, backs, and heads, webbed feet, and white under parts. They are graceful fliers and swimmers and nest in large colonies on rocky islands or in marshes. Gulls eat fish, other water animals, insects, carrion, garbage, and the eggs or young of other birds.

Best known are white herring gulls. Adults are two feet long and in addition to the typical gray and white gull motifs have black wing tips, yellow bills, and flesh-colored legs. They eat fish, shellfish, garbage, and carrion. Often commercial fishermen, cleaning catches, see gulls swarming behind their boats, awaiting fish offal. Herring gulls mate and lay about six eggs. Females incubate them for three weeks and feed the offspring until, at six weeks old, they strike out on their own.

Vulturelike Marabou Storks

Marabou storks (marabou) combine stork and vulture anatomy. Found throughout Africa, the adults are five feet tall. Like other storks, marabou have long legs and sharp, straight bills. Their heads and necks are bald, as in vultures, minimizing slop from blood and gore. Marabou wade in deep water, eating frogs, snakes, and small mammals. On land, they eat insects. However, most marabou food is deer, antelope, and zebra carrion.

Marabou plumage is gray-green on the back and wings. This gives way to white bellies and ruffs encircling bare, red-pink necks. Marabou heads are also red-pink. From their throats hang twelve-inch, featherless, red-pink pouches of unknown function.

Most marabous inhabit Africa's prairies, wetlands, rivers, and lakes. Each breeding pair builds a nest in a tree or on rocky terrain. Most often, three eggs are laid and incubation is shared by both parents. Chicks hatch during the dry season when carrion, from mammals who die of thirst, is plentiful. Chicks stay with parents for six months. Marabou live up to twenty-two years.

Sharks

There are over three hundred shark species. They differ from bony fish in having skeletons made of cartilage, not bone. Many sharks eat nearly all large marine animals. They vary from forty to fifty foot long, to six-inch-long species. Most abundant in tropical and subtropical waters, nearly all sharks are viewed as aggressive carnivores.

Sharks are usually gray, having leathery skins and gills behind the head. Shark tails are not symmetrical and shark skeletons end in upper tail lobes. Shark fins and tails are rigid, not erectile, as in bony fish. Sharks also have a keen sense of smell, sensing traces of blood and homing in on their sources. Despite their great strength, sharks are mostly scavengers, eating injured fish and carrion. They also eat seals, whales, and fish.

Benefits of Scavenging

Scavengers consume carrion, preventing its decay and the endangerment of the health of other animals. This is one of their main ecological functions. Species such as the sea mouse, the carrion beetle, scarabs, vultures, and condors choose to eat carrion. Others, such as American black bears, jackals, raccoons, kites, sharks, and gulls, given a choice much prefer catching live prey.

Also, some scavengers' perceived food sources may be based on incomplete data. For example, laughing hyenas were dubbed scavengers based on their awkward appearance and a few observations. More careful study showed that they are more predator than scavenger. In addition, regardless of preference in obtaining their food, scavengers such as sharks and vultures have another important ecological role in the oceans and on land, killing the injured or weak members of other species. This activity helps those species to select for strong individuals, enhancing chances of species survival.

—*Sanford S. Singer*

See also: Carnivores; Digestion; Ecological niches; Ecology; Ecosystems; Food chains and food webs; Herbivores; Hyenas; Ingestion; Omnivores; Raccoons; Vultures.

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SCORPIONS

Types of animal science: Anatomy, classification, ecology
Fields of study: Anatomy, ecology, invertebrate biology, systematics (taxonomy), zoology

Scorpions are one of the most ancient land animals, having evolved over 400 million years ago. There are over 1,300 species of scorpions occurring over every continent except Antarctica. Scorpions are known for their stinging apparatus, but relatively few species pose any danger to humans.

Principal Terms

ACULEUS: the sting, either a single or double hollow barb that delivers the venom to prey

EXOSKELETON: an external, jointed skeleton made up of chitin and protein

OVAL GLAND: the poison gland in the scorpion telson

OVARIAN DIVERTICULUM: used to house embryos and to obtain nutrients via absorptive cells among viviparous species

PECTINES: comblike structures on the ventral surface of the scorpion that are used in chemoreception

PEDIPALPS: clawlike appendages that are used to catch and hold prey

Scorpions are members of the phylum Arthropoda, and more specifically of a subphylum of that taxon known as Cheliceriformes. Scorpions are members of the subclass Arachnida, those arthropods having eight legs and chelicerae mouthparts, and lacking antennae. Scorpions are the oldest arthropod terrestrial group, whose aquatic ancestry dates back to Silurian times over 400 million years ago. Their terrestrial invasion occurred in the Devonian period.

Scorpions are cosmopolitan in distribution, occurring on all continents except Antarctica. Although most people envision scorpions as desert creatures, scorpions are found in the tropical jungles, temperate forests, and savannahs and in high elevations on mountains. They are mostly nocturnal creatures as they have little defense against the ultraviolet radiation of the sun. They are quite variable in size: Some are as small as thirteen millimeters, while others (the South African *Hadogenes troglodytes*) range up to eighteen centimeters in length.

Scorpion Physiology

Scorpions are segmental in form, the body being divided into an anterior prosoma and a segmented abdomen. A one-piece carapace covers the prosoma. The abdomen is divided into a preabdomen of seven segments and a postabdomen of five segments, ending in a stinging apparatus. The pedipalps are pincerlike and are used to capture and hold prey. The chelicerae are pincerlike as well and are used to macerate the prey. There are four pairs of walking legs, all ending in a pair of claws. All scorpions are carnivorous and are essentially liquid feeders. Copious amounts of digestive enzymes are poured over macerated areas of the prey and the liquid is then pumped into the stomach.

Scorpions are well equipped with sensory structures. They have a pair of simple eyes located in the center of the carapace. Additionally, there are from two to five pairs of eyes located along the anterior and lateral margins of the carapace. Scorpions have many setae or sensory hairs located over the dorsal surfaces of the body. These hairs function to pick up vibrations and air movement and are used to detect prey. The hairs are large on the pedipalps and are called trichobothria.

Unique to scorpions is a pair of ventrally located, comblike appendages called pectines. These structures are mainly chemoreceptors and are used to pick up pheromone trails of insects. Pectines are also used to dig burrows, although the legs mainly perform this function.

Scorpions breathe by means of book lungs that are ventrally located and open to the outside via a pair of spiracles. In this way, the book lungs are kept moist for oxygen diffusion. A circulatory system is present, with a dorsally situated heart that opens via ostia or pores into the hemocoels and book lungs. Scorpions are also well equipped to deal with excretory wastes, using Malpighian tubules. These tubules filter nitrogenous wastes from the hemocoels and deposit the waste into the gut tube for elimination.

Mating and Reproductive Strategies

There are separate sexes and the gonads are tubular in construction in both sexes. The gonopore opens on the ventral surface of the mesosoma. Males lay a spermatophore sac that is picked up by the female during a courtship dance. This dance is initiated by the male, who grasps the female's pedipalps in his and dances back and forth in a face-to-face position. When the female touches the opening lever of the spermatophore, sperm are released. Fertilization is internal, as is the development. Scorpions are either ovoviviparous or viviparous. The time from conception to birth in scorpions is quite variable. In some groups, birth requires up to five months' gestation, while in others the gestation period can last up to eighteen months. In viviparous species, the embryo is fed via a tube that extends from the digestive caeca to the embryos living in the ovarian tubes. The juvenile scorpions will exit the mother via the gonopore and climb atop her back, where they will mature and go through a molt. After this first molt, they will take up their own independent existence. Scorpions will molt from four to seven times before they reach the adult stage. As an adult no molting occurs, and limbs lost during life are not regenerated.

Scorpion Fluorescence

Looking for scorpions is made easy by the fact that scorpions will fluoresce under an ultraviolet black lamp. Scorpions appear light green under ultraviolet radiation. Fluorescence may be caused in part by chemicals known as carotinoids that are found in the epicuticle.

—*Samuel F. Tarsitano*

See also: Arachnids; Arthropods; Bioluminescence; Poisonous animals; Spiders.

Scorpion Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Arthropoda
Subphylum: Cheliceriformes
Class: Chelicerata
Subclass: Arachnida
Order: Scorpiones
Families: Bothriuridae, Buthidae, Chactidae, Chaerilidae, Diplocentridae, Euscorpiidae, Hemiscorpionidae, Heteroscoripionidae, Ischnuridae, Luridae, Microcharmidae, Pseudochactidae, Scorpionidae, Scorpiopidae, Superstitioniidae, Troglotaoysicidae, Vaejovidae, Urodacidae

Geographical location: Every continent except Antarctica

Habitat: Strictly terrestrial, found in both arid and tropical regions

Gestational period: Varies among species; lengths of between five and eighteen months have been reported

Life span: Depending on the species, the life span may be only one year, while other scorpions are known to live for twenty-five years or more

Special anatomy: Eight legs, chelicerae mouthparts and simple eyes like other arachnids; clawed pedipalps for grasping prey; telson with a sting that can deliver venom; special sensory organs, called pectines, that act in an olfactory capacity

Image Not Available

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SEAHORSES

Types of animal science: Classification, reproduction
Fields of study: Anatomy, conservation biology, ethology, marine biology, physiology, reproduction science, wildlife ecology

At least thirty-five species of seahorses, classified in the genus of Hippocampus, *live in shallow subtropical coastal areas around the world. They swim in an upright position and have a head suggestive of a horse, a prickly looking body, and a prehensile tail. The male incubates eggs in a pouch in its abdomen and gives birth to live young.*

Principal Terms

DORSAL FIN: fin on the back of a fish
OVIPOSITOR: a tube that extends from the female's body for depositing eggs
PECTORAL FIN: one of a pair of fins just behind the head of a fish, where arms of terrestrial vertebrates are attached
PREHENSILE: adapted for seizing or grasping

Seahorses are highly unusual fish. First, they swim upright and poorly. They lack the tail fin that provides other fish with most of their swimming power; instead seahorses use a small dorsal fin to move forward, pectoral fins near the head to turn and steer, and a swim bladder to move up or down in the water. Second, their shape is unique: They have a pronounced horse-shaped head at a right angle to their rough body, and a prehensile tail. Their snout is adapted for aspirating passing crustaceans, filtering the water through their gills. Their eyes move independently, permitting them to observe prey and their environment without moving. Their body is prickly and knobby, due to bony rings perpendicular to their backbones. Their tail permits them to anchor themselves by grasping vegetation or coral. Third, as they use camouflage to escape predators, they can grow tendrils from their skin to look like sea plants and, like chameleons, can change color to match their surroundings. They can also change color in response to other seahorses, brightening in response to a mate and darkening in submission to a rival.

The thirty-five seahorse species differ in size, shape, color, and habitat. The smallest, *Hippocampus bargibanti* (called the pygmy seahorse), is a

Seahorses are unique in that the male of the species gestates the young in an abdominal pouch. (Digital Stock) mere 1.3 centimeters (0.5 inches) from snout to tail, while the largest, *H. ingens* (the Pacific seahorse), is 35 centimeters (14 inches) long. Although seahorses generally look alike, the species differ in the number of bony rings around their bodies and tails, and one, *H. abdominalis* (the big belly seahorse), has a very pronounced abdomen. They vary in color, including pink, orange, yellow, brown, gray, and black, with the male usually the more colorful. They live in salt water at a depth of one to twenty-five meters (three to eighty feet), at a temperature of 6 to 30 degrees Celsius (43 to 86 degrees Fahrenheit), and in one of three coastal habitats: sea grass, mangroves, and coral reefs. The species are specific to different locations; for instance, *H. bargibanti* is found around the island of New Caledonia in the west Pacific, *H. ingens* inhabits the subtropical west coasts of North, Central and South America, while *H. abdominalis* exists around New Zealand, as well as on the southern and eastern coasts of Australia.

Seahorse Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Pisces
Subclass: Teleostei
Superorder: Acanthopterygii
Order: Gasterosteiformes
Suborder: Syngnothoidei
Family: Syngnathidae
Genus and species: Hippocampus hippocampus, *H. guttulatus* and *H. kuda* (spotted seahorse), *H. zosterae* (dwarf seahorse)

Geographical location: Subtropical coastal regions around the world

Habitat: Shallow coastal areas that contain sea grass, mangroves, or coral reefs

Incubation period: Ten days to six weeks, depending on the species and habitat

Life span: One to four years, depending on the species and environment

Special anatomy: The male has a brood pouch on its abdomen in which the female deposits its eggs; the male fertilizes them inside the pouch and incubates them, expelling the newly hatched, fully developed, but minuscule offspring through an opening in the pouch; seahorses have a prehensile tail that permits them to attach themselves to vegetation or coral

The Life Cycle of Seahorses

Depending on the species and location, seahorses may have a breeding season (generally during the warmer time of the year) or may reproduce continuously. Most seahorses appear to form monogamous relationships, although *H. abdominalis* is promiscuous. When the male is receptive, the pair will perform a mating dance that may last for hours to a day, ending with the female depositing her eggs through her ovipositor into the brooding pouch of the male, who will fertilize them with his semen. That the male becomes pregnant is the most unusual feature of seahorses. He provides the fertilized eggs with oxygen and food through a capillary network in the pouch, which also removes waste products. The incubation period depends on the species and conditions, lasting from ten days to six weeks. When the fully formed young hatch, they are expelled from an opening in the pouch in a rhythmic process that may last up to two days. The number of offspring born typically varies from 10 for the smallest species to 200, although the record is 1,572. The male will usually become immediately pregnant again. The young must find food, such as larval crustaceans, and must avoid predation from fish, water birds, or crabs. In addition, storms may sweep them out to sea attached to seaweed, and disperse them to environments to which they may not be suited. If they find sufficient food and avoid predation, they can mature in four to six months, mate, and procreate. While most seahorses do not survive to maturity, they can live from one to four years, depending on the species.

Future of Seahorses

Overfishing is a serious threat to the future of seahorses. The demand for them is large in traditional Asian medicine, where they are touted as cures for everything from asthma and heart disease to incontinence and impotence. An estimated twenty million seahorses are so used annually. Live animals are also sold for aquariums, where maintaining them is difficult because of their nutritional preference for live crustaceans and their susceptibility to disease. In addition, drag net fishing in coastal areas harvests seahorses inadvertently. Any destruction of sea grass beds, mangroves, or coral reefs also poses a threat to these fascinating animals. Their future depends on sustainable fishing in the wild and developing seahorse aquaculture, as well as minimizing unintentional harvest and habitat destruction.

—James L. Robinson

See also: Courtship; Fish; Marine animals; Mating; Pregnancy and prenatal development; Reproduction; Reproductive strategies.

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SEALS AND WALRUSES

Type of animal science: Classification
Fields of study: Anatomy, ethology, genetics, marine biology, physiology

Essentially aquatic, warm-blooded mammals, seals and walruses are widely distributed throughout the world, although most of them gravitate to the colder areas.

Principal Terms

AMULET: an ornament worn as a charm against evil
CARNIVORES: meat-eating animals
CIRCUMPOLAR REGIONS: the regions around the North and South Poles
MOLLUSKS: a phylum of aquatic invertebrates, usually shelled, such as clams, mussels, and squid
MUZZLE: the area around the nose and mouth of an animal
PINNIPEDS: web-footed animals
SCRIMSHAW: a type of art that involves etching or engraving images on pieces of ivory taken from the tusks of walruses or other animals

Seals and walruses belong to the same general family. They are pinnipeds, the term used to indicate an animal with webbed feet. Walruses are distinguished from seals by their tusks, which in mature males grow up to two feet long.

Walruses use their tusks to aid locomotion when they are on land, as a means of defense when they are physically threatened, and as shovels to plow the ocean floor to turn up the mollusks that constitute the major part of their diets. Walruses have strong, bristly hairs around their muzzles that are used to separate the meat of the mollusks from the shells.

Seal are gregarious creatures. In captivity, it is easy to train them. They bond quickly with humans. In their natural state, they tend to cluster together in groups, often with as many as a thousand of them lying in close proximity to each other on the seashore or on an ice floe.

Seal and Walrus Habitats

Seals are found on every continent, including Antarctica. Although most of them prefer the cold waters of the circumpolar regions, seals swim toward warmer waters to mate, then return to more frigid areas to give birth, often delivering their young on ice floes. Monk seals are found as close to the equator as the Galápagos Islands.

Most seals live in salt water, although Saimaa seals live in Finland's freshwater lakes. Many of them were killed off by fishermen who claimed that they were eating all the fish in the lakes. The Finnish government intervened and made killing the seals illegal in 1955, but it was not until serious conservation efforts began in the 1980's that the population began to rebound. It is also illegal to use fishing nets in those parts of the lake where the Saimaa seals live and breed, because more than half of their offspring were getting tangled in nets and drowning.

Although they are warm-blooded animals that must have air to breathe, seals and walruses spend most of their lives in the sea. They are essentially aquatic. Their webbed feet and flippers provide them with easier locomotion in the sea than on land, where most of them move quite clumsily. Seals and walruses are strictly carnivorous animals whose diet consists almost exclusively of fish and mollusks. They may ingest some seaweed, but if they do so, it is by accident. These animals can close off their nasal passages so that water does not enter them when they submerged. They can remain under water for up to thirty minutes without having to return to the surface. Seals are more streamlined than walruses. Walruses usually are found in waters that are no deeper than sixty feet, although they can dive to three hundred feet. They explore the ocean bottom, using their tusks to dig into the sand for the mollusks they live on.

Seal and Walrus Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Craniata
Class: Mammalia
Subclass: Theria
Order: Pinnipeda
Families: Otariidae (eared seals, including fur seals and sea lions, seven genera, fourteen species); Phocidae (true, earless, or hair seals, ten genera, nineteen species); Odobenidae (walruses)

Geographical location: Seals, every continent; walruses, polar and circumpolar regions in the Northern Hemisphere

Habitat: Mostly water, but they give birth on land or on ice floes

Gestational period: Earless seals, ten to eleven months; eared seals, twelve months; walruses, fifteen to sixteen months

Life span: For males, twelve to thirty years in the wild; females may have a life span of only eight to twelve years, although some live to twenty or even thirty

Special anatomy: Strong hind flippers, strong arms; webbed digits, five toes and fingers

Physical Characteristics of Seals and Walruses

Most seals and walruses have substantial layers of blubber, constituting almost half of the body weight of most seals. When melted down, the blubber of a mature male elephant seal can yield ninety gallons of oil. Blubber serves as the chief insulating material in the cold waters where most seals and walruses swim. The blubber also provides buoyancy. Walruses can puff up blubber-rich areas in their necks to keep their heads above water when they are bobbing about in the ocean.

There are two families of seals, the true or earless seals, family Phocidae, and the eared seals, family Otariidae. The largest species of seal is the elephant seal. It is sometimes twenty feet long and can weigh as much as four tons. Even the smallest species of seal, the ringed seal, is quite large, weighing in at about two hundred pounds. At maturity it is about five feet long. In some species, notably the monk, Weddell, leopard, and crabeater seals, the male is smaller than the female. Among Phocidae seals, the male and female are of about equal size, but among the Otariidae, the male is larger than the female.

Seals communicate at various volumes. The northern elephant seal has such a loud call that it can be heard a mile way. The Ross seal has a chirping sound that can be mistaken for bird song. The Weddell seal has a soft, gentle call.

Walruses, of the family Odobenidae, are distinguished from seals by their two upper canine teeth that grow into ivory tusks harder than those of elephants. These sometimes reach lengths exceeding two feet. Walruses have small heads and no protruding ears. The eyes are small and deep-set. The body is small, but overdeveloped in the neck area. Bulls are up to twelve feet long and five feet wide. They often weigh a ton. The female is two-thirds the size of the male.

Mating and Reproduction

Most seals swim south to spawn, while walruses usually spawn in their northern water habitats. Male seals and walruses have multiple spouses, sometimes as many as forty at one time. The older, seasoned animals stake out the most attractive territory and attract females to it, creating substantial harems within their own venues. Older males often fight off younger males, who in the end must settle for inferior pieces of land and fewer spouses. Males mature at about five years of age and often continue to mate until past twenty.

Female walruses give birth to one baby eleven months after they mate. Female seals have similar gestation periods but sometimes deliver twins, although more typically they deliver single offspring. Walruses tend to mate again within a month of the delivery of a cub; seals in some cases mate every other year, although some deliver cubs annually.

Although some seals are solitary in winter, they gather at breeding time in rookeries on islands or ice floes, but also sometimes along stretches of beach. As few as a dozen seals may gather in a rookery, but sometimes there are as many as a million within a fifty-mile radius. The males arrive at the rookeries first to stake out their territory, the most favorable locations being directly on the water. In the northern hemisphere, females usually arrive in July.

Human Uses of Seals and Walruses

Seals and walruses are benevolent creatures that seldom attack and that are accepting of humans. They are trusting enough to be vulnerable to those who engage in mass slaughters of the animals for their fur, their blubber, and, in the case of walruses, for their ivory tusks, from which scrimshaw is made.

Inuit and other people of the Arctic depend upon seals and walruses as part of their survival strategy in hostile environments. After they kill an animal, they treat it with reverence, sometimes making a replica of it from one of its bones or from a tooth or tusk. They wear such amulets around their necks to demonstrate their gratitude to the dead animal. When these native people slaughter an animal, they waste no part of it. They eat the meat, render the blubber into oil with which they light their lamps and warm their dwellings, convert the hides into clothing and tentlike coverings, and use the tusks and bones to carve into scrimshaw.

When Europeans and Americans began to raid the seal and walrus populations, they did so indiscriminately and came close to annihilating these animals completely. Fortunately, governments stepped in to protect the endangered species and to end the brutal slaying of newborn cubs for their fur.

Kinds of Seals

Elephant seal: The largest species of seal. It has a loud call that can be heard at great distances.

Fur seal: These seals were hunted nearly to the point of extinction by hunters wanting to sell their skins in the fur trade. Baby fur seals were brutally clubbed to death and skinned, sometimes when they were still conscious. Since 1974, when it became illegal to hunt them, their numbers have grown to more than five thousand.

Monk seal: The main varieties of the monk seal are the Caribbean monk seal, the Hawaiian monk seal, and the Mediterranean monk seal. The first two have been bordering on the edge of extinction and may already be extinct. The Mediterranean monk seal is still seen occasionally in the warm waters off Greece, Turkey, and North Africa, but its total population is estimated to be below five hundred.

Ross seal: Found mostly in Antarctica, this seal has large amounts of blubber. It is characterized by the birdlike chirping sounds it makes.

Saimaa seal: A freshwater seal, this variety dwells in the lakes of Finland. It was on the verge of extinction until the Finnish government, in 1955, intervened to make it illegal to kill the Saimaa and to string fishing nets near its habitat. This species is slowly rebounding, with a total population of about two hundred.

South African fur seal: This coastal seal has a limited range, seldom straying far from home. Most of its population is found within a hundred-mile range from shore.

South American fur seal: Found off the coast of South America, this species has three subspecies: sea lions, hair seals, and northern hair seals.

Weddell seal: Found mostly in the Southern Hemisphere, it prefers the frigid waters of the South Atlantic and South Pacific. It is one of the few forms of vertebrate life in Antarctica.

Walruses use their long, ivory tusks to defend themselves, to pull themselves along when they are on land, and to dig in the ocean floor for mollusks and other foods. (Digital Stock)

Those who quested after fur attacked seal cubs only days old, beating them bloody with clubs, stripping them of their fur, often while the cub was still conscious, and leaving their stripped bodies on the ice. People around the world were outraged by pictures they saw of such predation by humans upon defenseless seal cubs. They eventually called for this brutality to stop. Multinational agreements were drafted to protect these animals. The results have been encouraging as seal and walrus populations have finally begun to increase.

—*R. Baird Shuman*

See also: Dolphins, porpoises, and toothed whales; Endangered species; Fins and flippers; Marine animals; Otters; Teeth, fangs, and tusks; Whales, baleen.

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SENSE ORGANS

Type of animal science: Anatomy
Fields of study: Anatomy, behavior, ethology, neurobiology, physiology

Sense organs are responsible for detecting events that occur both outside and within the body and translating those events into the electrical and chemical language understood by the brain. As such, sense organs are the means for the perception of the surrounding world and the body's internal state, and supply the information necessary for the organization of appropriate behaviors. There are many different types of sense organs in animals, but all serve the same basic function of informing the brain of events transpiring in the internal and external environments.

Principal Terms

ADAPTATION: the decrease in the size of the response of a sense organ following continuous application of a constant stimulus

MODALITY: a specific type of sensory stimulus or perception, such as taste, vision, or hearing

PHASIC RECEPTORS: receptors that adapt quickly to a stimulus

RECEPTIVE FIELD: the area upon or surrounding the body of an animal that, when stimulated, results in the generation of a response in the sense organ

RECEPTOR CELLS: sensory cells within sense organs that are directly responsible for detecting stimuli.

RECEPTOR POTENTIAL: a change in the distribution of electric charge across the membrane of a receptor cell in response to the presentation of a stimulus

TONIC RECEPTORS: receptors that typically show little or no adaptation to a continuously applied stimulus

TRANSDUCTION: the translation of a stimulus's energy into the electrical and chemical signals that are meaningful to the nervous system

Plants are able to form complex organic compounds for nutrition from simple molecules such as carbon dioxide and water via the process of photosynthesis. Animals, on the other hand, rely upon obtaining complex organic compounds already formed by other organisms to meet their nutritional needs. Since such sources generally take the form of other organisms, these must be located and consumed by the animal. In short, animals, unlike plants, must use behavior, a set of responses to internal and external events occurring in their environment, to survive. It is the need for behavior that has formed the basis of virtually all of animal evolution.

The first and most vital element of behavior is the detection of events occurring both within the body of the animal and in the surrounding external environment. The role of the sense organs is to detect these events (which are called stimuli) and translate them into the complex series of electrical and chemical signals that is the language of the brain. It is important to understand that the stimuli (such as sound, light, or heat) which animals detect and which may possess behavioral significance are meaningless to the brain. Brains are capable of interpreting only those signals that are in its language of electrical impulses and chemical interactions. Thus sense organs have two vital functions: the detection of environmental stimuli and the translation of that stimulus into the language that is meaningful to the nerve cells of the brain. This latter process is called transduction, and it is the ultimate role of sensory organs.

Receptor Cells and Transduction

Sensory organs typically consist of several different types of cells. Receptor cells are directly responsible for transducing the stimulus into the electrical language of the nervous system. Supporting cells play a number of different roles and in some cases may themselves become receptor cells. For example, in mammalian taste buds the receptor cells routinely die after ten to fourteen days and are replaced by supporting cells that transform to become receptor cells. Accessory structures assist in the process of transduction, such as the lens of the eye. Finally, sensory nerve fibers are stimulated chemically by the receptor cells and send information concerning the presence of a stimulus into the central nervous system.

The process of transduction occurs when a stimulus interacts physically with a sense organ, causing a change in the distribution of electrical charge across the cell membrane of the receptor cell. This change in transmembrane voltage is referred to as a receptor potential, and the size of the receptor potential corresponds directly to the intensity of the stimulus applied to the receptor cell. There must therefore be a minimum intensity of the stimulus required to generate a receptor potential, referred to as the sensory threshold. In general, the sensory threshold corresponds to the smallest stimulus intensity that an animal can detect. At the same time there is a maximum receptor potential that can be generated by a receptor cell, no matter how intense the stimulus. The intensity at which this occurs is known as receptor saturation. Above this level, when the receptor is saturated, it is impossible for the animal to discriminate whether one stimulus is more intense than another. Between the upper and lower limits of threshold and saturation, a change in the intensity of the stimulus will result in a corresponding change in the magnitude of the receptor potential. This range of intensities is known as the dynamic range of the sensory organ and within this range of intensities animals can discriminate between stimuli of different intensities.

When a continual stimulus is applied, and a receptor potential is generated across the membrane of the receptor cell, the nature of the receptor potential may change with time. If the receptor potential decreases with time, even though the applied stimulus remains constant, adaptation is said to occur. If one jumps into a pool of cool water on a warm summer day, the initial sensation is that of coolness against the skin. However, this perception disappears with time as the temperature receptors in the skin adapt until the water has no perceptible temperature. There are limits to adaptation, however; immersing one's hand in very hot water does not result in an eventual disappearance of the perception of heat. Some senses exhibit sensitization, the opposite of adaptation, in which progressively less stimulus is required to elicit a sensation with increasing time. The responses to certain types of painful stimuli demonstrate sensitization.

The rates and degrees of receptor adaptation vary among different types of receptors and the specific types of information they detect. Some receptors adapt very quickly to an applied stimulus; after a short period of steadily applied stimulation the receptor potential disappears. Such receptors are said to be phasic receptors. For example, if one carefully deflects a hair on the back of one's arm with a pencil point and then holds it steadily in the deflected position, the sensation generated by the deflection quickly disappears. Other receptors show very little adaptation over time; such receptors are said to be tonic receptors. Many sorts of pain receptors are tonic, as anyone who has experienced a toothache may attest. Phasic and tonic receptors represent the extreme ends of a continuum. Most receptors can be said to be phasic-tonic receptors, which exhibit a greater or lesser degree of adaptation to continuous stimulation. Phasic and tonic receptors send different types of information concerning the nature of the stimulus to the brain. Tonic receptors send precise information concerning the duration and the intensity of a stimulus to the central nervous system. Such information may be useful, for instance, in determining the degree to which a limb is flexed. Phasic receptors, on the other hand, relay precise information about changes in the stimulus rather than its duration. Since animals live in a dynamic world, detecting small changes in the environment caused by the presence of a predator or prey may be of first importance. Both types of information are crucial to survival.

The Senses

Classically, there are considered to be five senses (vision, hearing, touch, taste, and smell), but in reality there are many different senses and these can be further divided into subsenses. For example, the sense of temperature actually consists of two different sensory systems, one that detects heat and another that detects cold stimuli. Furthermore, these are both linked, at some level, with the detection of pain (intensely hot stimuli are also painful, but mild heat is not). Neurobiologists refer to a type of sense as a modality (such as taste) and the detection of variations within that modality as a quality (such as sweet versus sour). There are numerous different modalities, and more are being discovered every year. The ability of animals to detect and use many different types of complex information from their environment is a fascinating and continually unfolding story.

Because changes in electrical and chemical activity are the only language understood by the central nervous system, information arriving in the brain from different sensory systems must be kept segregated from each other to avoid confusion. Thus, any activity arriving from the eyes via the optic nerve is interpreted by the brain as "light," whether or not light is actually present. Electrical or physical stimulation of the optic nerve in the absence of actual light will also be perceived by the animal as "light." The sensory systems within the brain are thus organized into a series of labeled lines, each dedicated to a specific sensory modality. Any electrical activity in a labeled line is interpreted by the brain as the presence of that modality.

Sensory organs can generally be broadly classified by the nature of the events that they are capable of detecting and transducing. Mechanoreceptors detect mechanical forces applied directly or indirectly to the body. The sense of touch is the most familiar sense employing mechanoreceptors, but there are others, such as hearing and balance, that are equally important. Chemoreceptors detect signals that occur when chemicals of different types come in contact with sensory organs (such as in taste or smell). Electromagnetoreceptors detect energy contained in the electromagnetic spectrum. The most familiar, and one most heavily relied on in most mammals, is vision. Visual sensory organs (eyes) detect the energy contained within a limited range of frequencies within the electromagnetic spectrum commonly referred to as visible light. Other familiar electromagnetoreceptors detect heat (infrared radiation) or its lack (cold). Other animals detect other portions of the electromagnetic spectrum and in some cases are capable of directly detecting electrical and magnetic fields. These three categories are not absolutely rigid, however. Some types of receptors such as hygroreceptors (that detect the water content of air) seem not to fall conveniently in any one category, whereas others, such as nociceptors (pain receptors) straddle several categories and may respond to mechanical, chemical, or thermal stimuli. Similarly, the sense of balance employs information from several kinds of sense organs responding to a number of discrete stimuli, such as the direction of the earth's gravitational pull, rotational acceleration of the head, and body position.

Exteroreceptors and Endoreceptors

Sensory receptors of all three types may be used to detect either stimuli originating in sources outside the body (exteroreceptors) or stimuli originating within the body itself (endoreceptors). These latter receptors play an absolutely vital role in the maintenance of a constant internal chemical environment and temperature (homeostasis). If the internal environment varies outside of a narrow set of parameters, death can quickly ensue. It is the task of endoreceptors to detect fluctuations in the internal environment and signal the body's involuntary control mechanisms (the autonomic nervous system) to effect corrections. For example, the detection of a drop in the core body temperature in mammals can result in a variety of responses, including the shunting of blood away from the skin surface (to minimize loss of heat to the environment), erection of hair or fur on the skin (what humans experience as goose bumps) to trap a layer of warmed air next to the skin, and shivering, which generates heat via muscular contractions. There are many other endoreceptors in the body, which detect stimuli such as the amount of dissolved gases in the blood (oxygen and carbon dioxide), sugars, salts, and the amount of water present in the body. Another important role of the endoreceptors is proprioception, the detection of the relative positions of the body's parts in relation to one another. It is this sense that allows an individual to touch their nose with the tip of their finger when their eyes are closed. "Muscle sense," or kinesthesia, and the detection of the amount of flexion of the joints are included as parts of the modality of proprioception.

There are very many different types of exteroreceptors, and they comprise all three general classes of receptors. All of them, however, are dedicated to detecting external events that impinge in some manner upon the body. Exteroreceptors may be scattered across the surface of the body (such as in the sense of touch) or confined within specialized structures (such as the eyes or ears). The twofold function of all of these receptors is essentially the same: Exteroreceptors relay information about the nature of a stimulus as well as its location with respect to the animal (localization). This latter purpose is crucial; it may be important to know that a given sound indicates the presence of a predator, but it is equally critical to know from whence the threat originates so that appropriate behaviors can then be generated.

All sensory organs typically possess a receptive field, that area of space on or around the body which, when stimulated, results in the generation of a response in the receptor. The size of the receptive field may vary widely among different types of receptors, and it is the receptive field size together with the density of the receptors in a given area that determines the acuity, or spatial resolution, of the sense system. For example, in humans the skin of the fingers and lips contains a very large number of tactile (touch) receptors, most of

The Electric Sense of Fishes

Many types of aquatic vertebrates, including lampreys, sharks, sturgeon, and lungfish, are able to detect the weak electrical fields produced by living organisms in the aquatic environment. This sense, known as electroreception, is a very ancient sense. Studies on the distribution of electroreception among different animal groups have demonstrated that it is as old as the other vertebrate senses, such as vision. Electroreception is useful to aquatic animals in that it can help them detect prey and potential mates by localizing the source of the bioelectric fields. It may also be a useful aid in navigation and orientation; for instance, these animals are capable of detecting the electric field produced by a large, ore-containing rock in a moving current.

Electroreception evolved early in vertebrates, but has been lost in several major groups, including most bony fishes and in terrestrial vertebrates. In the latter case, the almost infinite electrical resistance of air compared to water makes the possession of an electrosense useless. However, certain vertebrate groups have reevolved electroreception, including catfish and, in mammals, the platypus. Certain other South American and African bony fishes have also evolved a second electric sense that is designed to detect the electrical signals produced by special electric organs in these animals. They use these signals to locate objects in turbid water: The animals detect the changes in the electric field produced by objects with electrical properties different than the water. The electric sense is also used for communication among these animals, to attract mates and warn off rivals.

The Forest Fire Beetle

Animals that rely upon very specific conditions at some point in their lives frequently possess very specialized sense organs that are adapted to detect those conditions. A good example is the beetle *Melanophila acuminata*. The larvae of this beetle are unable to survive the chemical defenses of trees in the European forests in which they live, and so this species depends absolutely upon trees that have been freshly killed by forest fires. Mating takes place when the fire is still in progress and the female lays her eggs on the charred trees as soon as the flames subside. The ability to detect a forest fire from a considerable distance is therefore very important to the survival of this species. Recent studies by H. Schmitz and H. Bleckmann at the University of Bonn have demonstrated that these beetles possess pit organs on their thorax that are sensitive to the wavelengths of infrared radiation produced by forest fires, and that they can use these organs to "see" the heat signature produced by a ten-hectare fire at distances of up to twelve kilometers. Flying beetles thus localize and home in on fires where they are most likely to find potential mates and suitable locations for laying eggs, and they do so in massive swarms. Incidents have been related in which these beetles have even swarmed large outdoor sports stadiums where events were taking place. Apparently the large infrared signal produced by thousands of individuals smoking in the stands was mistaken by the beetles as a forest fire in progress.

which possess very small receptive fields. This allows individuals to discern to a very high degree precisely where on the skin a stimulus is occurring. In other areas of the body, like the back of the neck, the density of receptors in the skin is much lower and it is more difficult to localize exactly where a stimulus is being applied. The density of the receptor cells (rods and cones) in the eye decreases from the central portion of the retina toward the edges. That is why visual acuity is greatest when looking directly at an object and why it is very difficult to read using one's peripheral vision.

The localization of a given stimulus is critical to the organization of an appropriate response. The location of a given sense organ on the body corresponds to a location within the central nervous system, and adjacent receptors are represented by adjacent locations within the brain. Thus, there is a sensory map of the body within the brain, and it is via this topographic organization that information about stimulus location is maintained. There are many sensory maps within the brain and they play a prominent role in the organization of behaviors.

Responding to Sensory Data

Sense organs may be sensitive to a wide array of different qualities and provide the animal with a general sensory scene of the surrounding environment (as in mammalian vision) or may be restricted to a narrow range of stimuli that serve as channels of communication between animals of the same species. This latter case is particularly true for special chemical senses that detect chemicals that have specific behavioral meanings for members of the same species (pheromones). Very often, the sensitivity of sensory systems lies between these two extremes, with the system showing greatest sensitivity to ranges of stimuli that have greater behavioral significance to the animal. Dolphins, for example, locate objects underwater by echolocation, emitting a high-frequency call and then listening for the returning echoes. The greatest sensitivity of the dolphin auditory system is to the range of sound frequencies that are reflected back as echoes, although dolphins can hear other sounds as well.

As animals and their behaviors have evolved, so have their sense organs, providing the animals with the competitive advantages that allow them to survive and reproduce. Furthermore, natural selection frequently results in the evolution of very similar sense organs in widely divergent animals. The eyes of mammals closely resemble those of octopuses, despite the fact that these animals are not at all closely related and their common ancestor lacked complex eyes.

Such convergent evolution of sense organs has resulted from the adaptive pressures on both of these animal groups that depend strongly upon vision to organize behavior. Sometimes the sensory systems of different animal species evolve in tandem: This coevolution of sensory systems is a direct result of the interactions of the species. Bats hunt for flying moths by echolocation, emitting ultrasonic calls and homing in on the echo reflected from the moth. Many moth species, in response, have evolved "ears," located on either side of their abdomen, that are specialized to detect the calls of hunting bats. Depending upon the intensity of the detected call (and thus, the nearness of the bat) the moths display different behaviors. If the intensity is low, indicating the bat is still at a distance, the moth will fly away from the side of the body upon which the call is loudest. If the intensity of the bat's call reaches a certain level, however, the moth will execute an erratic, fluttering crash dive toward the ground in a final attempt to escape. In an additional twist, the dogbane tiger moth emits ultrasonic pulses of its own when it detects the calls of an approaching bat. Such calls may jam the bat's echolocation by interfering with the detection of the returning echoes.

A review of all of the different types of sense organs currently known in animals and the manner in which they are used to organize and shape behaviors would fill an entire volume, and more are being continually discovered. Sense organs are, in a very real sense, the keys to our individual understanding of the world. They provide the information upon which the daily understanding of reality is entirely based.

—John G. New

See also: Anatomy; Beaks and bills; Bone and cartilage; Brain; Circulatory systems of invertebrates; Circulatory systems of vertebrates; Claws, nails, and hooves; Digestive tract; Ears; Endoskeletons; Exoskeletons; Eyes; Fins and flippers; Hearing; Immune system; Kidneys and other excretory structures; Lungs, gills, and tracheas; Muscles in invertebrates; Muscles in vertebrates; Nervous systems of vertebrates; Noses; Physiology; Reproductive system of female mammals; Reproductive system of male mammals; Respiratory system; Skin; Smell; Tails; Teeth, fangs, and tusks; Tentacles; Vision; Wings.

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SEX DIFFERENCES: EVOLUTIONARY ORIGIN

Type of animal science: Evolution
Fields of study: Anatomy, evolutionary science, reproduction science

In asexual reproduction, genetic material is not exchanged; offspring are genetically identical to the parent. Sexual reproduction involves the exchange of genes. Natural selection favors asexual reproduction in the exploitation of dependable resources, but selection favors sexual reproduction whenever the future is uncertain.

Principal Terms

ANISOGAMY: reproduction using gametes unequal in size or motility

ASEXUAL REPRODUCTION: reproduction in which genes are not exchanged

FEMALE: an organism that produces the larger of two different types of gametes

GONOCHORISM: sexual reproduction in which each individual is either male or female, but never both

HERMAPHRODITISM: sexual reproduction in which both male and female reproductive organs are present in the same individual, either at the same time or at different times

ISOGAMY: reproduction in which all gametes are equal in size and motility

MALE: an organism that produces the smaller of two different types of gametes

PARTHENOGENESIS: asexual reproduction from unfertilized gametes, producing female offspring only

SEXUAL DIMORPHISM: differences in morphology between males and females

SEXUAL REPRODUCTION: reproduction in which genes are exchanged between individuals

SEXUAL SELECTION: selection for reproductive success brought about by the behavioral responses of the opposite sex

The evolutionary origin of sex differences can be understood only by examining the relative benefits of sexual as compared to asexual reproduction. Those forms of reproduction in which genes are not exchanged are considered asexual. Asexual reproduction may take place from already developed body parts (vegetative reproduction) or from special reproductive tissue. In either case, however, asexual reproduction results in the rapid production of numerous individuals genetically identical to their parents. Because asexual reproduction allows numerous offspring to be produced in a short time, it is favored in situations in which a species can gain an advantage by exploiting an abundant but temporary resource, such as a newly discovered cache of food. There is also a further advantage: The individual that finds a resource that it can effectively exploit, if it can reproduce asexually, is assured that all its offspring will possess the same genotype as itself, and will thus be equally able to exploit the same resource for as long as it lasts. Despite these advantages, asexual reproduction is much less common than sexual reproduction among animals. It is a temporary stage in many species, alternating with sexual reproduction. Asexual reproduction is far more common among microorganisms such as bacteria.

Forms of Sexual Reproduction

Sexual reproduction may take many forms, but all of them involve the exchange of genes. Some algae and protozoans exchange chromosomes without gametes in a process called conjugation. Most other forms of sexual reproduction use special sex cells called gametes, which exist in different "mating types." Two gametes can combine only if their mating types are different. Some simple organisms, such as the one-celled green alga *Chlamydomonas*, have gametes that are indistinguishable in size or appearance, a condition known as isogamy. Most other organisms have gametes of unequal sizes, a condition called anisogamy. Selection often intensifies the differences between gametes, producing a small, motile sperm and a much larger, immobile egg, laden with stored food (yolk).

Some sexually reproducing organisms have separate sexes, a condition called gonochorism. Individuals producing eggs are called female, while individuals producing sperm are called male. Since sperm are generally small and can be produced in great numbers, males tend to leave more offspring if they reproduce prolifically, indiscriminately, and often. Females, on the other hand, have fewer eggs to offer, and in many species they must also invest nutritional and behavioral energy in the laying of eggs and the care of the resultant offspring. Selection in these species favors females who choose their mates more carefully and take better care of their offspring.

The differing selective forces operating on the two sexes often give rise to sexual dimorphism, or differences in morphology between the sexes. Sexual dimorphism can also be reinforced by competition for reproductive success, a phenomenon first studied by Charles Darwin. Darwin called this type of competition sexual selection. It takes two basic forms—direct competition between members of the same sex, and mate choices made by members of the opposite sex.

Direct male-male competition often takes such spectacular forms as rams or stags fighting in head-to-head combat. Similar fights also occur in many other species, including a variety of turtles, birds, mammals, fishes and invertebrates. Many more species, however, engage in ritual fighting in which gestures and displays substitute for actual combat. Male baboons, for example, threaten each other in a variety of ways, including staring at each other, slapping the ground, jerking the head, or simply walking toward a rival.

Although male-male rivalry has attracted more attention in the past, female-female competition also occurs in many species. Now that more ethologists and sociobiologists are looking for evidence of such direct competition among females, it is being discovered that it is a fairly widespread occurrence which had previously escaped notice only because so few scientists suspected its existence or were interested in looking for it. Female-female competition has been found among langur monkeys, golden lion-marmosets, ichneumon wasps, and several other species.

Sexual Selection

Sexual selection in mating is selection in which reproductive success is determined at least in part by mate choice. No matter what form sexual selection may take, it results in greater reproductive success for those individuals chosen as mates, while those not chosen must try again and again if they are ever to succeed in leaving any offspring at all.

Sexual selection of this kind occurs in nearly all gonochoristic species. In some species, males will attract females by means of a visual display or by various sounds (also called calls or vocalizations). Females in such species will exercise choice by selecting among the available males. For example, male peacocks, lyre-birds, and birds of paradise will court females by showing off their elaborate tail feathers in bright gaudy displays. In other species, the females perform the display and the males do the selecting.

Sometimes, the display will include an object such as a nest constructed by one partner as an attraction to its mate. Bowerbirds, for example, construct elaborate nuptial bowers as a means of attracting their mates. These bowers, which contain a nest in the center, are sometimes adorned with attractive stones, flowers, and other brightly colored objects. In some species of animals, males and females will respond to one another by performing alternating steps; in this manner, each sex selects members of the other.

Many sexually reproducing organisms have both male organs which produce sperm and female organs which produce eggs, a condition known as hermaphroditism. Earthworms and many snails are simultaneous hermaphrodites, meaning that both male and female organs are present at the same time. Hermaphrodites often have their parts so arranged that self-fertilization is difficult or impossible. One system that guarantees cross-fertilization is serial hermaphroditism. In this system, each individual develops the organs of one sex first, then changes into the opposite sex as it matures further.

Some sexually reproducing organisms have become secondarily asexual through a process called parthenogenesis, in which gametes (eggs) develop into new individuals without fertilization. In bees and wasps, males develop parthenogenetically from unfertilized eggs, while females (with twice the chromosome number) develop from fertilized eggs.

The Cost of Sexual Reproduction

Sexually reproducing organisms experience a cost associated with the energy devoted to courtship behavior and to the growing of sexual parts. In addition, the act of courtship usually exposes an individual to a greater risk of predation, and the distractions of mating further increase this risk. In view of these costs, many evolutionists have wondered how sex ever evolved in the first place, or why it is so widespread. Any adaptation so complex and so costly would long ago have disappeared if the organisms possessing it were at a selective disadvantage. The widespread occurrence of sex, and of numerous sexual systems, shows that there must be some advantage to all the various forms of sexual reproduction, and that this advantage is sufficient to overcome the recognized advantages of asexual reproduction in terms of rapid proliferation with relatively low investment of energy.

The answer to this puzzle is based on the fact that asexually produced offspring are all genetically similar to the parent, while sexually produced offspring differ considerably from one another. Organisms exploiting a dependable habitat or food supply often leave more offspring if they produce numerous genetically similar offspring rapidly and asexually. On the other hand, organisms facing uncertain future conditions have a better chance of leaving more offspring if they reproduce sexually and therefore produce a more varied assortment of offspring, at least some of which might have the adaptations needed to survive in the uncertain future. Examination of those species that are capable of reproducing either way confirms this hypothesis: Whenever favorable conditions are likely to persist, they reproduce rapidly and asexually. Faced with conditions of adversity or future uncertainty, however, these same species reproduce sexually. In species that alternate between sexually produced and asexually produced generations, the asexual phases typically occur during the seasons of assured abundance, while the sexual phases are more likely to occur at the onset of harsh or uncertain conditions. Sex, in other words, is a hedge against adversity and against an uncertain future.

Studying Sexual Reproduction

Most biologists who study reproduction are either ecologists, ethologists, or geneticists. Their methods include counting various kinds of offspring and measuring their genetic variability. Reproductive ecologists and ethologists also measure parental investment, or the amount of energy used by individuals of each type (and each sex) in the courting of their mates, in the production of gametes, and in caring for their young. Energy costs of this kind are generally measured by comparing the food consumption of individuals engaged in various types of activity using statistical methods of comparison among large numbers of observations.

The morphology of sex organs in various species is also studied by comparative anatomists and by specialists on particular taxonomic groups such as entomologists (who study insects), helminthologists (who study worms), malacologists (who study snails and other mollusks), and ich-

Lions exhibit marked sexual dimorphism, with males not only being much larger than females but also developing distinctive manes when they reach maturity. (Corbis)

thyologists (who study fishes). In most hermaphroditic species, for example, the organs are so arranged as to make cross-fertilization easier and self-fertilization more difficult.

The above explanation of sexual reproduction as resulting from the greater variability among offspring facing an uncertain future is partially confirmed by studying species that can reproduce either sexually or asexually. Among these species, asexual reproduction is always favored in situations in which an individual discovers a resource (such as a habitat or a food source) too large to exploit by itself. These conditions favor individuals that can reproduce rapidly and asexually produce numerous individuals genetically similar to themselves, who then proceed to exploit the resource. Aphids, for example, produce one or several asexual generations during the spring and early summer, when plant food is abundant. In seasons or situations of great risk or uncertainty, however, the same species often reproduce sexually at somewhat greater energetic cost, leaving a wider variety of offspring but a smaller total number. Under unpredictable conditions (such as those associated with wintering in a cold, temperate climate), the greater energetic costs of reproducing sexually are more than made up by the greater genetic and ecological variability among the offspring. Sexually reproducing individuals leave more offspring (on the average) than asexual individuals under these conditions. Similarly, among hermaphroditic species, cross-fertilization results in more varied offspring than self-fertilization, and is therefore favored under such conditions.

Testing Theories

The several reproductive methods studied by biologists provide a natural laboratory for the testing of several theories. Among these are theories concerned with genetic variability, natural selection, the evolution of sex, and the allocation of resources, including the theory of parental investment in the care of their offspring.

In terms of the two most general types of reproductive strategies, those species using a system called the r strategy (reproducing prolifically at small body size) may be either sexual or asexual, or may alternate between these two methods of reproduction. On the other hand, species following the K strategy (reproducing in smaller numbers at larger body size and investing time and energy in parental care) are invariably sexually reproducing and most often gonochoristic as well.

In addition to the theoretical considerations mentioned above, the study of alternative methods of reproduction gives us important insights into the reasons that our species, like other K strategists, is sexually reproducing and gonochoristic. In most species, sexual behavior is largely controlled by instincts, but learned behavior plays a major role among higher primates. Beyond what is necessary in copulation and childbirth, much of sex-specific behavior in humans is culturally defined and may differ from one society to another. This includes the norms of what behavior is appropriate (or inappropriate) for each sex and what personal qualities are considered masculine or feminine. All attempts to redefine sex roles will lead nowhere, unless one is aware of both the biological and the social underpinnings of these roles.

—Eli C. Minkoff

See also: Asexual reproduction; Copulation; Development: Evolutionary perspective; Gametogenesis; Gene flow; Genetics; Isolating mechanisms in evolution; Natural selection; Nonrandom mating, genetic drift, and mutation; Parthenogenesis; Reproductive systems of female mammals; Reproductive systems of male mammals; Sexual development.

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SEXUAL DEVELOPMENT

Type of animal science: Development
Fields of study: Anatomy, embryology, genetics, physiology, reproduction science

The development of an organism into a male or female involves a complex series of interactions, including differential growth, influence of the external or internal environment, and genetic factors.

Principal Terms

ANDROGENS: the general term for a variety of male sex hormones, such as testosterone and dihydrotestosterone

GENITAL TUBERCLE: a small swelling or protuberance toward the front of an embryo's genital area; it is destined to become the penis tip or clitoris

GENITALIA: the external sex structures

GONAD: the structure that produces eggs or sperm cells and sex hormones; the ovary or the testis

HERMAPHRODITE: a single organism that produces both eggs and sperm

LABIAL FOLDS: the paired ridges of tissue on either side of the embryo's genital area, which become penis and scrotum in males and labia in females

MÜLLERIAN DUCTS: the embryonic ducts that will become the female oviducts or Fallopian tubes, uterus, and vagina

PARTHENOGENESIS: the development of an unfertilized egg

UROGENITAL GROOVE: a slitlike opening behind the genital tubercle that will become enclosed in the penis but remain open in females

WOLFFIAN DUCTS: an embryonic duct system that becomes the internal accessory male structures that carry the sperm

While some lower forms of life with no recognizably different sexes exchange genetic material in a form of sexual reproduction, sexual reproduction in most organisms involves individuals with some obviously different physical and behavioral features. Biologically, the real difference between males and females is the type of sex cells they produce—whether large eggs specialized to support embryonic development or tiny sperm specialized for moving to the egg. Eggs and sperm are produced in gonads—the ovaries of females and the testes of males. The gonads of higher animals also produce sex hormones, chemical messengers that affect both embryonic and adult sexual development.

Even these basic sex distinctions are rather flexible in some organisms. Sometimes, sex is determined entirely by the environment. One kind of marine worm becomes a female unless it attaches as a larva to an adult female, whereupon it becomes a male—probably because of hormones secreted by the female. Temperature can control sex development in some animals, such as mosquitoes and amphibians. Sex may also be determined by size. Since it takes more energy to produce eggs than sperm, when food is scarce it may be more adaptive to be male. The European oyster begins adult life as a male, changes to a female as it grows larger, and reverts to being a male after shedding eggs.

In territorial animals, being a large male may be an advantage. A tropical wrasse, or "cleaner fish," travels with a harem of smaller females. If he is removed, the largest female becomes a male within a few days. Many organisms, including earthworms, snails, and some fish, are hermaphrodites—functional males/females that can fertilize themselves or exchange sperm with others. Some insects, worms, crustaceans, goldfish, whip-tailed lizards, and even turkeys lay eggs that can develop without fertilization, a process called parthenogenesis. This strategy is not sound in the long run, since it does not promote genetic diversity. It is an advantage for an organism living under good conditions, however, where an all-female population can exploit the ideal environment most efficiently.

The Origin of Sex Differentiation

Sex differentiation probably originated as differential growth of either the ovary or the testis, mediated in various ways by hormones or other environmental factors. Later in evolution it came under genetic control, which made the process more independent of environment and made possible the development of more complex reproductive structures and behavior.

The genetic sex of an animal is determined by the father at fertilization. In most species, females have two matching X chromosomes, males have an unmatched X and a smaller Y chromosome. If a normal egg with one X chromosome is fertilized by an X-bearing sperm, the XX embryo is genetically female. A Y-bearing sperm will produce a genetic male, XY. In butterflies, fishes, and birds, however, females have XY chromosomes and males have XX. Initially, XX and XY embryos look identical and in a sense are still sexually bipotential. Their gonads are “indifferent,” that is, able to form either an ovary or a testis. Each has two sets of undifferentiated sex ducts. One set, the Wolffian ducts, will become the sperm ducts and other male structures. The other set, the Müllerian ducts, form the female oviducts, uterus, and vagina.

Soon, however, genes on the Y chromosome direct the inner part of the indifferent gonad to become a testis, which then produces the male sex hormones (androgens) and Müllerian-inhibiting substance (MIS), which control further events in male development. An androgen called testosterone causes the male duct system to persist and develop, and MIS makes the female duct system degenerate. Testosterone has other developmental effects, as indicated by the fact that in monkeys, male behavior is linked to the length of embryonic exposure to testosterone.

Without the influence of the Y chromosome an XX gonad begins to develop into an ovary. The role of female sex hormones in development is unclear, since in mammals female embryonic development can occur in the absence of female hormones. The mammalian embryo has a tendency to develop in the female direction unless specific influences prevent it. The Wolffian ducts are actually remnants of a drainage system from a temporary embryonic kidney that disappears before birth. Only the presence of male sex hormones will keep these tubes from disintegrating. The Müllerian ducts, on the other hand, tend to persist unless acted upon by the anti-Müllerian substance. In birds, the embryonic ovary is the dominant gonad, and it actively feminizes the reproductive tract. It has been suggested that the early male development in mammals is necessary to allow male differentiation in the female-hormone-rich uterine environment.

Until differentiation begins, both sexes also have the same vaguely female-looking external sex structures or genitalia. In both sexes, a small protuberance called the genital tubercle is found toward the front or belly side of the embryo. Behind the genital tubercle is a slitlike opening, the urogenital groove; it is flanked by two sets of paired folds or swellings, like a river valley paralleled by two sets of ridges on either side. In the female, the genital tubercle will form a small structure called the clitoris. The urogenital groove will remain open, forming a vestibule into which the vagina and the urethra open, which empties the urinary bladder. The folds on either side of the groove will remain relatively unchanged to form labial folds.

In the male, the genital tubercle will become the tip of the penis, and the innermost urogenital folds will fuse together to form the body of the penis; the “scar” of this joining may be seen on the underside of the penis. This fusion closes off the urogenital groove and encloses the male’s urethra within the tubelike penis. The outer pair of ridges will fuse to form the scrotum, the sac that encloses the two testes, which descend into the scrotal sac before birth. Another androgen, dihydrotestosterone, may be responsible for the development of these external male structures.

Studying Sexual Development

Many sex-determining mechanisms can be studied by simple modification of the environment. For example, by varying temperature, hormone level, social-group composition, or other environmental factors it is actually possible to reverse the sexes of some invertebrates, fish, and amphibians. Castration experiments are commonly used to study the effects of hormones on the sexual development of birds and mammals. For example, castrated mammals of either sex develop in the female pattern. Since in birds only the left ovary develops, castration of hens may result in the transformation of the right gonad into a testis, with complete functional sex reversal.

Sex development can be studied with naturally occurring hormone imbalances, as in freemartin calves—sterile, masculinized females whose male twin exposed them before birth to male sex hormone. The same masculinizing effect on female fetuses can be achieved by injecting a pregnant mammal with androgens or even by growing an embryonic ovary and testis together in an organ culture outside the body. In each case, the female structures are masculinized by the male hormones.

Sex chromosome mutants in animals as diverse as fruit flies, mice, and birds can be used to study chromosomal influences in sex determination. To use a human example, there are sterile XX men with a tiny piece of the short arm of the Y chromosome attached to one X. There are also XY females who show a deletion of the same short arm of the Y. These observations have led geneticists to think that the testis-determining genes are on the short arm of the Y, since without it an individual—even one with a Y—is female.

The Evolutionary Advantage of Sexual Reproduction

In spite of its great biological costs, sexual reproduction is practiced by almost every kind of living thing. It confers tremendous evolutionary advantage on a species by producing a new individual with the genetic characteristics of two parents but with unique combinations of features that may make the offspring more successful than either parent. The advantage of having separate sexes for reproduction is that it permits the development of extremely specialized reproductive organs for the very different requirements of sperm or egg production, and, when needed, intrauterine support for the embryo. Though some organisms show great sexual flexibility, higher animals and plants have tended toward sexual stability, probably because of the high cost of sex reversal for organisms with highly specialized sexual structures.

The study of sex differentiation helps advance scientific knowledge in many areas. Modes of sex determination often provide clues to evolutionary relationships among groups of organisms. In addition, the development of sex differences makes a good model system for the study of more general questions. For example, one might use the control of sexual size differences to attack the broader question of what makes mice smaller than elephants. The control of sex differentiation by environmental factors, to use another example, might provide geneticists with a way to study how genes are turned on by hormones, temperature, or other external influences.

For embryologists, the stepwise determination and differentiation of the mammalian reproductive system is an excellent general development model; it involves a genetically controlled sequence of events that includes both the preservation of one embyronic structure (the Wolffian duct) and the removal of another (the Müllerian duct). Hormonally controlled events include a wide variety of developmental sequences, from the externally visible large-scale changes involved in the shaping of the external genitalia to the biochemical differentiation that programs the brain hypothalamus for its complex control of the menstrual cycle.

—Michele Morek

See also: Determination and differentiation; Embryology; Endocrine systems in invertebrates; Endocrine systems in vertebrates; Gametogenesis; Hormones and behavior; Hormones in mammals; Reproduction; Reproductive systems of female mammals; Reproductive systems of male mammals.

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SHARKS AND RAYS

Type of animal science: Classification
Fields of study: Anatomy, systematics (taxonomy), zoology

Cartilaginous fishes constitute one of the seven living classes of vertebrates. There are about seven hundred living species of sharks, rays, skates, and ratfishes in this vertebrate group that has ancient origins.

Principal Terms

CARTILAGE: a gristlelike supporting connective tissue that forms the entire skeleton of cartilaginous fishes

CHONDRICHTHYES: the scientific name for the taxonomic group, or class, in which the jaw-bearing cartilaginous fishes are placed; it includes sharks, rays, skates, and ratfishes

DEVONIAN: a geological period from about 400 million years ago to about 350 million years ago; during this period, ancestral sharks were abundant and diverse

PLACOID SCALES: hard, toothlike scales, sometimes called denticles, that are embedded in the skin of most sharks, rays, and skates

SILURIAN: a geological period from about 440 million years ago to about 400 million years ago; the first jawed fishes appeared during this period

VERTEBRATE: a member of the chordate subphylum Vertebrata, characterized by the possession of a vertebral column made of cartilage or bone

The Chondrichthyes, or cartilaginous fish, constitute a large group of cold-blooded fishlike vertebrates. Like other fish they are characterized by gills, fins, and a dependence on water as a medium in which to live. Unlike the more primitive jawless fishes (class Agnatha), they possess well-developed jaws; unlike the bony fish (class Osteichthyes), they possess a skeleton composed entirely of cartilage, although this is often highly calcified (strengthened and hardened by calcium compounds).

Additional features characteristic of cartilaginous fish include teeth, lack of a swim bladder (the buoyancy organ present in most bony fishes), a spiral valve intestine, internal fertilization, and osmoregulation (salt balance) by means of the nitrogen compound urea. The fossil record for the Chondrichthyes begins in the late Silurian period, over 400 million years ago. They were abundant throughout the next period, the Devonian. Within the class Chondrichthyes are two distinct subclasses, the Elasmobranchii and the Holocephali; this separation dates back to the Devonian period.

Most living cartilaginous fishes are members of the Elasmobranchii. This group includes at least six hundred, perhaps seven to eight hundred, living species of sharks (order Selachii) and rays (order Batoidea). The elasmobranchs are characterized by five to seven separate gill openings on each side of the head region; members of this group also usually have placoid scales. Sharks and rays are almost exclusively marine, although there are about ten ray species (the river stingrays) that inhabit only freshwater environments and several other rays and at least one shark species (the bull shark) commonly found in rivers.

Sharks

Sharks are a diverse group of carnivorous species, ranging in size from the tiny dwarf shark (*Squaliolus laticaudus*), which matures at less than fifteen centimeters in length, to the enormous whale shark (*Rhincodon typus*), which reaches fifteen meters or more in length and represents the largest fish species of any kind. Curiously, the whale shark and the nearly-as-large basking shark (*Cetorhinus maximus*) are plankton feeders. They capture their tiny food organisms by swimming open-mouthed through the water and straining out the plankton with fine comblike structures in their gills, called gill rakers.

Most sharks, however, have sharp, bladelike teeth, suitable for attacking and feeding on more active prey. The white shark (*Carcharodon carcharias*) is a voracious roving predator that may grow to twelve meters in length. It has been implicated in more fatal shark attacks than any other species.

In addition to well-developed eyes, inner ears, and olfactory (smell) organs, sharks possess a lateral line system, as do most bony fishes. This is a sense organ consisting of a canal beneath the skin, on each side of the body, connected to the surface by numerous pores. It is sensitive to vibrations in the water, giving sharks a sense of "distant touch" that enables them to navigate and hunt their prey in murky water. Another sensory feature of sharks and other elasmobranchs is an electroreception system, consisting of receptors, called ampullae of Lorenzini, on the surface of the snout. Apparently, this system is useful in hunting, since it allows the weak electric fields produced by the muscle contractions of prey species to be detected. It may also function in intraspecific communication (communication with others of the same species), since many elasmobranchs possess electric organs.

Sharks are typically torpedo-shaped and slightly depressed in form—that is, flattened from top to bottom. They swim by means of rhythmic undulations of the body, which are produced by sequential contraction of the myomeres (body-muscle segments). The tilt of the shark's pectoral fins (the paired fins toward the front of the body) and heterocercal tail (the upper lobe of the tail fin being larger than the lower lobe) enable it to maintain its relative depth position as it swims forward, despite the fact that the shark lacks a swim bladder. Also improving the buoyancy of sharks are their cartilage skeletons, which are lighter than bone, and their large, oily livers. Some shark livers contain a unique low-density oil called squalene.

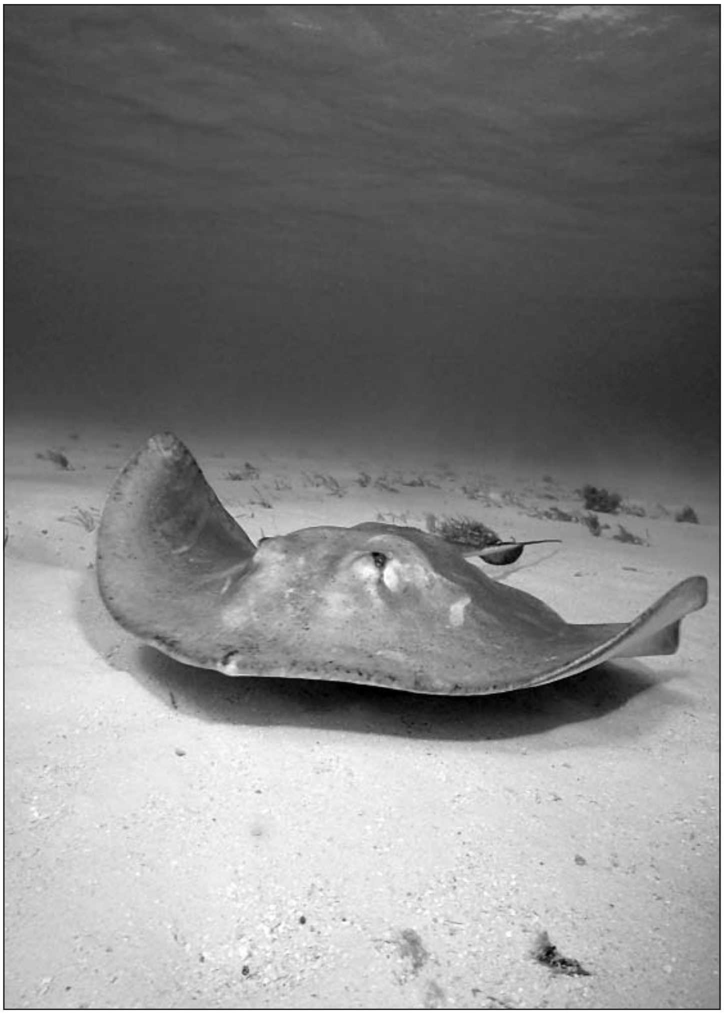
Sharks and other cartilaginous marine fishes regulate the concentration of solutes (dissolved substances) in the body in a manner very different from that of the bony fishes, which either retain salt (freshwater bony fishes) or secrete salt (marine bony fishes). Sharks maintain a concentration close to or higher than that of seawater by retaining urea and trimethylamine oxide, two relatively nontoxic nitrogenous waste products.

Reproduction in the sharks and other cartilaginous fishes is characterized by internal fertilization. A pair of intromittent, or copulatory, organs called claspers are located on the pelvic fins (the paired fins nearer the tail region) of the male. These are used to transfer sperm to the female genital opening. Embryos remain in the body or are released in egg cases, for a long gestation, or development, period. A small number of young either are born alive or hatch from an egg case in active, well-developed form.

Common Shark Species

Among the more familiar shark species are members of the family Lamnidae. This family includes the dreaded white shark and other "mackerel sharks," such as the shortfin mako (*Isurus oxyrinchus*)—a popular game fish and food fish, but a dangerous species as well. Another family, the Carcharhinidae (requiem sharks), with dozens of species, includes two man-eaters, the tiger shark (*Galeocerdo cuvieri*) and the bull shark (*Carcharhinus leucas*). Bull sharks have been found in rivers and lakes in Central and South America; they have penetrated the Amazon River as far as Peru.

Yet another group of dangerous sharks is the family Sphyrnidae, the hammerheads. These species are distinguished by a laterally expanded head, having the eyes and nasal openings at the ends of the hammerlike extensions. The function of this arrangement is unclear, but it probably aids in detecting and homing in on prey organisms. To students of comparative anatomy, the spiny dogfish (*Squalus acanthias*) is perhaps the most famil-



The unusual flat body shape of rays is an adaptation to living on the bottom of the ocean. (Digital Stock)

iar shark, since it is often dissected in the classroom as a typical representative of the lower vertebrates. This worldwide species, inhabiting temperate coastal areas, is also an important food fish in many parts of the world. It commonly appears in England, for example, in fish and chips.

Rays and Skates

Most of the more than three hundred living species of the order Batoidea, the rays and skates, are adapted for living on the bottom. In body form they are strongly depressed (flattened), with enlarged pectoral fins extending forward to the head region. Their teeth are usually pavementlike, for crushing their hard-shelled invertebrate prey. Most species give birth to live young, except the skates (family Rajidae), in which the eggs develop in a leathery egg case (the "mermaid's purse" that beach visitors often find in the sand).

Several ray families include members with a venomous spine on the tail, including the Dasyatidae (stingrays), the Potamotrygonidae (river stingrays), and the Myliobatidae (eagle rays). The largest species among rays and skates is the giant manta ray or devilfish (*Manta birostis*), which may attain a width of over six meters between the tips of its pectoral fins and a weight in excess of 1,300 kilograms. Like two other cartilaginous fish giants mentioned earlier (the whale shark and basking shark), the giant manta ray is a plankton feeder. It directs plankton into its mouth as it swims by means of large scooplike extensions on its head—the "horns" responsible for the name "devilfish." It then filters out the plankton with its comblike gill rakers.

Rays and skates swim by means of flapping movements of their winglike pectoral fins. Some species, including eagle rays and manta rays, can make spectacular leaps from the water. Among the more remarkable rays are the electric rays (family Torpedinidae). These sluggish fishes use electrical discharges of up to two hundred volts, produced by a pair of disk-shaped electric organs on the sides of the head, to stun their prey and perhaps to repel predators. Another specialized group among the rays is the sawfish family (Pristidae). A sawfish resembles a somewhat flattened shark in body form but has a long, flat, toothed extension (the "saw") on the end of its snout. This is used to slash through a school of prey fish.

Ratfish

The other major subgroup of cartilaginous fishes, the subclass Holocephali, comprises about twenty-five or thirty living marine species, most or all of which are placed in a single family, the Chimaeridae. They have a single gill opening on each side, like the bony fishes, but unlike them have a soft (rather than bony) gill cover. These fishes, commonly called chimaeras or ratfish (because of their long, slender tails), live and feed on the ocean bottom, usually in deep water. They have pavementlike teeth for crushing their mollusk and crustacean food, and they have a venomous spine on the leading edge of the first dorsal fin (the forwardmost of the unpaired fins on the upper surface of the body) for defensive purposes. Male ratfishes have a fingerlike barbed clasper, of unknown function, on the top of the head, and two pairs of claspers on the ventral (belly) side of the body. At least one pair of these ventral claspers is involved in mating. The female lays eggs in leathery capsules somewhat like skate egg cases.

Ichthyology

The study of sharks, rays, and related species is part of the larger discipline known as fish biology, or ichthyology. This science has its origins in the writings of Aristotle more than twenty-three centuries ago. He was the first to report, for example, that the sex of sharks can be determined by the structure of the pelvic fins, that is, by the presence of claspers in the male. Aristotle also contrived some rather fanciful interpretations of shark anatomy and behavior, as in his explanation for the fact that the shark mouth is on the under side of the head, far back from the tip of the snout, unlike the mouths of most other fish. In his view, this made it difficult for the shark to feed on its prey, requiring it to turn on its back, and thus nature allowed some chance for the poor animals to escape the jaws of this ravenous predator.

Modern study of cartilaginous fishes, like fish biology in general, involves several disciplines. Ichthyology, or systematic ichthyology, is particularly concerned with the naming and classifying of species and higher taxa (taxonomic categories) and determining their interrelationships. Living cartilaginous fishes are probably better known (that is, more of the extant species have been discovered) than living bony fishes, simply because they tend to be larger, more conspicuous, and less secretive. Yet it was not until 1976 that one of the largest shark species, a deep-water filter-feeding species called the megamouth shark (*Megachasma pelagios*), was discovered near Hawaii. There may exist many additional Chondrichthyes species in deep ocean waters and remote coral reef areas.

Chondrichthyes systematics (that is, the classification of the fishes) has undergone many changes and revisions as more has become known about fossil representatives and about the characteristics of the anatomy, biochemistry, and the like, of the living species. Studies of fossil cartilaginous fishes are limited almost entirely to samples of teeth, since these are virtually the only body parts durable enough to be preserved in the fossil record. Nevertheless, there is enough information in the characteristics of the teeth so that knowledge of the interrelationships of fossil species, both among one another and with living species, is quite advanced. It is known, for example, that the enormous hand-sized fossil teeth of *Carcharodon megalodon*, which lived about twenty million years ago, are so similar to the smaller teeth of the white shark (*Carcharodon carcharias*) that they both belong in the genus *Carcharodon*.

Systematic study of modern species requires collection of specimens, generally by means of nets, traps, hooks, and lines, or spearing. Specimens are then preserved in some way and maintained in a museum collection. Entire specimens, if they are relatively small, can be maintained in diluted alcohol after fixation in formalin (formaldehyde solution). Other specimens, especially large ones, are dissected, and only certain parts are preserved, particularly the head skeleton with jaws and teeth. Certain new techniques provide taxonomic information from samples of living tissue. Karyotyping (analysis of the chromosomes), protein analysis (determination of the amino acid sequence), and DNA hybridization (estimation of genetic similarities) are all techniques that can elucidate interrelationships among the Chondrichthyes. Other disciplines concerned with the study of cartilaginous fishes include fisheries biology (the science of management and exploitation of commercially important fish species) and comparative physiology.

The Place of Sharks and Rays in Evolution

Cartilaginous fish represent an early line in the evolution of vertebrates. Understanding their interrelationships is crucial to an understanding of the ancestry of other fishes and of tetrapods (amphibians, reptiles, birds, and mammals) and thus, ultimately, of humans. Even though humankind's ancestors split from the ancestors of sharks and rays more than 400 million years ago, many anatomical and physiological features are shared. A prime example is the eye, which is extraordinarily similar in all vertebrates. The same system of eye movement, involving six muscles innervated by the same three cranial nerves, has remained unchanged throughout vertebrate evolutionary history. Thus, the study of shark eyes, or any other aspect of shark biology, deepens the understanding of the evolution of higher animals.

Sharks and their relatives are important and interesting in other ways as well. Many species have importance as food, especially in Asia and the South Pacific. Other products derived from sharks include shark liver oil (which was an important vitamin A source before the development of synthetic vitamin A), shark skin (for leather products), and shark cartilage derivatives (used in medicine).

Even though the real risk of shark attack anywhere in the world is statistically very small, sharks have been known to be such brutal killers that interest in preventing shark attacks is widespread. Various chemical shark repellants such as "shark chaser" have been tried. This water-soluble mixture of dye and copper acetate was given to U.S. military personnel during World War II for use if they were stranded in the sea after their ships were sunk or planes downed. It was, however, later shown to have little or no effect on sharks. Other techniques have included the cartridge-loaded "bang-stick," which is probably more dangerous to the untrained user than to a shark. A more promising device is the "shark screen," a floating plastic bag that can be filled with water and entered—masking the odors, sounds, and movements that might attract sharks.

Much remains to be learned about sharks, rays, and other cartilaginous fishes. Studying their ecology, behavior, and evolutionary relationships is important for further understanding of their basic biological nature. It is also essential for maximizing the benefit of commercially important species and minimizing the risk posed by dangerous species.

—*George Dale*

See also: Amphibians; Evolution: Historical perspective; Fish; Invertebrates; Lungs, gills, and tracheas; Marine animals; Marine biology; Systematics; Whale sharks; White sharks.

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Pough, F. H., J. B. Heiser, and W. N. McFarland. *Vertebrate Life*. 5th ed. New York: Macmillan, 1999. This is a thoroughly revised edition of one of the best undergraduate texts in vertebrate biology, reflecting the extraordinary advances in philosophy and methodology of vertebrate taxonomy. It is a rather large volume, but three of its twenty-four chapters (6, 7, and 8) are a particularly useful account of the origins of cartilaginous and other fishes.

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SHEEP

Type of animal science: Classification
Fields of study: Anatomy, zoology

Over nine hundred breeds of sheep have been identified worldwide, and four hundred have significant research data available to allow for distinctive, productive evaluation.

Principal Terms

BLOOD SYSTEM: grading for fleece, as in fine, ½, ¾, ¼, low, and braid
CLIP: the fleece that is removed from a single sheep
EWE: female sheep
FLEECE: wool fiber, which comes in various colors
FLOCK: group of sheep
LAMB: baby sheep, either ram or ewe, under one year of age
RAM: male sheep, also called a buck
WOOL: outer covering of sheep, similar to hair but with a crimp

Sheep are estimated to have evolved over two million years ago. They were the first agricultural animal to be domesticated, about twelve thousand years ago, just after the end of the last Ice Age. It is estimated that sheep domestication occurred in the Middle East, with the nomadic tribesmen that lived near the current Iran and Iraq. The sheep herding practice spread west to the Mediterranean Sea area to Africa and Spain. By 4000 B.C.E., sheep could be found in northern Europe, India, and China. The domesticated sheep evolved from either the European mouflon or the Asiatic mouflon, which can still be found in the wild. These sheep were very large in comparison to current sheep, and weighed about the same as some breeds of cattle. They had huge curved horns, and had thick woolen coats covered with long guard hairs that helped repel water and snow. Modern sheep resemble the sheep of old, but only weigh about one third as much. The shepherds strove to improve their flocks, and culled out the sheep that did not improve the breeding.

In general, sheep are classified as either carcass animals, developed for meat consumption, or fiber animals, which were used primarily for wool clothing. If a sheep is used for food consumption and is under one year of age, its meat is called lamb, but if it is a year old or older it is referred to as mutton.

Description

Sheep come in all shapes and sizes, with many different variations. Many have horns that are large and curving, others are polled and have no horns at all. Depending on the breed, some sheep have horns in the male, where the female has none; in other breeds, both sexes have horns. Some sheep are covered with wool and need to be sheered on a regular basis; others have no wool and are hair sheep, raised for either meat or hides. Most hair sheep were developed in the tropics and are relatively immune to parasites. Sheep are excellent grazers and prefer a varied diet of green soft plants of almost every description. Sheep prefer to eat as they walk up hills rather than grazing when walking down. They can be very selective in choosing what they eat, as their mouths are flexible due to a cleft in their lips that serves them like fingers. Sheep are agile and can move very quickly on cloven hooves. Sheep are ruminants and have a four-compartment stomach that allows them to regurgitate the herbage they have eaten and then

Sheep Facts

Classification:
Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Ungulates
Suborder: Artiodactyla
Family: Bovidae
Genus and species: Ovis aries (domestic sheep)

Geographical location: Every continent except Antarctica

Habitat: Land, including mountainous regions, desert and dry land, forested areas, tropics

Gestational period: Approximately five months, depending on breed

Life span: Up to ten years, although some have survived up to twenty years

Special anatomy: Narrow muzzle divided by a center cleft; very flexible lips, which allow them to graze close to the ground and to be very selective as to the plants and food eaten; wool

chew cud. Sheep do not have teeth on the upper front of the jaw but have a hard pad, where food is pressed between the pad on top and the teeth on the bottom. The sheep uses a jerking, upward motion to pull up its food, then swallows it.

Most sheep have wool as an outer cover, although several of the more primitive breeds are covered by hair. The color white is the most dominant of colors, but other colors and spots are present in several breeds. A sheep's skin is very thin, less than 0.1 inches in thickness. The skin also has sweat glands, which are missing in most other domesticated animals. The number of fibers that grow out of the skin of a sheep varies from breed to breed. The carcass-bred sheep have the least, whereas the fine wool sheep the most. The fiber number can be as low as 4,500 follicles, to as much as 80,000 follicles per square inch.

Sheep Life

Sheep in general live for about eight to ten years. Depending on the breed, they will mature in one or two years. The ram is able to reproduce earlier than the ewe, and can be put into service before the female can. Sheep tend to breed during the late autumn or early winter. The gestation period for a ewe is five months.

When the lambs are born, the average weight is about nine pounds, about the same size as the average domestic cat. Most are single births, but twins are frequently born. Lambs nurse for about eight weeks.

Sheep are followers, and they will follow a leader in groups. At the first sign of danger, they run. They would rather live in totally dry conditions, and do not do well where it is moist and muddy, even though they have cloven feet. Sheep also have the ability to do without water

Bighorn sheep retain the large, curved horns possessed by the moufflon ancestors of today's domesticated sheep. (Digital Stock) for extended periods of time, but prefer to have it available.

—*Earl R. Andresen*

See also: Cattle, buffalo, and bison; Domestication; Fur and hair; Goats; Herds; Horns and antlers; Ruminants.

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SHELLS

Types of animal science: Anatomy, evolution, physiology
Fields of study: Anatomy, biochemistry, evolutionary science, invertebrate biology, physiology, zoology

External shells have been produced by many phyla, including both plants and animals. The majority of external shells are composed of calcium carbonate, but there are also examples of silica shells or tests.

Principal Terms

CARAPACE: the exoskeleton of arthropods

CARBONIC ANHYDRASE: an enzyme used in the mineralization process to convert carbon dioxide to bicarbonate

LAMINATE STRUCTURE: having a layered shell, as in the exoskeletons of crustaceans and the valves of clams

MATRIX: composed of proteins or protein-chitin polymers that act as nucleation sites for mineralization

NACREOUS LAYER: the pearl-like inner layer of molluscan shells

PORE CANALS: sites that house the cytoplasmic extensions of the crustacean hypodermis

PRISMATIC LAYER: the outer crystalline layer of the molluscan shell

Shells are external coverings that are produced by an organism. As such, they require a process by which the constituents of the shell are deposited in a site-directed fashion. What this means is that calcium and carbonate cannot come in contact with one another when their concentrations exceed their solubility product; otherwise, they will precipitate (form a solid). Thus, these ions must be directed to the area where the preferred precipitation is to take place. For this reason, a matrix is needed to provide a negative attractive force for calcium or other bivalent ions, such as magnesium. Other parts of the matrix may be composed of or house the enzyme carbonic anhydrase for the conversion of carbon dioxide reversibly to bicarbonate. The bicarbonate will degrade to carbonate ion that can then react with the positively charged calcium ion. Calcium can be taken out of the seawater or diet and concentrated; likewise, bicarbonate ions can be formed in the gills of some of these organisms and transported to deposition sites. However, having a matrix containing the enzyme carbonic anhydrase ensures that the calcium will only precipitate at that matrix site and nowhere else. In this way, the organism can control the shape of the shell by laying down a fiber matrix, usually composed of protein, as in mollusks, or a protein-chitin mixture, as is found in arthropods. The dumping of bicarbonate outside of a tissue where calcium is present will cause precipitation on the tissue membranes, a consequence with detrimental effects on the cells of the tissue. How calcium and carbonate ions are brought together varies from phylum to phylum.

The Protozoa

Among protists, mineralization is usually accomplished within a membrane-bound vacuole. The precipitated calcium carbonate is then exported by exocytosis to reside on the external surface of the cell. A matrix is secreted in the vacuole to facilitate the mineralization process. External calcium carbonate shells are found among the order Sarcodina of the phylum Sarcomastigophora. The shells of these amoebas become chambered with growth and are perforated by small openings, through which protrude slender pseudopodia that may be interconnected to form reticulopodia. Other sarcodines, the radiolaria and heliozoa, use silica as their shell material. In this case, too, the shell or test is perforated with puncta, or small openings, through which extend slender axopodia that will collect food.

Shells of Arthropods

The mineralized shell makes up the exoskeletons of the subphylum Crustacea and the subphylum Merostomata, which includes the horseshoe crabs. The mineralization process in the Crustacea is more complex than that of mollusks because the exoskeleton must be periodically shed and a new exoskeleton must be formed in the growth process. A percentage of the old exoskeleton is reabsorbed prior to molting and then redeposited in the new exoskeleton. Like mollusks, an epithelial, sheetlike tissue, the hypodermis, is responsible for the formation of the fiber matrix upon which is deposited calcium and carbonate. Unlike mollusks, the hypodermis forms cellular extensions that elongate as the layered exoskeleton is constructed. These cellular processes come to lie in pore canals as mineralization proceeds. The first layers laid down are the first to be mineralized, so new matrix layers are being formed while the mineralization of earlier deposited layers is proceeding.

Other differences found between the mollusks and crustaceans is the amount of protein-chitin matrix of Crustacea and the mainly protein matrix of the Mollusca. The fiber matrix of crustaceans averages about 40 percent by volume, a volume as high as the protein matrix of bone. Because the enzyme becomes entombed in the matrix during the mineralization process, new matrix must be laid down in stepwise fashion. This gives the exoskeleton a laminate structure that is divided up into an outer epicuticle, a middle exocuticle, and an inner endocuticle. A noncalcified membrane lies between the hypodermis and endocuticle.

Shells of arthropods are quite variable, but most have a carapace covering the dorsal part of the body (the head and the thorax). The jointed plates of the abdomen are also calcified, as are the legs and antennae. Ostracod arthropods have a clamlike shell that is hinged dorsally. Barnacles are the other crustacean group that has a different sort of exoskeleton. Their exoskeleton is composed of plates called parietes that form a wall around the organism.

Shells of Mollusks

The shells of mollusks are usually arranged into two major layers: an outer prismatic layer and an inner nacreous or pearly layer. The prismatic layer is composed of vertically oriented prisms that are bounded by matrix to separate each prism from one another. The prisms are elongated and extend upward to the organic layer of the shell, termed the periostracum. The nacreous layer is composed of cross-laminated lamellae. The lamellae are oriented in different directions, much like plywood layering. This serves to increase the strength of the shell in its resistance to cracking. The amount of matrix in the shells of mollusks is quite low and may be less than 1 percent of the shell volume. The mantle tissue that lines the shell is responsible for

Mineralization Debate

There is currently a debate concerning the mineralization process of the Crustacea and Merostomata. While it is clear that these hypodermal extensions are supplying the calcium ions for mineralization, it is still unclear as to the origin of the carbonate ions. Presently there are two views. First, bicarbonate ions are supplied by these cellular extensions to the mineralizing tissues. Second, the large quantities of carbonic anhydrase deposited into the external matrix of the shell function to maintain the bicarbonate concentrations in a reaction that is favored at a pH above 7.0 found in seawater. It is likely that both hypotheses are valid. Carbonic anhydrase has been extracted from formed shells and has been found to be active. This strongly implies that carbonic anhydrase is indeed active in the mineralization process.

Image Not Available

exporting the matrix, calcium, bicarbonate, and carbonic anhydrase for shell mineralization. A space, the extrapallial space, lies between the mantle and the shell and is filled with fluid to facilitate the transfer of ions to the shell. Whereas shell is deposited along the area of the mantle, new shell is deposited along the edge of the mantle.

The shells of mollusks are found in many members of this taxon. The class Monoplacophora have a single cap-shaped shell covering a muscular foot. The class Polyplacophora have an elongated body and eight shell plates covering their dorsal surface. More familiar shells of mollusks are found among the classes Gastropoda and Bivalvia. Gastropods have a single coiled shell that may be twisted, with an opening for the protrusion of the foot and head. The opening may be covered by an operculum that, in some groups, is calcified. The coiling of the shell may keep the weight of the shell over the foot for balance. The shell is used for protection against predation and to prevent desiccation in land forms. The animal can retreat into the shell when frightened or if poor water conditions occur. Many groups lose the shell in both terrestrial and marine forms and are sluglike.

Bivalves, as the name implies, have two shells or valves that enclose the animal and are hinged dorsally with an elastic ligament. Some species of both gastropods and bivalves grow spines by the evagination and elongation of the mantle to export a matrix for mineralization. This is carried out along the edge of the mantle; a ventral slit in the spine often remains to show where the mantle was during spine formation. Spine formation appears to be a device used by gastropods and bivalves to thwart predation, although this idea has not been fully tested. Spines may make these animals difficult to grasp, for example, by the claws of crabs or lobsters. In addition, the spines may make the animal difficult to swallow or crush in the mouths of fishes. Another strategy seen by these mollusks is the thickening of the shell, especially around its lip or edge. This makes it difficult for a crab to start breaking the shell from the edge, which is usually the thinnest part of the shell as this area represents new shell deposition.

Other molluscan groups with external shells are the nautiloids and extinct ammonites. These cephalopods often have coiled shells that resemble those shells of gastropods in their external appearance. Their shells are chambered, with the animal living in the endmost chamber. Gas can be secreted into the old chambers to act as a buoyancy device. The chamber partitions add strength to the shell to withstand ocean pressure at great depths. Nautiloid shells lack a periostracum. Ammonites were a similar cephalopod that occurred in great numbers during the Mesozoic era. Their shells were coiled or straight and developed complex sutures between the separate chambers. Rib patterns developed as well.

The class Scaphopoda has tusklike shells that are open at both ends. The animal extends out the lower opening and the upper opening extends above the sediment in this burrowing form for water flow into and out of the mantle cavity.

—Samuel F. Tarsitano

See also: Anatomy; Beaks and bills; Bone and cartilage; Brain; Claws, nails, and hooves; Defense mechanisms; Endoskeletons; Exoskeletons; Muscles in invertebrates; Muscles in vertebrates; Physiology; Predation; Skin; Teeth, fangs, and tusks.

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SHREWS

Types of animal science: Anatomy, behavior, classification, reproduction
Fields of study: Anatomy, classification, zoology

Small, ferocious shrews sometimes have venomous saliva. They are ecologically useful because they eat carrion and harmful insects.

Principal Terms

CARRION: dead, decomposing animal bodies
GESTATION: the time developing mammalian offspring are in the uterus
VENOM: a poison made by an animal

Shrews are usually very small; the Savi's pygmy shrew is probably the smallest known mammal on earth, less than 1.5 inches long and weighing 0.07 ounces. The shrew family, Soricidae, is the largest family of the order Insectivora, and shrews inhabit all major land masses except polar regions, Australia, New Zealand, and Greenland. Shrews are useful to gardeners because they eat many insects. They also inhabit fields, marshes, and woodlands. Some shrews are semiaquatic.

Shrews are often mistaken for mice because of their small size and vaguely similar bodies. Their habits and bodies are actually more like those of moles. Shrews have long, mobile snouts, tiny ears and eyes, and bodies covered with short, thick hair colored gray, brown, or black. Smaller shrews are under two inches long, while the largest are one foot long. They eat insects, worms, small fish, and plants. Weasels, foxes and owls eat shrews. However, the shrew's unpleasant odor and taste protects it from excessive predation.

Physical Characteristics of Shrews

Shrews have sharp teeth and are both vicious and ferocious. When attacked or disturbed, they fight wildly. They live alone, stake out territories, and hold them against invaders. As added protection, some shrews have venomous saliva, which they use to poison prey. Shrews also have whiskers that aid detection of prey at night. Shrews live in gardens, forests, woodlands, and grasslands. Most dig burrows, though some species do not burrow and others are semiaquatic.

The largest shrew is an elephant shrew, also called the golden-rumped shrew. These "giant" shrews have maximum body lengths of one foot, tails ten inches long, and weigh one pound. Elephant shrews are so named for their long snouts. Their tails are like rat tails and their hind legs are designed for hopping. A small elephant shrew, the short-eared shrew, has maximum body length of four inches, a tail of five inches, and a weight of 1.5 ounces. Elephant shrews inhabit South Africa and eat insects, snails, and plant roots, fruits, and seeds.

Shrews forage day and night and must eat every two to three hours to survive. This great need for food leads shrews to eat anything available. Depending on habitat and species, they eat insects, worms, carrion, seeds, nuts, plants, shellfish, frogs, and fish. Shrews hear and smell well. This helps them find prey and avoid predators. Some creatures kill shrews, but most will not eat them because they smell and taste bad. The smell and taste is due to secretions from skin glands most plentiful at knee and elbow.

The Life Cycles of Shrews

Shrews live alone except when mating. This occurs year round, except in cold climates, where mating is from March to September. Gestation, two to three weeks, takes places in nests that females dig. A female can have ten litters a year.

Each litter contains three to ten furless, blind young. An exception to standard litter size occurs in elephant shrews, who have one or two offspring. Offspring are full grown four weeks after birth.

Because of long mating seasons, some mothers nurse a litter while pregnant. Young leave nests after two to three weeks. Females mature in 1.5 months and males in 3 months. Courtship is short since shrews fight, even with mates. The life spans of shrews range from one to five years, depending on species.

The American Short-Tailed Shrew

American short-tailed shrews inhabit southeastern Canada, the northeastern United States, Texas, and Louisiana. They have thick, gray-black fur, are four to five inches long, have one-inch tails, and weigh one ounce. Like other shrews, American short-tailed shrews constantly seek food, eating insects, earthworms, snails, small vertebrates, centipedes, spiders, mice, frogs, and plants. They have venomous saliva, used to stun and kill prey, which is also painful to humans and large animal predators. Predators of the shrews are owls and other raptors.

American short-tailed shrews live alone except when mating, which happens from late winter to the next September. Courtship is short because shrews are harsh, even to mates. Females give birth after two to three weeks to litters of four to nine young. Young leave after a month. As with other shrew species, males are mature in 1.5 months, females in three. The life span of these shrews is two to three years.

Shrew Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Insectivora
Family: Soricidae (shrews), with twenty-two genera and 246 species
Geographical location: Worldwide except for poles, Australia, New Zealand, and Greenland
Habitat: Most in gardens, fields, marshes, and woodlands; some are semiaquatic and spend much time in freshwater
Gestational period: Thirteen to twenty-four days
Life span: One to five years in the wild
Special anatomy: Mobile snout, venomous saliva, glands that make offensive excretions to dissuade predators

Most shrews are harmless to humans, though bites of some species cause severe pain. They are useful in gardens and farms, where their consumption of insects and grubs cuts down harmful insect populations. Shrews are also useful ecologically because they eat carrion, preventing its decay and resultant endangerment of humans and other animals.

—Sanford S. Singer

See also: Gophers; Mice and rats; Moles; Poisonous animals; Predation; Rodents.

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SKIN

Types of animal science: Anatomy, physiology
Fields of study: Anatomy, cell biology, histology, invertebrate biology, physiology

Skin is the organ that covers the body surface of an animal, and it is composed of cells. The specialized structures and cells associated with the skin are involved in a variety of physiological functions, including protection, communication, regulation of body heat, and respiration.

Principal Terms

CHROMATOPHORES: pigment-producing cells
DERMIS: layer beneath the epidermis, primarily connective tissue but also containing nerves and blood vessels
EPIDERMIS: surface layer of epithelial cells
INVERTEBRATE: animal without a backbone
MITOTIC CELLS: cells capable of dividing and forming new cells
VERTEBRATE: animal with a backbone made up of individual bones called vertebrae

Survival in animals requires that the internal body components be separated and protected from the external environment. Most single-cell organisms are separated from the environment only by the plasma membrane (cellular membrane). In multicellular organisms the body surface is covered by a tissue consisting of epithelial cells and connective tissue. The covering is commonly referred to as skin, but the skins of invertebrates and vertebrates have distinct differences. Invertebrates often have a single layer of surface epithelial cells, which is generally referred to as an integument. However some invertebrates, specifically flukes and tapeworms, have a unique, living surface covering called a tegument. In this situation, the epithelial cells have fused and formed a single bag of cellular components called a syncytial epidermis. Thus, the word "skin" is often reserved specifically to describe the surface covering in vertebrates, but the word "integument" is also used.

The Structure and Physical Properties of Skin

The general structure of the skin is similar in all vertebrates. There are two primary regions, an epidermis and a dermis. The upper region, the epidermis, is made up of multiple layers of epithelial cells. All vertebrate skin has a basal layer (the stratum germinativum) consisting of mitotic cells. These mitotic cells divide to replace the cells closer to the surface as they are worn away, and to heal skin wounds. In most vertebrate species, the outermost layer of cells (the stratum corneum) is dead. The dead cells are filled with a waterproofing protein called keratin, which is produced by keratinocytes, the major type of cells forming the epithelium. An exception can be noted in many species of fish, where the epidermis is composed entirely of living cells and the stratum corneum is absent. The epidermis will differ the most between aquatic (water dwelling) and terrestrial (land dwelling) organisms. When compared to mammals and reptiles, the epidermis of amphibians, birds, and fish is thinner and the stratum corneum may only be one or two cells thick. The epidermis lacks its own blood supply (is avascular). Nourishment reaches the living cells by diffusion from the underlying dermal blood supply. No nerves are present in the epidermis.

The underlying region, the dermis, is primarily composed of connective tissue. Although epidermal and dermal thicknesses vary between groups of animals and thickness may vary along an individual's body surface, the dermal layer is always thicker than the epidermis. The hypodermis, a layer of subcutaneous tissue immediately beneath the dermis, connects the skin with underlying tissues such as muscles and bone. In birds and mammals in particular, this layer often contains a significant amount of fat, which provides insulation and a reserve source of energy.

The protective aspect of skin does not mean that it is entirely impenetrable or that the body is completely isolated from the environment. Materials that are fat-soluble or that disrupt cellular membranes can be absorbed across the skin surface. In some cases, beneficial chemicals cross skin. For example, frogs, which are amphibians, actively take up oxygen and expel carbon dioxide across the skin as well as the surface of the lungs. Amphibian skin is also permeable to water and, in fact, some species absorb amounts comparable to that obtained by drinking in other organisms. In other cases, detrimental materials such as solvents and potential environmental pollutants cross the skin. Acetone present in nail polish remover, methanol which is sometimes used to remove old finish on furniture, and salts of heavy metals such as mercury or lead are some examples.

Skin, like muscle, has the properties of extensibility (stretch) and elasticity (ability to return to the original shape after being stretched). These properties are made possible by the presence of collagen and elastic fibers as major components of the tissue comprising the dermis. When the elastic properties of the skin have been exceeded, white lines known as stretch marks appear.

Specialized Secretions and Structures Associated with Skin

Some epithelial cells produce and release protective secretions onto the external surface. Vertebrates and invertebrates both have mucous-secreting cells. On internal surfaces, such as the digestive tract, mucus protects cells from being broken down along with the food. On the external surface, mucus may trap bacteria or, as in earthworms, prevent death from desiccation (drying out). Another example of an invertebrate secretion is a covering called a cuticle. In insects this cuticle includes a mixture of proteins that eventually harden and form the exoskeleton.

Vertebrates, including fish, birds, and humans, as well as invertebrates, insects, secrete a group of antimicrobial (bacteria-killing) proteins called defensins (originally called magainins). Species of poison dart frogs have another type of protective secretion which is toxic to potential predators. Some of these secretions are used on poison dart arrows.

Changing Protective Layers

Snakes and other reptiles shed their skin, arthropods shed their exoskeleton, and some worms shed their cuticle in a process called ecdysis. In snakes, the mitotic cells of the basal layer replicate to form a new layer of epidermal cells that will be beneath the cells that are breaking down. There is a layer of cells in a region between the mitotic cells and the outer epidermal layers that is not keratinized and begins to break down. A separation or fission zone occurs at the level where the cells are breaking down. This results in the old epidermal layers breaking away above the newly formed layers. The old skin can now be shed and the new skin will be exposed. The surface of the new skin will be keratinized and scaly just like the old. Most snakes shed their skin in one piece.

Arthropods, which includes the insects, shed their exoskeleton many times during the growth stage. The epidermis detaches from the old exoskeleton and secretes a new epicuticle that will be the new exoskeleton. Molting fluid, which contains enzymes, is secreted into the region between the old and what will be the new exoskeleton. The enzymes degrade the inner region of the old exoskeleton. The old skeleton now splits and the animal emerges with a new exoskeleton. However, this skeleton will remain soft for some time and during that time it is able to stretch to accommodate the larger body size of the arthropod.

Structures with quite varied functions are derived from skin cells, particularly the epithelial cells. The feathers of birds function in flight but they also provide insulation. A bird's beaks and claws provide a method of defense and a way to secure food. Mammalian hair is an epithelial derivative. Body hair provides protection from abrasion and sunlight and has some insulation value. In animals that have them, sweat, oil, and mammary glands are groups of specialized epithelial cells. Reptiles, for example, lack sweat glands. Light organs of deep-water fish are modified epithelial glands. The scales of reptiles, the rattles of snakes, and the claws of turtles are other examples of epithelial derivatives. Geckos are able to walk up walls because they have modified epidermal scales on the tips of digits which serve as suction cups.

Cells of the dermis also are the origin for specialized structures in some organisms. Although there are fewer examples, dermal derivatives include shark teeth, fish scales, and the protective armor plates of an armadillo.

Skin and Temperature Regulation

The skin is a major organ in controlling body temperature. Mammals and birds are animals that generate internal body heat (warm-blooded or endothermic). Species of reptiles, fish, and amphibians, which are often called cold-blooded (ectothermic), are unable to control their body temperature through internal regulators in the same way that warm-blooded animals can. Both groups of animals depend upon the rich supply of blood vessels in the dermis as one mechanism for maintaining a safe body temperature. When internal body temperatures rise in endotherms, an increase in blood flow carries internal body heat to the surface, where it is lost to the environment. A similar increase in blood flow in ectotherms carries heat from the environment into the body and helps to warm internal organs and tissues. A decrease in blood flow will work in the opposite direction in both groups. In animals with sweat glands, the evaporation of sweat secreted onto the body surface also helps to lower body temperature. One unique feature of birds is a specialized region of skin, the brood patch, located on the ventral (stomach) surface. This area is rich in blood vessels (is highly vascularized) and is used to transmit heat from the female to the eggs or the hatchlings.

Skin Coloration

Vertebrate skin contains pigment-producing cells called chromatophores. Pigment production pro-

Hair-Raising Response

Originating in the superficial dermis and attaching to the hair shaft (long part of the hair) near its base is a small muscle, the arrector pili muscle. This is a smooth muscle, which means that its contraction and relaxation are involuntary responses. The muscle is innervated by a part of the nervous system (autonomic nervous system) that is under subconscious control. One part of the autonomic nervous system regulates specific responses during periods of stress. These responses are generally referred to as "fight-or-flight" responses.

When the muscle attached to a hair is stimulated to contract by the nervous system, the hair will stand up. In many mammals, dogs for example, this phenomenon occurs when a nonfriendly situation is detected. The raised hairs indicate alarm. In other cases, erected body hair serves as a protective method of defense since it will make animals appear larger than normal. In many mammals, elevated body hair traps air and assists in maintaining body warmth when exposed to cold temperatures, or helps in cooling when the core body temperature gets too warm. Hair normally emerges from the body surface at a slight angle. "Goose bumps," noticeable in humans who are frightened or experiencing some type of stress, are the result of a slight elevation of the skin when the hair shaft moves into a vertical position.

vides many benefits to animals. Skin pigments help to limit the amount of damaging ultraviolet light or irradiation to which the deoxyribonucleic acid (DNA) in the mitotic cells and the underlying tissues are exposed. Melanocytes located in the epithelium of mammals produce a brown-black pigment called melanin. They are the only pigment-producing cells in most mammals. In addition to epithelial melanocytes, amphibians, fish, reptiles, and birds have other types of pigment-producing cells which are located in the dermis. Examples are lipophores, which use carotene, a naturally occurring pigment in food, to synthesize yellow, orange, and red pigments, and iridophores, which use molecules called purines to synthesize pigments that are iridescent. The amount of pigment produced, the final location of the pigment in the cells, and the combination of cells producing it result in a range of body and feather coloration. Chromatophores account for the changes in body color that allow chameleons, flounders, and octopuses to easily blend in with different surroundings. Changes in body color also provide a means of communication between individuals.

Skin color, particularly in organisms with a thin, fair surface covering such as humans, is also influenced by the amount of oxygen bound to hemoglobin in the blood. Fully oxygenated hemoglobin is red and it gives a pink coloration to the skin. Hemoglobin that is not fully oxygenated can cause the skin to appear blue or take on a purplish hue, a condition called cyanosis.

—Robert W. Yost

See also: Anatomy; Beaks and bills; Bone and cartilage; Brain; Circulatory systems of invertebrates; Circulatory systems of vertebrates; Claws, nails, and hooves; Digestive tract; Ears; Endoskeletons; Exoskeletons; Eyes; Fins and flippers; Immune system; Kidneys and other excretory structures; Lungs, gills, and tracheas; Muscles in invertebrates; Muscles in vertebrates; Nervous systems of vertebrates; Noses; Physiology; Reproductive system of female mammals; Reproductive system of male mammals; Respiratory system; Sense organs; Shells; Tails; Teeth, fangs, and tusks; Tentacles; Wings.

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SKUNKS

Types of animal science: Anatomy, classification, reproduction
Fields of study: Anatomy, zoology

Skunks, related to weasels, are known for the vile odor of their musk. They are helpful to farmers, eating animals that prey on agricultural products. Their fur is used for garments and some people keep them as pets.

Principal Terms

GESTATION: the term of pregnancy
MUSK: vile-smelling liquids that skunks use for self-defense
NOCTURNAL: occurring at night
PERINEAL: located between scrotum and anus in males or the equivalent region in females

Skunks belong to the weasel family (Mustelidae), which also contains badgers, weasels, and otters. They form three mustelid genera found in southern Canada, throughout the United States, in Mexico, and in Central America.

The average skunk is sturdily built and cat-sized. It has a long, pointed nose or a hoglike nose, an arched back, and short legs. Skunk fur is long, soft, shiny, and black with wide, white stripes down the back. Stripe patterns differ among skunk species. Many skunks also have white forehead patches. Skunk tails are long, bushy, and usually black on top and white underneath.

Skunks live in hollow trees, burrows, or under sheds when dwelling among humans. They eat insects, mice, gophers, reptiles, squirrels, birds, and eggs. They help farmers by killing other animals that eat or prey upon agricultural products. Skunks are best known for their vile-smelling musk, originating in perineal glands on either side of the anus. When frightened, a skunk squirts out this fluid with considerable force. The musk's vile odor usually keeps enemies away. A human or animal sprayed with the fluid smells bad for weeks. For this reason, most people and animals learn not to attack skunks. One predator of skunks is the great horned owl, unaffected by the musk.

Physical Characteristics of Skunks

Striped or common skunks live in small groups in underground dens in pastures, meadows, and fields. They eat insects, gophers, reptiles, squirrels, birds, grubs, and eggs. These skunks are noc-

Image Not Available

Skunk Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Carnivora
Family: Mustelidae
Subfamily: Mephitinae
Genus and species: Three genera and thirteen species, including *Mephitis mephitis* (striped skunk); *Spilogale angustifrons* (southern spotted skunk), *S. gracilis* (western spotted skunk), *S. putorius* (eastern spotted skunk), *S. pygmaea* (pygmy spotted skunk)
Geographical location: The United States, Mexico, southern Canada, and Central America
Habitat: Rocky crevices or hollow trees; may live in the suburbs, where they make dens in burrows or under buildings or sheds
Gestational period: Two to seven months
Life span: Up to seven years in the wild, ten years in captivity
Special anatomy: Musk-secreting perineal glands; long, very bushy tails

turnal hunters. They either dig their own dens or use those vacated by other animals. Striped skunks are the largest skunks, reaching body-to-tail lengths of 3.5 feet and weights of five pounds. Their coats are glossy and black, with two wide, white stripes running from head top to tail tip. They spray musk in self-defense up to 6.5 feet. The musk hurts the eyes of predators and its vile odor lingers for many days.

Another type of skunk is the hog-nosed skunk. There are seven hog-nosed skunk species. They differ in habitat from striped skunks, living in rocky areas and inhabiting rocky crevices. They have sharp claws for digging hard, rocky soil. Hog-nosed skunks are two feet long from nose to tail tip and weigh about 3.5 pounds. Their glossy black coats have a white head-to-tail stripe. Unlike other skunks, they lack white stripes down the middle of the face and their tails are all white. Their long, bare snouts look like pig snouts, hence the name. Hog-nosed skunks are nocturnal and eat the same food as striped skunks.

Spotted skunks differ from striped and hog-nosed varieties in having four to six broken stripes or spots in different patterns on body and tail. Some dig burrows; others live in rock crevices. They are much smaller than other skunks, being only 1.25 feet long from nose to tail tip and weighing only one pound. Spotted skunks are like other skunks in nocturnal predation and diet.

The Life Cycle of Skunks

Striped and hog-nosed skunks mate during February and March in dens lined with grass and leaves. Males do not help raise young and live alone during the summer. Gestation lasts 2 to 3.5 months and a female gives birth to between two and ten babies, depending on species. The babies initially weigh about an ounce and can spray musk before they can walk. They are nursed for 1.5 months and then follow their mother around, learning to hunt. At six months old, they strike off on their own. These skunks can mate when they are eleven months old, and can live for six to seven years in the wild and ten years in captivity.

Mating of eastern, southern, and pygmy spotted skunks occurs in the usual February to March period, but gestation is only five weeks. In contrast, western spotted skunks mate in the late summer. Females of all four spotted skunk species give birth to two to six babies. Nursing and life spans are the same as for hog-nosed and striped skunks.

Skunk Fur and Skunk Pets

Wild skunks produce a valuable fur, but skunk farming is not profitable because of the low prices paid for each small pelt. However, skunk fur is beautiful. Coats made of this fur were once sold as "black marten," but are now sold under their real name due to Federal regulations. Buyers like skunk fur for its appearance and durability compared to most other furs. Skunks, often "destunk" by surgical removal of perineal glands, have some popularity as pets because they are attractive, friendly, and cat-sized.

—*Sanford S. Singer*

See also: Defense mechanisms; Fauna: North America; Otters; Weasels and related mammals.

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SLEEP

Type of animal science: Behavior
Fields of study: Ecology, ethology, neurobiology

Almost all animals exhibit behavioral sleep, a form of rest, but only birds and mammals have the same kinds of brain states as humans when they sleep.

Principal Terms

CIRCADIAN RHYTHM: a physiological or behavioral cycle that occurs in a twenty-four hour pattern

DIURNAL: habitually active during the day

ELECTROENCEPHALOGRAM (EEG): a chart of brain wave activity as measured by electrodes glued to the surface of the skull

NOCTURNAL: habitually active during the night

NONRAPID EYE MOVEMENT (NREM) SLEEP: sleep characterized by relaxed muscles and slow brain waves

RAPID EYE MOVEMENT (REM) SLEEP: sleep characterized by fast brain waves, during which dreaming typically occurs

Behaviorally, sleep can be recognized by four basic features. It generally consists of 1) a prolonged period of physical immobility during which there is 2) reduced sensitivity to environmental stimuli, and which 3) typically occurs in specific sites and postures and 4) in a twenty-four hour (circadian) pattern. Using this broad definition of sleep, almost all animals can be said to sleep.

The Ecology of Sleep

Since animals are more vulnerable to danger when sleeping than when awake, most animals sleep in sites and postures that help to maximize their safety. For an insect or a small lizard this might mean wedging into a crack in tree bark or burying themselves under leaf litter. For a snake, small bird, or mammal it might mean sleeping in a nest, burrow, or tree hollow. Some animals can adopt a particular sleep posture that helps them to blend into the background to avoid detection. Animals that cannot hide or camouflage themselves might try sleeping while semiprotected in the center of a family or larger group.

Animals can also modify their sleep sites and postures to help regulate their temperature. In cold temperatures, sleep sites and postures can be chosen so as to cover exposed skin on the face or feet; birds fluff their feathers and mammals fluff their fur to trap air like a blanket; small animals huddle together to keep warm. In particularly hot temperatures, well-chosen sleeping sites may protect an animal from direct exposure to the sun, and specific postures can be adopted to facilitate heat loss.

Sleep periods also tend to be taken at times that are most safe. Diurnal species are those that are typically active in the day and do most of their sleeping at night; nocturnal species those that are more active at night and do most of their sleeping during the day. In general, birds, reptiles, and shallow-water species tend to be active during the day while mammals and deep-water species tend to be active at night, but there are many exceptions to this generalization. Whether a particular species is primarily diurnal or primarily nocturnal depends upon many aspects of its ecology and physiology, but most exhibit some kind of circadian pattern of rest and activity.

The Physiology of Sleep

Neurophysiologically, "sleep" can be distinguished from "rest" in vertebrate animals only by

Do Animals Dream?

While we can never ask animals whether they dream, there is every indication that some of them do. During sleep, the brain activity of birds and mammals cycles between slow and fast waves just like that of humans going in and out of the dream state. During fast-wave sleep, birds and mammals also have rapid eye movements which, in humans, are associated with the visual imagery of dreams. Because the neurophysiology of rapid eye movement (REM) sleep in birds and mammals is so similar to that of humans, it is reasonable to think that they, too, are dreaming.

In mammals, a specialized part of the brain suppresses most muscle activity during REM sleep. Experiments show that if this area is destroyed, an animal will move around just as if it is awake, presumably because it is acting out its dreams. In an undamaged animal, small body movements and twitches during REM sleep are often visible. Many people know when their dog is dreaming because they see it making tiny running motions or hear it making muffled barking sounds. Cats often twitch their limbs and whiskers as they go through a period of REM sleep.

In birds, REM sleep takes place in very brief bursts of only a few seconds or a minute at a time, so the dreams of birds, while probably visual, could never follow much of a story line. Part of the reason for this is related to body size: The larger an animal, the longer its REM sleep periods. Since most birds are small, their REM sleep cycles tend to be short.

measuring changes in brain state. Fish, amphibians, reptiles, birds, and mammals all show changes in brain waves that accompany the progressive muscle relaxation that characterizes deeper and deeper states of sleep.

During their sleep periods, fish, amphibians, and reptiles slowly progress into more and more relaxed stages of sleep, then remain in their deepest state for a prolonged period of time, eventually returning slowly back to the waking state. Birds and mammals, on the other hand, show a pattern of alternating states of sleep within each sleep period. The first state is called NREM sleep (for "nonrapid eye movement sleep"). NREM sleep is characterized by relaxation of the muscles, slowed breathing and heart rate, and slow waves in the EEG (a measure of brain activity). Alternating with periods of NREM sleep are periods of REM sleep. REM sleep is characterized by rapid eye movements, irregular heart rate and breathing, and fast waves in the EEG that look identical to brain activity while awake. Although the brain is very active during REM sleep, most muscles are deactivated, leading some people to refer to REM sleep as "paradoxical sleep." In humans, it is during REM sleep that dreaming typically occurs.

Amazingly, some birds and marine mammals can sleep on one side of their brain and body while the other side remains awake. In marine mammals, it is thought that one-sided sleeping may enable an animal to keep swimming and stay near the surface in order to breathe. In birds, one-sided sleeping is thought to be a wayn for a particularly vulnerable animal simultaneously to get some rest and still remain alert for predators.

Across-Species and Developmental Patterns of Sleep

Large animals have longer sleep periods than small animals. Large animals also sleep more deeply (are more relaxed and have fewer arousals) than small ones and, among birds and mammals, have a greater proportion of REM sleep. According to the vigilance model of sleep, this is because large animals are less vulnerable than small animals, and so can afford to be less alert. Supporting this idea is the fact that for a given size animal, species that are predators typically sleep more and sleep more deeply than animals that are prey. Cougars, for example, sleep more and sleep more deeply than the deer they hunt, while falcons sleep more and sleep more deeply than pigeons and ducks.

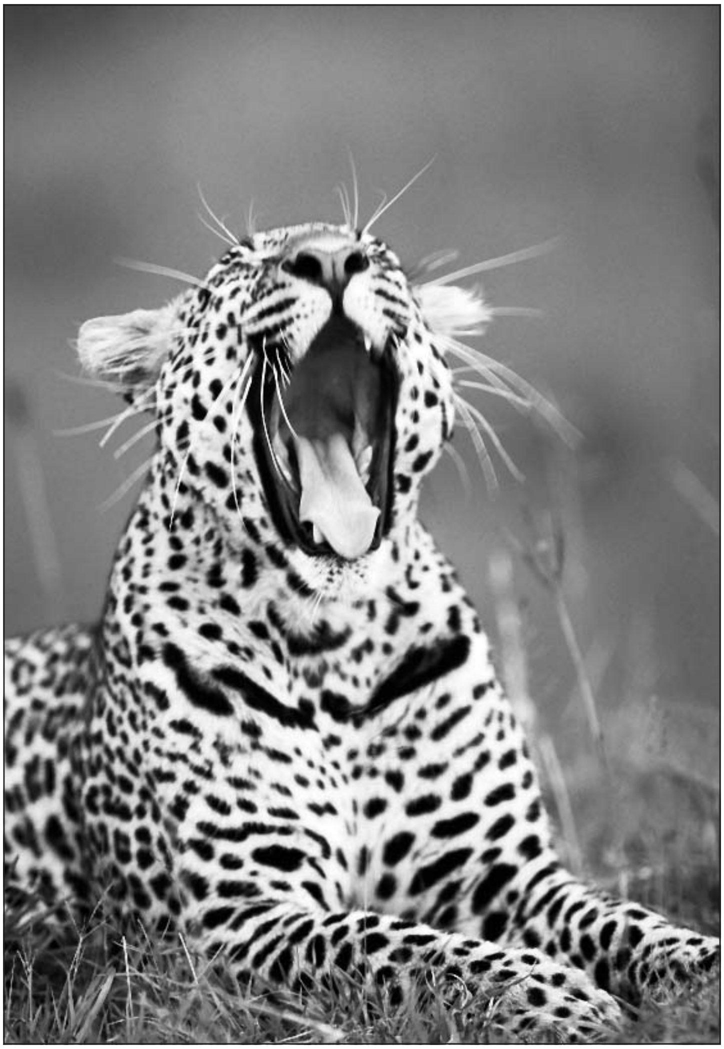
Although large animals tend to have longer sleep periods than small animals, small animals generally have more total sleep time than large animals because they sleep more often. It is not known whether this pattern results because small animals need more sleep or because what sleep they do get is shallower and more disrupted.

Consistent with the fact that small animals sleep more than large animals is the fact that in any particular species, young animals sleep more than adults. Not only does total daily sleep time drop as an animal ages, so does the relative percentage of time spent in REM sleep. Human babies have more total sleep time and a greater percentage of REM sleep than adults, and young adults have more sleep time and a greater percentage of REM than elderly adults. The same pattern seems to hold true for other species as well.

Possible Functions of Sleep

Besides the vigilance model, there are three other models which try to explain across-species and across-age differences in sleep. One of these suggests that sleep is necessary for learning. Since large animals generally live longer than small animals, they typically have a greater capacity for learning. Likewise, for a given size animal, predatory species typically rely more on learning, while prey species rely more on instinct. (A prey animal who makes a mistake is dead, whereas a predatory animal who makes a mistake can always try again.) According to this model, larger animals and predatory animals not only can afford to sleep long and deeply, they actually need more sleep in order to process and encode information. This model also accounts for the facts that young animals sleep more than older ones (they have more to learn), and that after accounting for body size and predator/prey status, mammals sleep more than birds.

A second model suggests that sleep is necessary for visual-motor coordination. This model was originally formulated to try to explain why birds and mammals have REMs during sleep but fish, reptiles, and amphibians do not. Birds and mammals have a much more complex visual system than other vertebrates. This model also attempts to explain why young animals sleep more



It is theorized that large animals sleep more than small animals because they are less vulnerable to predation. (Corbis)

Do Animals Sleepwalk?

In humans, sleepwalking occurs during NREM sleep when muscles are relaxed but not deactivated. Birds that sleep on the water are known to go through automated swimming movements while they are in NREM sleep—what might be called "sleepswimming." It is also thought, but not yet proven, that some birds can "sleepfly." Albatrosses, for example, are known to fly for extended periods without landing; it is possible that they fly on a kind of autopilot while they sleep.

When humans sleepwalk, they certainly autopilot. Although sleepwalkers are not conscious of any visual input, lower brain centers use information from the open eyes to navigate around objects. Presumably birds that are sleepswimming or sleepflying also have their eyes open in order to navigate, so it would be difficult to tell whether they were awake or asleep unless one had a very long range radio transmitter measuring their EEG.

In fact, birds sleep with their eyes open much more often than humans or other mammals. They also open their eyes frequently during sleep quickly to assess the status of the environment. This "peeking" is particularly common in birds that are especially vulnerable. Brightly colored breeding male mallard ducks, for example, peek more often than their camouflaged mates. Birds sleeping alone are also more vulnerable than birds sleeping in pairs or groups and, not surprisingly, they sleep less, are more easily aroused, and are more likely to peek than are birds sleeping in groups.

than older animals—their visual and motor systems are not yet fully developed—and why young animals of altricial species (those born or hatched relatively helpless) sleep more than young animals of precocial species (those born or hatched at an advanced stage of development).

A third model suggests that sleep functions as a mechanism for thermoregulation. Among warm-blooded species, small animals, having a greater surface-to-volume ratio, both lose heat and overheat more rapidly than large ones; thus, they would need to rest more frequently but for shorter periods. Young animals, according to this model, need to sleep more than older animals because their thermoregulatory abilities are not yet fully developed. Likewise, altricial animals sleep more than precocial animals because their thermoregulatory mechanisms are less well developed.

All or none of these models may be correct; although virtually all animals sleep, no one yet really knows why.

—*Linda Mealey*

See also: Aging; Brain; Camouflage; Defense mechanisms; Groups; Invertebrates; Learning; Predation; Thermoregulation; Vertebrates.

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SMELL

Types of animal science: Anatomy, behavior, development, evolution
Fields of study: Anatomy, biochemistry, biophysics, cell biology, developmental biology, genetics, herpetology, histology, human origins, immunology, marine biology, neurobiology, ornithology, pathology, physiology, reproduction science, zoology

For most animal species, smell is the main sense that is used in locating food and in detecting harmful agents and predators. Smell is used to recognize or exclude members within a social group, such as a pack, herd, or flock, and to find appropriate home sites. In some species, smell is also used to attract and identify mates.

Principal Terms

ANOSMIA: the clinical term for the inability to detect odors

CHEMOTAXIS: an oriented response toward or away from chemicals

OLFACTION: the sense of smell

OLFACTORY RECEPTORS: receptor organs which have very high sensitivity and specificity and which are "distance" chemical receptors

PHEROMONES: species-specific compounds (odors) which, acting as chemical stimuli at a distance, have a profound effect on an animal's behavior

Responses to chemicals are fundamental at all stages in biological organization. Chemotaxis, an oriented response toward or away from chemicals, has been observed in species ranging from single-cell animals such as bacteria and protozoa to very complex multicellular animals including humans. An attraction to a chemical is referred to as positive chemotaxis whereas a rejection or repulsion is called negative chemotaxis. The development of sensitivity (both positive and negative) to particular chemicals is the dominant sense in most animals. In general, receptor organs which have very high sensitivity and specificity, and which are distance chemical receptors, are called olfactory; the receptors of moderate sensitivity, usually found in the mouth, which are associated with feeding and are stimulated by dilute solutions are called taste receptors. Smells can be delivered to the olfactory receptors through air, as is the case with terrestrial animals ranging from insects to humans. On the other hand, smells can be delivered to the olfactory receptors through water, as is the case with aquatic animals such as insects and fish.

Smell in Insects

In insects, the olfactory (smell) receptors are located on the antennae. Because of the superficial location of their receptors and, more especially, because of their suitability for electrophysiological studies, insects have contributed much basic information about the mechanisms of olfaction. The olfactory receptors of most insects are highly specialized and can detect very trace amounts of compounds that are biologically important to the animal.

Olfaction is an important sensory modality for insects, particularly in mating, egg laying, and food selection. Numerous male insects, such as moths and cockroaches, are attracted by species-specific compounds called pheromones that act as chemical stimuli at a distance. Pheromones can be thought of as a language based on the sense of smell. Pheromones are often divided into two categories. Releaser pheromones initiate specific patterns of behavior. For example, they serve as powerful sex attractants, identify territories or trails, signal danger, and bring about swarming or similar types of grouping behavior. Primer pheromones trigger physiological changes in metabolism related to sexual development, growth, or metamorphosis. These changes are usually mediated through the endocrine system.

Male silk moths and gypsy moths may be attracted from a distance of a mile or two by a releaser pheromone from the scent glands of the females. Males will attempt to mate with any object that has touched the female scent gland; however, males deprived of their antennae do not even orient toward the female. Synthetic releaser pheromones are now being used in traps to attract pest insects such as the gypsy moth and the Japanese beetle.

Chemical communication in social insects is used for alarm, attraction, recruitment, and recognition of nest mates and of castes. Ants give off alarm releaser pheromones from mandibular glands and so are able to warn other ants of impending danger. Army ants deposit releaser pheromones on trails to food sources or to nest sites. Primer pheromones secreted by the queen bee cause the worker bees to cluster and swarm, and they suppress the rearing of other queens in the hive.

Mosquitoes are attracted chemically to warm-blooded animals and are sensitive to several chemicals. Carbon dioxide (the metabolic waste product excreted through the lung) attracts them and they are able to orient themselves and fly to the source of this compound. They also react positively to other mammalian body products. Most common insect repellants work by interfering with the olfactory ability of the mosquito, so that the insect can no longer follow an odor toward its source.

Smell in Fish

The olfactory receptors in most fish are located in olfactory sacs in a pit on the head. Chemicals are brought to the receptors while swimming or during respiratory movements.

Odors and the olfactory sense play a major role in the life of many species of fish. For example, homing in salmon is controlled mostly by the "smell" of the water in which the fish was born. By following the smell trail composed of the minerals found in the water, salmon are able to return to breed in the same stream in which they were born.

Fish can also become rapidly conditioned to odors. For example, once a pike has attacked a school of minnows, the odor of other pike in the water becomes associated with an alarm response in the minnows.

Smell in Terrestrial Vertebrates

In vertebrates, the olfactory receptor cells are located in the nose along the respiratory airflow path. As a result, when air is brought into the nose either during breathing or sniffing, odorant molecules are delivered to the headspace above the mucus-coated olfactory receptors. The odor molecules then bind to hairlike cilia on the olfactory receptors, producing a signal that is transmitted to the central nervous system. Because they stimulate different receptors, different smells produce different patterns of electrical activity. These odorant-specific patterns are used by the brain in smell identification.

Olfactory receptor cells are primary receptors, with axons running directly to the brain. This makes olfactory receptor cells unique, since most other sensory cells send their signals through processing centers (called synapses) before the message is carried to the brain. In the case of the olfactory receptor cells, all the information recorded by the cell is transmitted to the central nervous system. Once in the brain, the output of the olfactory receptors is sent to the limbic system (a portion of the brain involved with memory), the endocrine system, and throughout the rest of the central nervous system. The connections to the limbic system result in the very strong association that odors have in memory recognition. In humans, smells can often trigger very vivid memories. The rest of the brain also sends messages back to the bulbs, amending the pleasure of a food aroma when the stomach is full. Unlike other neurons, olfactory receptor cells constantly replicate. As a result, after a life span of about thirty days, olfactory receptor cells are replaced.

Odors help bond mothers to their newborn babies. A mother cuddling her infant will invariably brush her nose in the baby's hair to inhale its sweet aroma. She can identify her baby by its smell as much as by its cry. Additionally, one-day-old infants of many species have been shown to be able to recognize the smell of their mothers. A mother rat licks her nipples so that her blind pups can follow the scent of her saliva to the milk. Likewise, a mother kangaroo produces a saliva trail so the newly born and blind babies can follow the trail from the uterus to the mother's pouch. Wash the nipples and eliminate the saliva trail, and the pups are lost.

Female rodents who periodically smell male urine will move more quickly into puberty than females that do not. If a pregnant female mouse smells the urine of a male of another colony, she will immediately terminate her pregnancy. Also, if the olfactory nerves of a newborn rat pup are cut, the rats will never develop sexually.

A diminished sense of smell is termed hyposmia. Hyposmia can occur following a cold or after head trauma, and humans experience some reduction in the sense of smell with age. Also, most conditions that reduce the flow of air through the nose will reduce olfactory acuity. For example, a stuffy nose as a result of an allergy, a cold, or a nasal polyp often creates hyposmia. Anosmia is the complete loss of the ability to detect airborne odorants. Head trauma and severe nasal obstructions can produce anosmia. If the cause of hyposmia or anosmia is related to a blocking in the nasal airflow passageways, then treatment with steroids and/or surgery often can restore the olfactory loss.

Human experience seems to draw a sharp contrast between taste and smell. Taste is the chemical sense related to sampling compounds that come in directed contact with the inside of the mouth whereas smell is the ability of the nose to monitor airborne chemicals, often from distant sources. However, the sensations of taste and smell are not completely independent, since smell can influence taste and vice versa. For example, a lemon smell in the nose can make distilled water appear to "taste" bitter, and a sugar solution in the mouth can affect the perception of a fruit smell such as cherry. Much of what is usually perceived of as being a taste is really a smell. For example, with the nose blocked, it is difficult to tell coffee from bitter water or an onion from a potato. As humans chew, volatile compounds in the food are released into the air in the back of the throat. These compounds then make their way up the back of the nasal cavity, where they stimulate the olfactory receptors, producing a smell sensation that dramatically enriches the perception of the taste. This combination of smell and taste is referred to as flavor. What is often thought of as "taste" is actually a combination of smells and tastes, with additional contributions to the flavor coming from temperature and pain receptors in the nose and mouth.

—David E. Hornung

See also: Brain; Communication; Hearing; Insect societies; Nervous systems in vertebrates; Noses; Pheromones; Vision.

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SNAILS

Types of animal science: Anatomy, classification, reproduction
Fields of study: Anatomy, invertebrate biology, zoology

Snails are marine, freshwater, and land mollusks belonging to the class Gastropoda. Some are used for food; others are ecologically useful.

Principal Terms

FOOT: muscular bottom portion of snails, on which they walk

HERMAPHRODITE: an organism having both male and female reproductive systems in the same individual

RADULA: a tonguelike, toothed organ used to grind food

The first gastropods appeared 600 million years ago. Among these mollusks are snails and slugs, related animals which have a single shell and an asymmetric body. There are thirty-five thousand species, varying hugely in structure and lifestyle. The smallest snails are barely visible, while the largest, sea slugs, weigh up to thirty pounds. They occur in marine, freshwater, and land habitats.

The first gastropods were bilaterally symmetrical. Later, many evolved into asymmetric snails, with gills and anus above the head and coiled shells. In land snails, the gill-holding cavity became a lung. The snail head has eyes and tentacles, enabling good sight and smell. The mouth has a rasplike radula, used to harvest food. Digestive, nervous, circulatory, and reproductive systems are also well developed. Some snails have sexes and lay eggs in water, where they hatch, settle down, and mature. In many snails, fertilization is internal and hermaphroditic, and they can mate with any mature animal of the same species.

Physical Characteristics of Snails

Most snails have hard outer shells and slimy bodies. Slugs have no shells or internalized shells. On their heads, snails and slugs have two pairs of antennae. One pair holds the eyes. The other antennae sense the environment. The bodies of

Most snails have hard, spiral shells that protect their soft, invertebrate bodies. (Adobe) these gastropods grow from 0.1 inch to several feet in length, depending on species. The shell of a snail may be rounded, long and pointy, or flattened. Shells are homes and protection. When afraid, snails close them up via plates under their bodies.

Snails and slugs eat algae, leaves, lichens, small insects, and small marine organisms. As they also eat decaying plant and animal matter, the gastropods are ecologically important. Snails are also important to food chains, serving as food sources for fish and birds. A snail or slug eats with a radula, a ribbonlike tongue having thousands of tiny teeth. Radulas are drawn along rocks, leaves, or plants to scrape off food. Carnivorous snails have radulas that bore holes through shells of other mollusks to eat their flesh. Snails move by wavelike muscle contraction along the bottom of their muscular feet. This motion is aided by cilia in aquatic snails or slugs and by a slime track on land.

Types of Snails

Abalone, marine snails of the family Haliotidae, live on underwater rocks near shores of warm ocean regions. Their flat, ovoid shells, often a foot long, are nice souvenirs. Their thick feet are tasty.

The common garden snail, *Helix aspersa*, a land snail, inhabits Great Britain and continental Europe. It lives in moist, shady places, not restricted to gardens, is nocturnal, and can be four inches long.

Conches, marine snails of the order Mesogastropoda, close their shells with their digging claws. The largest conches (queen conches) inhabit warm Atlantic regions. Their three-foot-long shells make beautiful ornaments. Humans eat conch feet.

Great pond snails, order Bassommatophora, occur in ponds in Europe, Asia, and Africa. Their shells grow two inches long and one inch wide. Air-breathers, with lungs, they frequently come to pond surfaces for air.

Limpets, marine snails of the order Archaeogastropoda, are found worldwide. Limpets have arched, nonspiral shells and are found clinging to rocks. They scrape out rock areas the size of their shells, returning to their safety nightly. The New England species is 1.5 inches long.

The Life Cycle of Snails

Most snails are hermaphrodites, having both male and female sex organs. However, they usually mate with another individual of the same species, passing sperm to its partner and getting sperm from the partner. Fertilized eggs hatch in two weeks to two months. They are usually laid on marine or land plants, depending on the species involved.

The offspring pass through complex developmental cycles before hatching. Often, they hatch as miniature replicas of parents. In some cases hatchling snails have weak shells and very fragile bodies. Such snails become stronger and obtain hard shells, as they grow. Snails of most types are sexually mature at one to two years of age and live for up to ten years.

Abundant snails and slugs are important to food chains. They are herbivores, carnivores, and omnivores. As they eat decaying flesh and plants,

Snail Facts

Classification:
Kingdom: Animalia
Phylum: Mollusca
Class: Gastropoda
Orders: Include Archaeogastropoda (limpets), Bassomatophora (land snails), Mesogastropoda (conches)

Geographical location: Europe, Asia, Africa, the Americas, and Australia

Habitat: Oceans; freshwater lakes, streams, ponds; moist land environments

Gestational period: Eggs hatch in two weeks to two months, yielding miniature versions of parents

Life span: Two to ten years, depending on species

Special anatomy: Antennae, radula, muscular foot for locomotion, univalve shells, eyes on stalks in head, hermaphroditic reproductive system these gastropods have another ecological function, environmental cleanup. They are also important human foods. Escargot, in French cuisine, are cultivated land snails. Other edible snails are abalone, periwinkles, and queen conches. A few of these gastropods are harmful. For example, snails and slugs damage crops and gardens. Others are pests in oyster beds.

—*Sanford S. Singer*

See also: Hermaphrodites; Home building; Marine animals; Mollusks; Shells.

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SNAKES

Types of animal science: Classification, evolution
Fields of study: Evolutionary science, herpetology, systematics (taxonomy)

Snakes are squamate reptiles with slender, elongate bodies that lack limbs. In spite (or because) of these features, snakes have successfully exploited many habitats and lifestyles.

Principal Terms

- CLADE: a group of animals and their common ancestor
- CONSTRICTION: a method of killing prey using increasingly tight coils around the body to trigger stress-induced cardiac arrest
- FANGS: enlarged teeth that are hollow like a hypodermic needle or grooved to facilitate the injection of venom
- KINETIC SKULL: a highly moveable arrangement of bones that allows independent action of the snout and jaws on both sides
- VENOM: a toxic substance that must be injected (instead of ingested) to immobilize or kill prey

Humans are fascinated by snakes, arguably more so than any other kind of animal. This fascination may be based on fear (some snakes are undeniably dangerous), religious fervor (snakes figure, for good or ill, in nearly all world mythologies and religions), or curiosity (how does an animal move without limbs?). Regardless, this fascination has led to myths and an inclination to attribute mystical powers or malevolent intentions to these bizarre (by human standards) creatures.

Snakes are fascinating for purely scientific reasons as well. Based on diversity and total numbers, they are very successful. They have adapted to amazingly varied lifestyles in spite (or maybe because) of many unique features, the most obvious of which is the combination of extreme body elongation and lack of limbs. These, in turn, help explain other features. For example, long, slender bodies limit the size of the body cavity, requiring that paired internal organs are offset (placed one in front of the other) or that one organ is disproportionately elongated and its counterpart reduced or absent. Similarly, all snakes are obligate carnivores (meat-eaters; that is, they eat other animals). Plants are difficult to digest, and the simple, straight digestive tracts that can be accommodated in a snake's body are not long enough to provide enough time in passage for vegetable matter to be adequately broken down. However, these characteristics that appear to define snakes are shared with many other squamate reptiles, whereas those that are unique to snakes (number of body vertebrae; modification, reduction, or absence of some skeletal features; location of the ophthalmic nerve; eyes without ciliary bodies to facilitate focusing) are comparable to differences between other squamate reptiles.

Relationships Among Squamate Reptiles

For many years, squamate reptiles were divided into three suborders, Sauria (lizards), Serpentes (snakes), and Amphisbaenia (odd, mostly limbless burrowers), but recent studies of relationships indicate that snakes and amphisbaenians are cladistically nested within lizards; in other words, instead of being "cousins" of lizards, they are siblings. Consequently, the traditional suborders no longer reflect true relationships. They are retained for the sake of convenience by some authors, but only because they reflect clades within Squamata. As suborders, they have no formal taxonomic status.

Several distinct groups of snakes are recognized. The Microstomata (small-mouthed snakes) include small burrowing forms with blunt heads and tails. Among other snakes, two primitive families (uropeltids and aniliids) are distinct from macrostomatan (large-mouthed) forms, but many relationships within the latter remain unresolved.

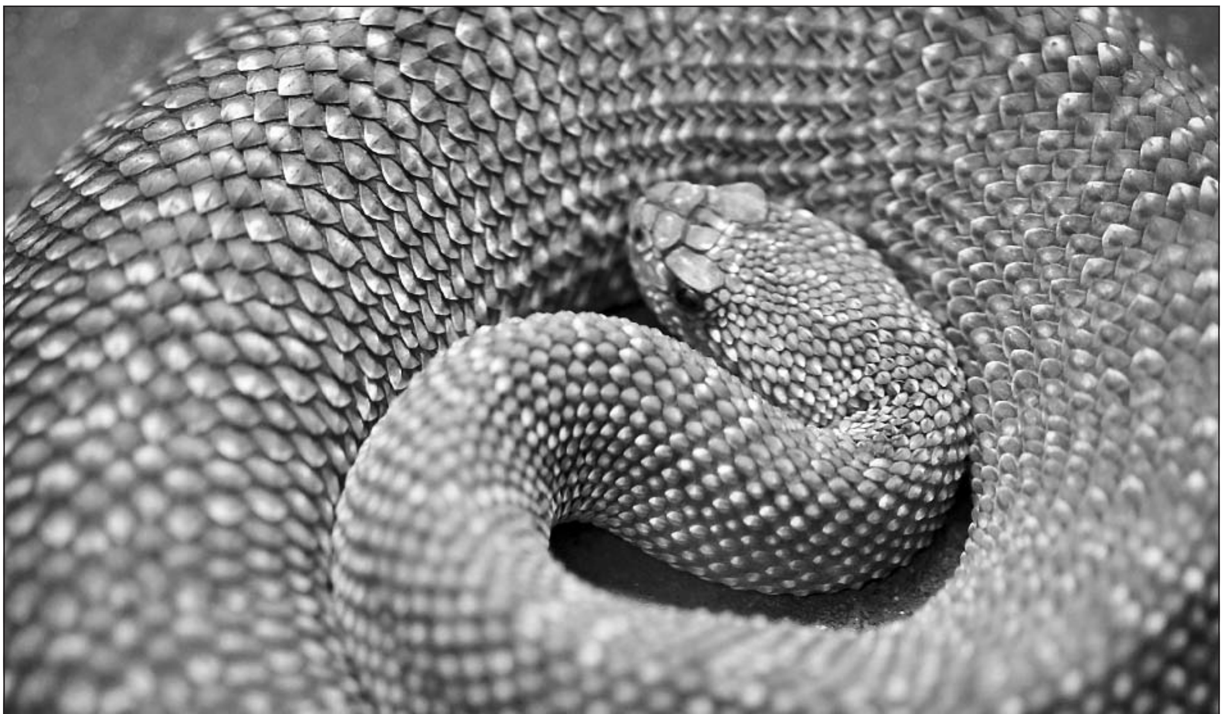
Body Forms and Habitats

Evidence suggests that snakes evolved as burrowers, but snakes in many families have subsequently and successfully exploited various habitats. Fossorial snakes (burrowers) are small, have conical heads (sometimes with modified snouts that help them dig), reduced scales that often overlap and reinforce sutures between skull bones, tiny eyes, and mouths located underneath the snout to avoid ingesting soil while burrowing. Many have spines on their tails for use as anchors when using the head to dig.

Arboreal snakes live in trees, and often are very slender, although the center of gravity may have shifted posteriorly so the rear of the body or tail can be used as an anchor while extending the head and anterior body over open spaces. To facilitate extension, many have laterally compressed bodies and enlarged scales along the back and belly; this allows them to form a structure much like an I-beam for support. Tails are long and may be prehensile (capable of grasping branches). Eyes are often large, as vision is more important than chemical cues when searching for prey in trees.

Snakes that inhabit loose ground litter in prairies or forests are small and often have enlarged scales on their snouts, with which they root for food. Like burrowers, body scales are usually smooth to reduce friction and ease passage through tight spaces.

Aquatic snakes often have eyes and nostrils on the tops of their heads, and nostrils may be equipped with valves. Many are heavy-bodied and laterally compressed to increase the surface



Snakes have remarkably flexible spines that allow them to coil tightly. (Corbis) area with which they push against water while swimming. Scales are generally rough to increase friction. Some sea snakes have fins supported by extensions of their vertebrae. Most aquatic snakes exhibit countershading (dark above, light underneath), reducing their visibility to both prey and potential predators.

Locomotion

Most snakes move by means of rhythmic waves of muscle contractions that cause the body to undulate laterally. Very heavy-bodied snakes often rely on rectilinear propulsion. Instead of muscles on the sides of the body working alternately, they work in concert, contracting and relaxing while drawing the body forward in a straight line. Enlarged belly scales or friction with the surrounding substrate (water in aquatic forms) prevents backsliding. Concertina locomotion and thrust creeping are used by burrowers. In the former, snakes first wedge the anterior part of the body and draw the posterior portion forward, then wedge the posterior region while extending the head and anterior body. Thrust creeping is very similar, except the spiked tail is used as a posterior anchor instead of a body loop. The most unusual form of snake locomotion is sidewinding, which is employed on loose or slick substrates. Loops of the body are elevated and thrown laterally to serve as the contact points while the intervening areas are raised. The advantage of this method is that force on the substrate is directly downward, which reduces slippage. Regardless of method, snakes are not very fast. The world's fastest snakes, large, slender mambas (*Dendroaspis*) can achieve top speeds on ideal substrates of about 12 kilometers per hour (about 7.5 miles per hour). Humans, in contrast, can sprint at speeds up to about thirty-five kilometers per hour (over twenty miles per hour).

Sensory Systems

Except for many arboreal and some actively foraging terrestrial forms, most snakes rely primarily on chemical cues to monitor their environment for food, prospective mates, or danger. Limbless forms are close to the ground and have a limited scope of vision (in fact, most are nearsighted). Snakes also lack external and middle ears, and are essentially

Snake Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Reptilia
Order: Squamata
Superfamilies: Typhlopoidea, Booidea, Colubroidea
Families: Fifteen recognized, including Typhlopidae (blind snakes or worm snakes); Leptotyphlopidae (slender blind snakes); Aniliidae; Xenopeltidae (sunbeam snakes); Uropeltidae (shieldtail snakes); Boidae (pythons, boas, and wood snakes); Acrochordidae (wart snakes); Colubridae, with subfamilies Dasypeltinae (egg-eating snakes), Pareinae, Dipsadinae, Xenodontinae, Homalopsinae, and Colubrinae; Viperidae (vipers, rattlesnakes, moccasins, and relatives), with subfamilies Viperinae (Old World vipers) and Crotalinae (pit vipers); Elapidae (cobras, mambas, coral snakes, and relatives); Hydrophiidae (sea snakes)
Genus and species: 450 genera, nearly three thousand species
Geographical location: Worldwide
Habitat: Terrestrial, aquatic, and marine habitats, except at very high latitudes
Gestational period: Some snakes lay eggs, whereas others bear live young; clutch sizes range from one or two (tiny threadsnakes and some sea snakes) to one hundred or more (large boas and pythons), and the incubation period varies according to temperature
Life span: Varies by species
Special anatomy: No legs

deaf to airborne sounds, although they are very sensitive to vibrations of the substrate. Thus, the importance of smell and taste is not surprising. Both smell and taste are very well developed in almost all forms, and are further enhanced by vomeronasal systems. The moist, forked tongue collects chemical molecules by flicking in the air or licking a substrate, and delivers these to paired sensory pits in the roof of the mouth. The importance of chemical senses is reinforced by the role of pheromones in snake reproductive ecology and observations that many snakes will follow a convoluted scent trail rather than rely on vision to directly approach a mate or food.

Specialized infrared (heat) receptors occur in several boid snakes and in pit vipers (Viperidae). In boids, receptors are in pits on the lips or snout, whereas pit vipers have a single pit between the nostril and eye on each side of the head. These sensors apparently are able to generate infrared images that are superimposed on visual images. Although obviously valuable to species that consume mammals or birds, which generate body heat, infrared imaging works equally well for species that eat frogs or salamanders. Amphibians have moist skins and lose evaporative heat to the environment, appearing as distinct "cold" spots in thermal images.

Some Types of Snakes

THREAD SNAKES (Leptotyphlopidae) include the smallest snakes, extremely slender forms less than ten centimeters (about four inches) long. Most are burrowers, but some have been found in bird nests. These were presumably brought to the nests by birds as food for their young, but escaped and subsist on the insects that also inhabit the nests.

BOAS and PYTHONS (Boidae) include the world's largest snakes. Although mythical accounts abound, individuals of some species (invariably females) may exceed twenty feet, and a very few may approach thirty. Tales of larger snakes are probably fanciful. Large snakes can exploit large prey, and can swallow deer, pigs, and even humans.

SEA SNAKES (subfamily Hydrophiinae) are the most aquatic snakes. Some species never leave water and give live birth. All are venomous and most feed on fish.

KING COBRAS (*Ophiophagus hannah*) are the longest venomous species, sometimes exceeding five meters (over sixteen feet) in length. King cobras feed largely on other snakes and are one of the few species that builds nests and cares for its eggs.

Killing and Consuming Prey

All snakes eat animal food. Some are know to scavenge or eat dead animals, but most hunt and kill live prey. Venom, often prey specific, is used by some to immobilize and kill especially large and dangerous prey. Constrictors use teeth to grab prey, then rapidly loop one or more coils of their body around it, tightening with each breath until the animal dies of stress-induced cardiac arrest and suffocation (constrictors do not crush their food). A few species may use loops of their bodies to press prey against the substrate. Some venomous forms constrict or compress prey while envenomating it; others quickly inject venom and then follow the prey's scent trail, ingesting it only after it dies. Other snakes eat animals with limited defensive capabilities, and prey is swallowed alive.

Snake teeth vary in number and size, but species that hunt prey that is hard to hold (slimy fish or snails that must be pulled from their shells) generally have the longest teeth. Bird-eaters often have long teeth to grasp the body of their prey and avoid a mouth full of feathers while the prospective meal escapes. Some snakes have upper jaw teeth of approximately equal size, rear-fanged species have enlarged posterior teeth that may be grooved, and others (cobras and their kin) have enlarged anterior fangs. Vipers and pit vipers have very large fangs on small maxillary bones that are rotated to erect the fang.

Most snakes can consume food much larger in diameter than their bodies by using a kinetic skull, a protrusible glottis (opening to the lungs) that is used like a snorkel when the mouth and throat are filled with food, and an elastic body wall not enclosed by ribs. Using teeth as anchors, upper and lower jaws on alternating sides separately "walk" over the prey until it is ingested. Rhythmic muscular contractions of the body wall then move the meal through the digestive tract. The ability to consume large prey reduces the need for frequent meals, allowing snakes time to rest and conserve energy before eating again.

Many snakes forage actively for food, rooting through debris or scanning their environment with one or more sensory systems. Some species, however, lie motionless, often well camouflaged, along a game trail, patiently waiting to ambush a meal. Because this sit-and-wait strategy does not require constant movement (other than the strike, which may be lightning quick), snakes that employ this method are frequently heavy-bodied and capable of eating the largest prey items relative to their body sizes.

Snakes in Need of Conservation

Snakes, because of the fear and revulsion they engender in many people, are subject to greater persecution than almost any other kind of animal. They often are actively hunted and, in many parts of the world, quickly killed whenever encountered. Nevertheless, habitat destruction and alteration are responsible for more declining snake populations than any other single factor. Many species are exploited as food, especially in parts of eastern Asia, and others are killed for body parts thought to have medicinal or aphrodisiac qualities. Introduced exotic species exact a toll. Many island populations of diurnally active terrestrial snakes have been extirpated by the mongoose, an effective predator introduced to control introduced rat populations. However, rats are nocturnal and mongooses active by day; consequently they have a much greater impact on ground-dwelling snakes than on rats. The leather industry is responsible for the deaths of hundreds of thousands of giant snakes each year. In addition, many wild snakes die each year as a consequence of being caught for the pet trade, much of it illegal. Many species become roadkills as they migrate. Only a few species are formally protected in at least some parts of their ranges, and many others may be nearing extinction in spite of increasingly frequent efforts to conserve them and their habitats.

—Robert Powell

See also: Camouflage; Digestive tract; Lizards; Poisonous animals; Predation; Reptiles; Scales; Smell; Vertebrates.

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SPARROWS AND FINCHES

Type of animal science: Classification
Fields of study: Anatomy, ornithology, systematics (taxonomy)

The finches and sparrows are some of the most widespread and successful of all songbirds. Of relatively recent origin and uncertain taxonomic status, they are united in possessing several basic characteristics: All are small, seed-eating songbirds that have a bill adapted for gathering, holding, and, in some cases, crushing seeds.

Principal Terms

CONVERGENT EVOLUTION: unrelated animals that have evolved similar features which enable them to exploit a habitat in a similar fashion, and have the same way of life

PASSERIFORMES: the largest order of birds, consisting mostly of perching songbirds

PRIMARY FEATHERS: feathers of the hand that provide most of the lift and thrust for bird flight

The name "finch" at one time was applied to ten different subfamilies of songbirds such as the chaffinches, goldfinchlike birds, buntings, grosbeaks, tanagers, weaver-birds, and sparrows. All of these birds have large jaw muscles that power cone-shaped bills. They differ, however, in skull structure and in the ways they open seeds. These differences suggest that at least some "finches" may have evolved independently and share characteristics as a result of convergent evolution. In view of these differences, most modern taxonomists agree that the name "finch" should be limited to the family Fringillidae in the order Passeriformes.

The 112 species of fringillids are among the most successful of the seed-eating passerines. All have conical bills or crossed bills adapted for eating seeds. Several fringillid subfamilies are recognized. The subfamily Carduelinae includes the New World rosy finches, purple finches, crossbills, redpolls, siskins, some grosbeaks, and saltators. Old World chaffinches and bramblings are placed in the subfamily Fringillinae. Two other New World fringillid subfamilies include the Hawaiian honeycreepers (subfamily Drepanidinae), which are restricted to the Hawaiian Islands, and Darwin's finches (subfamily Geospizinae), which are found only on the Galápagos Islands.

Several finchlike birds have recently been placed in a separate family called the Emberizidae. This family is further subdivided into the subfamily Emberizinae, which includes the New World sparrows, juncos, longspurs, and tropical brush finches, and the subfamily Cardinalinae, which includes the forty species of cardinals and their allies.

Old World sparrows, which include the familiar house sparrow (*Passer domesticus*), are more distantly related and placed in a separate family called the Passeridae. They are widespread seed eaters that occur in a wide variety of habitats throughout most of Eurasia and Africa. Some, such as the house sparrow, have been deliberately and successfully introduced in many other areas of the world.

The Ecology of the Finches

Most finches are forest-dwelling, seed-eating songbirds that have nine instead of ten primary feathers in the wing and twelve tail feathers. The outermost part of ten primary feathers is usually small and hidden.

Most species have sweet, melodious songs and often sing in winter, which is why they were

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named finch (from Latin *frigus*, "cold," because finches sing in the cold of winter). The female builds an open, cup-shaped nest with her tail feathers and also uses the feathers to incubate the eggs. Incubation and the fledgling period usually last between eleven and fourteen days. Members of the subfamily Fringillinae feed insects to their young and inhabit large territories while breeding. There are usually about three or four eggs and they are blue-gray with purple-brown spots. In the summer, the birds eat caterpillars from trees, and in winter seeds from farmland, including spilled grain and weed seeds. Over most of their territory they are migratory, but females tend to move farther away from their territory than males.

The Carduelinae form the largest branch of the finch family, with about 122 species. These birds are more specialized seed-eaters than Fringillinae and they feed their young mostly seed, sometimes augmented with insects. They nest either alone or in loose colonies and feed away from the nest in packs. Many feed directly on plants and are adept at clinging to stems or hanging on twigs. They demonstrate a wide range in bill shape and adaptation for extracting the seeds from different types of seed pods. The fringillids range in size from the *Mycerobas* grosbeaks of the Himalayas, which reach eight inches in length and 3.5 ounces in weight, to the relatively tiny Lawrence's goldfinch (*Spinus lawrencei*) of eastern North America, which just reaches four inches in length and weighs no more than 0.3 ounce.

Most fringillids are found in temperate regions, with fewer in the Arctic, deserts, tropics and subtropics. About sixty-eight species occur in Eurasia, thirty-six in Africa, and twenty-five in the New World. Fringillids are absent only from Madagascar and the islands of the South Pacific. Some species have been introduced into Australia and New Zealand.

Sparrows

The twenty-seven species of Old World sparrows are closely related to weaver finches and were once grouped with them in the family Ploceidae before being placed in their own family. They are all small, seed-eating birds that occupy a wide variety of habitats throughout Eurasia and Africa. Over half of the true sparrows (*Passer*) coexist well in human habitations and at least one, the house sparrow, has for so long adapted to exist in human-modified landscapes that it is no longer found naturally in the wild. House sparrows coexist with humans in habitats and climates ranging from tundra to tropics. Other *Passer* species occur in habitats as diverse as desert, woodlands, or tropical rain forests. Dry brush country and mountain habitats are occupied by species of rock sparrows (*Petronia*) which may range upward of fifteen thousand feet in the Himalayas.

Males claim nest sites and sing to attract females and deter other males. Following pair formation both sexes help build the nest. Many *Passer* species, such as tree sparrows (*Passer montanus*), are solitary nesters, usually nesting in tree cavities, but some are at least partly social and nest in loose aggregations. Several species also build a ball-shaped nest with a feather-lined interior and an entrance toward the side. Depending on species, from two to eight whitish or mottled eggs are laid in a clutch, generally fewer in the tropics and more in temperate zones. Incubation is brief, generally eleven or twelve days, and the young remain in the nest for another two weeks (up to seventeen days). The young are fed on a variety of foods, mostly seeds and insects, but discarded bits of human food, grains, and other discarded edible substances are often readily used to feed the young.

Tropical sparrows generally raise one brood a year, but temperate species may raise two or three broods or occasionally even four broods in good weather conditions and availability of sufficient food. Following breeding, the sparrows are gregarious, gathering in loose aggregations of foraging flocks that may include other species. In many locales their numbers may cause appreciable destruction of seed crops.

Some Typical Finches and Sparrows

The northern cardinal (*Cardinalis cardinalis*) belongs to the subfamily Carduinalleae. Males are bright "cardinal" red with black about the bill. Females are a duller brown-red. Both have a distinctive crest. The species is widespread throughout eastern North America, in western North America from the Great Plains south and west into California, Arizona, New Mexico, Texas, and into Mexico. It is essentially nonmigratory and winters in the same general area. The cardinal's range has expanded northward in recent years, especially into New England, and it has been successfully introduced in Hawaii.

Cardinals dwell in mostly edge habitats, especially the interface of woodland and meadow, and edges of swamps of shrubby wetlands, especially areas that offer shrubby evergreens for nesting. They have adapted well to human-modified landscapes and commonly nest in landscaped yards in which the mix of ornamentals and grass essentially mimics its natural habitats.

One of the earlier nesting species, cardinals may claim their territories in late February. The female typically constructs a nest of leaves, weeds, grasses, and thin bark strips in dense shrubbery, often in either evergreens or vine tangles from one to twenty feet

Sparrow and Finch Facts

Classification:
Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Class: Aves
Order: Passeriformes
Families: Fringillidae (finches and allies, New World sparrows); Emberizidae; Passaridae (Old World sparrows)
Subfamilies: Carduelinae (New World rosy finches, purple finches, crossbills, redpolls, siskins, some grosbeaks, saltators); Fringillinae (Old World chaffinches, bramblings), Drepanidae (Hawaiian honeycreepers); Geospizinae (Darwin's finches); Emberizinae (New World sparrows, juncos, longspurs, tropical bush finches); Cardinalinae (forty species of cardinals and allies)
Geographical distribution: All continents, except Madagascar and South Pacific islands
Habitat: Prefer temperate regions, although some species are found in Arctic, desert, tropic, and subtropical regions
Gestational period: Varies by species, but most eggs are incubated for eleven to fourteen days
Life span: Varies; three to ten years in the wild, five to eight years in captivity
Special anatomy: Beaks adapted for gathering, holding, crushing, and eating seeds; finches have nine primary wing feathers and twelve tail feathers; melodious song

high, but generally lower. Clutch size is generally three or four spotted white eggs which hatch in about twelve to fourteen days. Three broods may be raised in a season in southern states, about two broods in more northerly states. The young are fed seeds and small insects. Adults divide roles and responsibilities to raise a second and sometimes a third family; the male cares for the first brood while the female incubates the second brood. The young and adults also form family groups that may remain together in fall. Groups often form loose flocks of up to seventy birds in winter. Cardinals are common birds at feeders.

The American goldfinch (*Carduelis tristis*) belongs to the family Fringillidae. It is widespread in North America, breeding from southern Canada southward to Gulf Coast states, west to California. At least partially migratory, it winters along the Gulf Coast and Florida but may winter anywhere in its breeding range in mild winters.

The American goldfinch is a bird of fields and open woodlands. It is a late-nesting species, often not beginning until August in its northern range, late May or June in western and more southern states. Nests are constructed in branch forks, often from one to thirty feet high. The highly compact, cup-shaped nests are lined with thistle or thistledown and are so tightly constructed that they hold water—young sometimes drown following heavy rainstorms when the nest is flooded. Generally four to six (usually five) bluish eggs are laid and incubated by the female for about two weeks. The male attends the incubating female at the nest, bringing her food.

Young are fed by regurgitation as the parents first fill their crops with dandelion, burdock, thistle, or chicory seeds, berries, and insects, then regurgitate or cough them up to feed each of the young. Seeds are usually augmented by insects, especially caterpillars, grasshoppers, aphids, and plant lice.

The house sparrow (*Passer domesticus*) belongs to the family Passeridae. It is the most widely distributed of Old World sparrows, ranging across Eurasia and Africa and successfully introduced in South America and Australia. Repeated introductions of birds in North America between 1850 and 1867 resulted in the establishment of this aggressive songbird. At the turn of the last century (1900), it was probably the most abundant bird in North America but has declined with the switch to combustion engine vehicles, for it fed on the scattered feed grain fed to horses. The house sparrow gathers in large winter roosts in urban and suburban areas or evergreen plantations.

House sparrows are aggressive cavity nesters. Their success has at least partly been at the cost of other cavity nesters such as bluebirds and swallows. Nesting sites are selected in cultivated areas, especially buildings, outbuildings, farms, and edge habitat between urban and suburban landscapes and natural landscapes. Artificial cavities, including nest boxes, are also readily appropriated by this adaptable species. The nest of small twigs and leaves is lined with grasses, feathers, hair, and bits of paper and other discarded materials. The four to six white or greenish eggs are incubated for about fourteen days. Young are brooded by the female and fed mostly insects and spiders, along with seeds and blossoms.

—Dwight G. Smith

See also: Beaks and bills; Birds; Domestication; Feathers; Flight; Molting and shedding; Nesting; Respiration in birds; Wildlife management; Wings.

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SPIDERS

Types of animal science: Classification, ecology, evolution, geography
Fields of study: Ecology, evolutionary science, systematics (taxonomy)

Spiders are members of phylum Arthropoda, the dominant animals on earth in terms of both number of species and number of individuals. Of an estimated ten million species of arthropods, only 10 percent have been identified. A close examination of spiders helps to understand other arthropods.

Principal Terms

BOOK LUNGS: specialized respiratory structures of arachnids, such as spiders

CLASS: the taxonomic category composed of related genera; closely related classes form a phylum or division

COMPOUND EYES: eyes that are made up of multiple lenses or light detectors

EXOSKELETON: an external skeleton that encloses the body like a suit of armor

MOLTING: in animals with an exoskeleton, the process of shedding the old shell to allow the increase in body size due to growth

PHYLUM (pl. PHYLA): the taxonomic category of animals and animal-like protists that is contained within a kingdom and consists of related classes

TRACHEA: a network of narrow, branching respiratory tubes

The major classes in the phylum Arthropoda include the insects (class Insecta), the spiders and their relatives (class Arachnida), and the crabs, shrimps, and their relatives (class Crustacea). Arthropods are everywhere, cohabiting with humans: ants, yellow-jackets, spiders, dragonflies. It is only fitting to look at the factors that contribute to the huge army of arthropods before examining one of their members: spiders.

Traits Contributing to the Success of Arthropods

Several adaptations are responsible for the spread of arthropods to nearly every habitat on earth: an exoskeleton, segmentation, the efficient use of oxygen, and a well-developed body plan, including circulatory, sensory, and nervous systems. The exoskeleton is formed via secretion by the epidermis (the outer layer of skin) and is made up mainly of protein and a polysaccharide called chitin. The exoskeleton protects against predators and is responsible for arthropods' increased agility over their wormlike ancestors. The exoskeleton allows precision movement, making possible the flight of the bumblebee and the intricate, delicate manipulations of the spider as it weaves its web. By providing a watertight covering for delicate, moist tissues, the exoskeleton also contributed enormously to the arthropods' invasion of dry land habitats. However, the exoskeleton also creates some unique problems for arthropods. First, it cannot expand as the animal grows, and thus must be shed, or molted, periodically and replaced with a larger one. In the process of molting, arthropods are vulnerable to predators. Second, the weight of the exoskeleton increases exponentially as the animal grows, placing a cap on the size arthropods can reach. No wonder some of the largest arthropods (crabs and lobsters) reside in buoyant watery habitats.

In general, segmentation in arthropods is less distinct than the worms (annelids). Three main segments are evident: the anterior segment forms

The spider's web is made of silk created from fluid proteins produced in glands and excreted through spinners at the rear of the abdomen. (Digital Stock)

the head; the posterior segment holds digestive structures as the abdomen. Between the head and the abdomen is the thorax, consisting of structures used for movement, such as wings and legs.

The efficient gas exchange in arthropods is accomplished by gills in aquatic forms, and by either tracheas or book lungs in terrestrial forms. Arthropods also have a well-developed open circulatory system, by which blood not only travels through vessels but also bathes the internal organs directly.

A well-developed sensory and nerve system is another feature of arthropods. Most have compound eyes and acute chemical and tactile senses. The nervous system consists of a brain with fused ganglia in the head and a series of ganglia running through the body, coordinating movement and other complex behaviors.

Common Characteristics of Spiders

Spiders, scorpions, mites, ticks, and their relatives are members of the class Arachnida. The arachnids comprise about seventy thousand species of terrestrial arthropods. Animals in this class have eight walking legs; most are carnivorous, and many subsist on a liquid diet of blood or predigested prey. Spiders are the most numerous arachnids, accounting for forty-two thousand species belonging to one hundred different families. The number of spiders can be larger than anyone expected. A study in Great Britain counted spiders in a meadow, coming up with 131 spiders per square meter. Within the area of 36,150 square kilometers that composes the Netherlands, there are approximately five trillion spider inhabitants. Put together, these spiders could consume all fifteen million Dutchmen in merely three days.

Many people confuse spiders with insects. Although many similarities exist between spiders and insects, such as the presence of an exoskeleton, the gas exchange system, and the circulation system, three conspicuous traits can serve to distinguish spiders and insects. First, spiders usually have four pairs of legs compared to insects' three. Second, insects have compound eyes whereas spiders have singular eyes with lenses. Third, insects have antennae while spiders do not.

The body of a spider has two distinct parts: the cephalothorax, consisting of the head and breast, and the opisthosoma, or abdomen. The back of a spider is referred to as its dorsal side and the bottom is its ventral side. The eight legs, two jaws, and two feelers (palps) are connected to the cephalothorax. The males have a bulb at the end of their palps, which is used to store and inject semen into the sexual organs of the female. There are usually eight eyes on the cephalothorax, although the number may vary from none to twelve. An extensive nerve system is made up of a brain located in the cephalothorax, and ganglia (the equivalent of nerves in mammals) that run through various sections of the body. The heart is situated at the front upper side of the abdomen. The silk-making spinners are found at the rear of abdomen. These spinners are linked to glands that produce a variety of proteins, which when mixed polymerize to form silk. As the fluid silk is pressed through the spinners, a thread is made. The reproductive organs are located between the book lungs and the spinners. Running though the whole body is the alimentary canal, at the end of which is the excretory system.

Spider Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Arthropoda
Class: Arachnida
Order: Araneae
Suborders: Mygalomorphae (the primitive spiders); Aranaeomorphae (the modern spiders); Mesothelae, with one family of spiders, the Liphistiidae

Geographical location: Every continent except Antarctica

Habitat: Diverse; mostly on land, inside and outside buildings, on or close to the ground, under stones, logs, litter, low or medium foliage, tall shrubs and trees, under bark; some live in freshwater and very few in salt water

Gestational period: Varies; some female spiders can carry sperm for some time after mating until ready to produce an egg sac

Life span: Many live for up to two years

Special anatomy: Eight walking legs, four on each side of the thorax; eight simple eyes, each with a single lens, that are particularly sensitive to movement; an extensive nerve system; silk-making spinners; muscular jaws equipped to inject poison into prey

Various Body Parts and Their Functions

Most spiders are equipped with poison glands to kill prey. The jaws are used to grab and crunch the prey. A pair of syringelike structures, which are hollow and extremely sharp, are found at the end of the jaws. They are used to puncture the body and inject poison into a prey. The venom is produced in special glands and stored in a special bladder, around which is a spiral muscle. This muscle contracts to eject the poison through the syringe into the victim. The poison, made up of proteins, amines and polypeptides, causes paralysis by disrupting the communication between the nervous system and the muscles. The poison and digestive enzymes cause the death of cells and dissolve the contents of the prey. The spider then sucks the prey empty, leaving a shell behind. Many spiders can give a nasty bite comparable to the stinging of a wasp; a spider sting can even be fatal to children and persons with weak constitutions.

Spiders use a trachea, a slit above the spinners that can be opened and closed, for admission of oxygen. Long small tubes run from this slit into the body. Gases are exchanged with the blood by diffusion. Many spiders also have book lungs, which are hollow, leaflike structures through which the blood flows. Many modern spiders have both tracheas and book lungs. With these two systems together providing extra oxygen, the modern spider has an advantage in having quicker and more sustained reaction times than the primitive counterparts with only book lungs. The circulating blood in a spider's body is colorless and called hemolymph. It transports nutrients, hormones, and cells in addition to oxygen. It is also used locally to raise blood pressure during molting and stretching the legs. Spiders have an

The Black Widow: Small but Deadly

The black widow spider, *Latrodectus mactans*, is found in the United States from northern Massachusetts, south to Florida, and west through Louisiana, Texas, Kansas to California, and also throughout Central America. The body length of the female reaches up to 5 inches, but males are smaller. Leg span for the female is 0.75 inches, with that of males slightly longer. The main diet includes beetles, cockroaches, crickets, flies, scorpions, and spiders.

The black widow possesses one of the most powerful venoms. She earns her name from her gruesome habit of devouring the tiny, harmless male spider after mating with him. The black widow's poison is called a neurotoxin—it attacks the nervous system and blocks the transmission of nerve signals to the muscles, causing convulsions, paralysis, and intense pain. Every summer, the male black widow goes searching for a mate. The female simply waits in her web, hanging upside down as usual. When he finds a female, the male approaches very carefully and signals to the female that he is not prey by tapping out a coded message on the web. As soon as the mating is over, however, he must escape or become an easy meal for the female.

open blood circulation system with the heart located in the back of the abdomen. Blood vessels transport the blood to the heart but thereafter the blood flows freely in the open spaces between organs. The heart is an open tube with valves which is hung in a cavity. Elastic muscles around this cavity contract, enlarging the tubes and forcing blood to flow in only one direction. The size of the heart is closely correlated with the size of the trachea system.

A number of nerves extend from the brain to the legs, eyes, and the rest of the body. The brain occupies about 20 to 30 percent of the cephalothorax volume. Spiders have several sensory organs with which to sense and react to their surroundings. They have simple eyes, each with a single lens, which are particularly sensitive to movement. Spiders have neither ears nor sense of taste. However, they are able to detect smell with scent-sensitive hairs located on their legs. With the brain and all sense organs, spiders are sharp hunters.

With its enormous strength, spider silk is an extraordinary material. A thread of silk the thickness of a pencil has enough strength to stop a Boeing 747 flying at full speed. Humans simply do not yet know how to duplicate such a material. Silk threads are produced by several glands located at the spider's abdomen. Every gland produces a thread for a special purpose: glandula ampulleceae for the silk of the walking thread, glandula pyriformes for the attaching threads, glandula acinoformes for the encapsulation of prey, glandula tubiliformes for the thread of cocoons, and glandula coronatae for the adhesive threads. A thread is made up of polymerized protein molecules. The smallest measured thread was only 0.02 micrometer yet a web made up of it is capable of stopping a bee flying at full speed. The thread is also very elastic and can be stretched 30 percent without breaking. Spider webs take a variety of shapes and function to trap prey, produce cocoons, and provide hiding places for the spiders.

Male spiders are often smaller and more colorful than the females. Males can also be recognized by what appears to be a fifth pair of legs. These are actually palps with bulbs for injecting their sperm into a female during mating. During breeding season, males search for females. Once the female is found, the male has to avoid being mistaken for prey by the female. Male spiders of different species use different ways to announce to the female that they are interested in mating. If the signals are right and the female is ready, mating occurs. After the mating, the males of some species must be extremely careful or they will become an easy meal for the female. The females lay their eggs and tend the young. The kingdom of spiders goes on.

—*Yujia Weng*

See also: Arachnids; Arthropods; Circulatory systems of invertebrates; Food chains and food webs; Molting and shedding.

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SPONGES

Types of animal science: Classification, ecology, reproduction
Fields of study: Anatomy, zoology

Thousands of sponge species occur, most in the oceans. They are sexual hermaphrodites, and also reproduce asexually. Sponges are useful commercially.

Principal Terms

FLAGELLUM: a long cell extension used in locomotion

GEMMULE: an asexual reproductive structure that becomes a new sponge

HERMAPHRODITE: an organism having male and female reproductive organs

OSCULUM: an opening through which a sponge ejects water

OSTIUM: a surface pore through which water enters a sponge

SPICULE: a needlelike structure that is part of a sponge skeleton

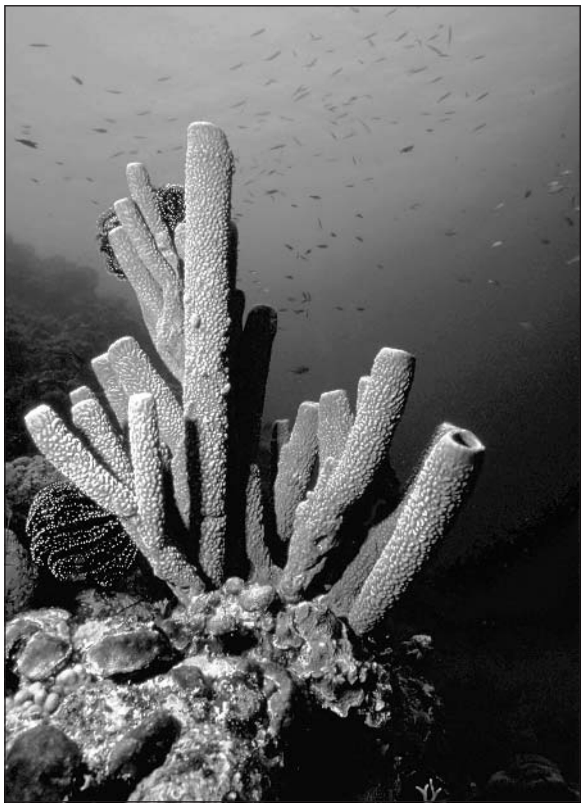
SPONGIN: a fibrous skeletal material in soft sponges

Sponges make up the phylum Porifera, the simplest multicellular animals. There are thousands of sponge species. Most inhabit oceans, although freshwater species exist. Each saltwater sponge has a stem that attaches it to a rock or other object on the ocean floor. Sponge remains are found in the oldest, fossil-bearing rocks.

Live sponges can be black, brown, gray, red, purple, or green. They are abundant in earth's oceans, from shallows to huge depths and from the equator to the Arctic. However, sponges are most numerous and varied in tropical to warm temperate habitats. The four sponge groups are the marine Calcarea, with calcium carbonate skeletons; deep sea Hexactinellida (glass sponges), with silica skeletons; marine and freshwater Demospongiae, comprising 95 percent of species, with skeletons made of flexible spongin (as in a bath sponge) and/or silica; and Sclerospongiae, with silica-, spongin- and calcium-containing skeletons.

The Physical Nature of Sponges

Live sponges have outer layers of cells, which provide their color, and inner-layer flagellate cells



Sponges are the simplest type of multicellular organism. (Digital Stock)

Bath Sponge Facts

Classification:
Kingdom: Animalia
Phylum: Porifera
Class: Demospongiae
Family: Spongidae
Genus and species: Spongia adriatica
Geographical location: Tropical and subtropical Adriatic Sea, the Mediterranean, the Gulf of Mexico, and the Caribbean
Habitat: Oceans and seas
Gestational period: Sexually, eggs are fertilized by sperm from a nearby sponge, and resultant larvae become sponges; asexually, pieces of sponge break off, settle down, and grow (regenerate), or buds or gemmules form new bath sponges
Life span: Indefinite and dependent on environment
Special anatomy: As sponges are the most basic form of animal life, there is little anatomy at all

that move water. The simplest sponge is a tube with many pores (ostia) on its surface. Water enters the tube, via ostia, in a current due to flagella attached to inner-layer cells. Flagellate cells absorb oxygen and digest tiny sea creatures. Then water is expelled through an opening, the osculum, atop the tube. Ejection, due to pressure from flagellar movement, moves depleted water away from the sponge, preventing its reuse.

Sponges form groups if a sponge develops young that remain connected to it. As more and more young develop, their body cavities become canal networks. Water then enters via ostia and passes through canals to chambers where flagellate cells absorb food and oxygen. Used water leaves by larger and larger tubes, reentering oceans via an osculum.

Between outer and flagellate cells a sponge has a skeleton made of structures called spicules. When a sponge dies, its flesh decays and the skeleton remains. There are three sponge skeleton types. Calcarea sponge spicules are made of lime. Hexactinellida (glass) sponges have glassy, silica spicules. Some glassy spicules form attractive skeletons, such as Venus' flower basket. In Demospongiae (including freshwater sponges) the skeleton is almost entirely spongin. Spongin skeletons may contain minute spicules of lime, silica, or both. Bath sponge skeletons have no spicules.

Many sponges begin life as fertilized eggs, which divide until becoming free-swimming larvae. Flagella transport larvae until they settle on the ocean bottom and attach to rocks and other objects in order to become adults. Sponge reproduction can also be asexual, via buds or gemmules. Sponges have a great ability to regenerate in order to replace lost body parts or even most of the body. Some sponges, treated so all their cells are separated but left in water, form a new sponge.

Commercial Sponges

Some Demospongiae have soft, elastic, spongin skeletons that absorb large amounts of water. These qualities have long made them useful tools for surgery, military gun-cleaning, and the clean-

Venus' Flower Basket

Venus' flower basket (VFB) sponges inhabit waters up to three thousand feet deep in warm Pacific Ocean regions. They are plentiful off China, Japan, and the Philippines. VFB, a glass (hexactinellid) sponge, has a skeleton of glassy spicules, interconnected into a one-foot-high, three-inch-wide basket or vase, seemingly made from glass threads.

VFB reproduces sexually or asexually. Sexual reproduction by this hermaphrodite uses cells that make sperm or eggs at different times. A VFB may release sperm into the water while a nearby VFB produces eggs. Conversely, it may provide the eggs. Regardless, sperm fertilizes the eggs in a "female" VFB, and larvae become new VFB. In asexual reproduction, VFB pieces break off, settle down, and regenerate a new VFB; sponge buds form on the VFB surface, break off, and become sponges; gemmules may also be released.

ing of automobiles, houses, and bodies. The best such sponges come from the eastern Mediterranean, off the Syrian and Greek coasts. Sponges are also fished for off Tampa Bay, Tarpon Springs, the Florida Keys, and the Bahamas.

In deep waters, suited sponge divers descend into the sea to dredge sponges. In shallow waters, off Florida, glass-bottomed boats from a mother ship are used. A pole ending in a pronged hook loosens sponges sighted and brings them to the surface. On return to the mother ship, sponges are spread on deck until their flesh decays, hung to dry in the rigging, or kept in seaside pens which tides fill and empty, removing sponge tissues and leaving skeletons.

—Sanford S. Singer

See also: Asexual reproduction; Fossils; Marine animals; Marine biology; Reproduction.

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SQUIRRELS

Types of animal science: Classification, ecology, zoology
Fields of study: Ecology, systematics (taxonomy), wildlife ecology, zoology

Squirrels are mammals belonging to the family Sciuridae. Consisting of 272 species, this family represents only about 5 percent of mammal species. Nevertheless, squirrels are very familiar mammals to most people.

Principal Terms

GROUND SQUIRRELS: those members of the family Sciuridae who burrow in the ground

OPPORTUNISTIC OMNIVORE: an animal who includes a variety of plant and animal material in its diet, depending on the availability of different foodstuffs

POLYGYNOUS: mating system in which one male mates with several females during a breeding season

SCIURIDAE: rodent family to which all squirrels belong

TREE SQUIRRELS: those members of the family Sciuridae who nest in trees

Most people are familiar with squirrels, but may not be aware that members of the squirrel family (Sciuridae) can be divided into two basic groups: tree squirrels and ground squirrels. Tree squirrels are arboreal. Not only do they nest in trees, but they also often mate and forage in trees. Ground squirrels are primarily terrestrial. Though some may climb several feet up the trunk of a tree, ground squirrels nest in burrows beneath the soil surface and forage and mate on the ground or in their burrows. Another big difference between ground-dwelling and tree-dwelling squirrels is that ground squirrels hibernate during the winter and tree squirrels do not. Typical ground squirrels include marmots, woodchucks, and chipmunks. Typical tree squirrels include fox and gray squirrels in North America and red squirrels in Europe.

Gray Squirrels

One of the most familiar tree squirrels in North America is the gray squirrel, *Sciurus carolinensis*. Gray squirrels live in deciduous forests and are also abundant in parks and yards in eastern North America. Their common name is somewhat misleading, in that some gray squirrels have a black pelage. There are even a few populations of albino gray squirrels in North America. Nevertheless, most gray squirrels have gray backs with light-colored ventral fur and light to white fur on the backs of the ears. Like other tree squirrels, gray squirrels have large, bushy tails almost equal in length to the squirrel's body. Though males are generally larger than females, there is no pronounced sexual dimorphism. Gray squirrels range in size from 330 to 750 grams.

Gray squirrels are not particularly social. That is, they do not form cooperative groups. Rather, gray squirrels are solitary. They do not defend territories, and home ranges of individual gray squirrels overlap widely. However, they may defend core areas in the autumn to ensure access to food.

Gray squirrels undergo one or two breeding seasons each year, depending on latitude. Squirrels in northern latitudes may only breed once a year, though squirrels in more moderate climates breed up to two times per year. Timing of the breeding season thus also varies with latitude. In the northern United States, gray squirrels begin to

Gray squirrels spend most of the autumn collecting and hoarding nuts to feed on throughout the winter. Unlike ground squirrels, gray squirrels do not hibernate. (Digital Stock)

breed in early to mid February. Gray squirrels are polygynous; one male may mate with several females during a single breeding season. Males compete with each other for access to females; several males may chase a female until one has an opportunity to mate with her. Some males, rather than participate in mating chases, wait behind trees and find opportunities to mate with females during times other than the mating chase. Mating takes place on the ground or in the trees, and thus can be dangerous to both participants, as there is a real risk of falling during mating.

Gestation in gray squirrels lasts approximately forty-four days. Litter sizes range from one to six, with an average of two to three. Gray squirrels are born in a relatively helpless state; they are born hairless and their eyes do not open until about twenty-five days after birth. Gray squirrels nurse for eight to nine weeks, after which time they are weaned. Some litters are at this point abandoned by their mother. Young gray squirrels can fend for themselves at about eighty days of age and begin to build their own leaf nests at about eighteen weeks of age. Sexual maturity is reached at ten months of age. Gray squirrels have an average life span of only eleven to twelve months. However, many individuals live longer than this, even up to ten years in the wild (longer in captivity).

Gray Squirrel Lifestyle

Gray squirrels might best be considered opportunistic omnivores. Commonly known to consume nuts and seeds as well as buds and fruits from hardwood trees, gray squirrels have also been known to consume baby birds, insects, and fungi. Nevertheless, during the autumn and winter, gray squirrels depend almost exclusively on the mast crop from hardwood trees as their food source. Beginning in late summer to early autumn, gray squirrels begin to scatterhoard nuts. Scatterhoarding entails burying

Squirrel Facts

Classification:
Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Subclass: Theria
Infraclass: Eutheria
Order: Rodentia
Suborder: Sciurognathi
Family: Sciuridae (squirrels), with forty-nine genera and 267 species

Geographical location: Worldwide, except Australia, Polynesia, and southern South America
Habitat: All habitats except deserts
Gestational period: Forty days
Life span: Ten years in the wild, sixteen years in captivity
Special anatomy: Large bushy tail used for balance and temperature regulation

single nuts in different places around the squirrel's home range and differs from larderhoarding in that gray squirrels do not cache large piles of nuts together in a single location. Memory and an excellent sense of smell allow the squirrels to find buried nuts later in the winter, even when buried under several inches of snow. Gray squirrels can be very selective about which foods to include in their diet. They are known to avoid nuts produced from the red subgenus of oaks, which tend to be high in tannin. When eating acorns from red oaks, squirrels generally consume those parts of the seed that are low in tannin.

Unlike ground squirrels, gray squirrels do not hibernate during the winter. Thus, even in the worst weather, they must leave the safety of their nests to obtain food. During the winter months, gray squirrels will den together in tree cavities, presumably to conserve heat. Females usually den with other females (often in mother-daughter groups) and males usually den with other males. Dens are lined with leaves as insulation. Squirrels also use a variety of anthropogenically produced materials in den construction. Foil-coated fast-food wrappers and laundry lint are not uncommon discoveries in squirrel nests. During warmer months, gray squirrels build leaf nests, called dreys, in the upper branches of hardwood trees.

—Erika L. Barthelmess

See also: Beavers; Gophers; Hibernation; Mammals; Mice and rats; Omnivores; Porcupines; Rodents.

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STARFISH

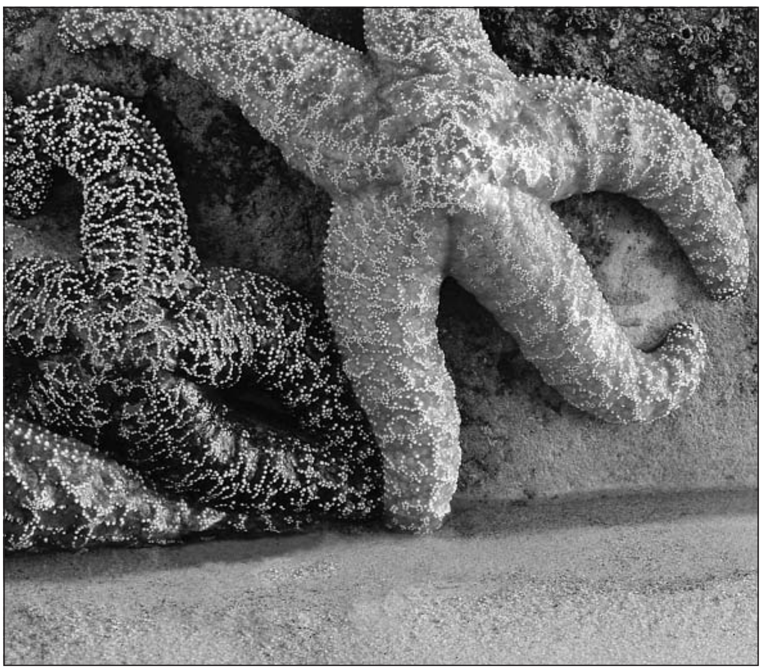
Type of animal science: Classification
Fields of study: Anatomy, invertebrate biology, zoology

Starfish are five orders (1,500 species) of marine invertebrate animals making up the echinoderm class Asteroidea. Their main foods include mollusks and coral.

Principal Terms

BIVALVE: a mollusk having two shell halves
CARNIVORE: an animal that eats only other animals
INVERTEBRATE: an animal lacking an internal skeleton

Starfish are carnivorous ocean animals that usually have five starlike arms. They are related to brittle stars, sea urchins, and sea cucumbers, all of which are known as echinoderms. Like these animals, starfish have spiny skins. Starfish make up five orders—1,500 species—of marine invertebrates, the class Asteroidea of the phylum Echinodermata. They have radially arranged arms which hold locomotor tube feet, and which reach diameters from six inches to four feet. They are abundant at all ocean depths and occur in all oceans except near the North and South Poles. Often, a starfish escapes its enemies by breaking off one or more of its arms, which regenerates. In fact, if a starfish is halved, quartered, or cut into smaller pieces, each becomes a new individual.


The starfish's arms are equipped with suction-cup feet, which it uses to pull itself along the ocean floor. (Digital Stock)

The Physical Characteristics of Starfish

Stiff-bodied, starfish move by crawling slowly. Their bodies may have five arms or many more. Starfish skin is leathery and has protective spines, which point upward. The spines are made of lime and develop from the skeleton. The animal also has a large gut, a complex system of body cavities, and a nervous system but no brain.

The central body of a starfish is located where its arms join. Its bottom surface holds a mouth at the point where all the arms meet. A groove also stretches from the mouth to each arm tip. There are rows of holes in the grooves from which tube feet can push out. The feet, with sucker ends, enable crawling. They are supported and moved by an internal hydraulic system inflated with seawater.

Most of the central body is a baglike stomach into which the mouth opens. Starfish also have well-developed senses of touch, smell, and taste, and respond to light. However, they lack the complex behavior patterns of animals having brains.

The Life of the Starfish

Starfish spend much of their lives searching for food, mainly clams, mussels, and oysters. To eat bivalve mollusks, a starfish uses its tube feet to open shell halves. It surrounds a mollusk, attaches the tube feet, and uses them to pull in opposite directions. Once the mollusk tires of resisting the starfish's force, the shell opens. Then the starfish pushes its stomach inside out through the mouth and surrounds the mollusk body. Its stomach releases digestive fluid and as the mollusk softens, the starfish eats its flesh and releases the shell. A similar technique is used with other foods, such as coral. Coral polyps (individual corals) are eaten. First, a starfish climbs onto a polyp and presses its stomach out through its mouth. Then, digestive juice softens the polyp's shell and turns the polyp into a soupy liquid, which the starfish eats.

Starfish are themselves eaten by fish and snails. Their most successful predators are giant carnivorous sea snails, such as tritons. A triton rips starfish open and eats their soft tissues. Fish also eat starfish by flipping them over and biting off and eating their soft centers.

Mating occurs in spring or summer, depending on species and habitat. Most starfish have two sexes and mate by secreting sperm and eggs into the ocean (spawning). External fertilization follows and the eggs become larvae. Larvae float in the ocean and sink to its bottom to become adults. Most starfish regenerate body parts. In some starfish, this is also their mode of reproduction: A bud grows and pinches off into a new starfish.

Starfish Facts

Classification:
Kingdom: Animalia
Phylum: Echinodermata
Class: Asteroidea
Orders: Include Forcipulata, Forcipulatida, and Spinulosida

Geographical location: All ocean depths in all oceans, except near the North and South Poles

Habitat: Ocean bottoms, from shallow water to great depths

Gestational period: No true gestation; sperms and eggs are spawned into oceans, where the eggs are fertilized; larvae drift, settle to the ocean floor, and become adults

Life span: Not known

Special anatomy: Radially symmetrical arms, locomotor tube feet, mouth and stomach cavity that can turn inside out, protective spines

Three Sample Starfish Species

Sunflower starfish (*Pycnopodia helianthodes*), the largest starfish, resemble sunflowers because of their many arms. They grow to diameters up to four feet and may have twenty-five arms. These starfish inhabit the west coast of North America from Alaska to California, from shallows to deep water. They eat bivalves, sponges, coral, worms, crustaceans, other starfish, and small fish. They mate in spring, by spawning.

Crown-of-thorns starfish (*Acanthaster planci*) are star-shaped with many body spikes (thorns). They grow to two-foot diameters and have up to twenty-four arms. A crown-of-thorns starfish also has a large, round midsection, which holds internal organs and many tube feet. Crown-of-thorns starfish inhabit tropical West Pacific and Indian Oceans. Feeding on coral, they live on or near coral reefs, such as Australia's Great Barrier Reef, where they hide during the day and feed at night. A single crown-of-thorns starfish can destroy 1.5 feet of coral reef per week.

European starfish (*Asterias rubens*) are five-armed starfish of the European and African coasts. They grow to 1.5-foot diameters and have tube feet. They feed on bivalves, sponges, corals, worms, crustaceans, other starfish, and small fish.

They find food via chemical signals picked up by tube feet. Their spring mating is by means of spawning.

The main foods of starfish are mussels, oysters, and clams. Starfish are thus serious pests on oyster and clam farms. In addition, they eat coral and can damage reefs. For example, crown-of-thorns starfish sometimes overgrow and damage coral reefs by eating too much coral.

—Sanford S. Singer

See also: Echinoderms; Exoskeletons; Marine animals; Marine biology; Regeneration.

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STEGOSAURS

Types of animal science: Classification, evolution
Fields of study: Anatomy, evolutionary science, paleontology, systematics (taxonomy)

Stegosaurs were a group of armored, herbivorous dinosaurs characterized by large plates set vertically along the back and spikes on the tail. The plates are thought to have acted as thermoregulatory devices.

Principal Terms

CRETACEOUS: a period of time that lasted from about 146 to 65 million years ago, the end of which was marked by the extinction of the dinosaurs

ECTOTHERMY: a form of metabolism in which internal temperature is regulated by ambient temperature

JURASSIC: a period of geological time that lasted from about 208 to 146 million years ago

ORNITHISCHIA: one of the two main dinosaur groups, characterized by a pelvis in which the pubis is swung backward

PUBIS: one of the three bones that make up the pelvis (the others are the ischium and ilium)

Stegosaurs are a group of quite large (up to eight meters long), quadrupedal, ornithischian dinosaurs. That is, they have a pelvis in which the pubis points backward, and thus they are allied with all other herbivorous dinosaurs except the gigantic sauropods. Their closest relatives are the other armored dinosaurs, the ankylosaurs, with which they are grouped as Thyreophora ("shield bearers"), characterized by rows of plates along the back and sides of the body. The earliest stegosaurs are represented by fragmentary remains from the Middle Jurassic of England, but by the Late Jurassic they are well known from complete skeletons from Africa, Asia, Europe, and North America. The Late Jurassic was the most successful time for stegosaurs and they are particularly well known from articulated skeletons of *Stegosaurus* of this age from North America. By the Early Cretaceous their distribution had contracted to Europe, Africa, and China, and by the Late Cretaceous they are absent from all continents except India. India was separate from all the other continents from the Middle Jurassic onward as it drifted away from Africa and toward Asia, and this isolation may have protected the stegosaurs as they became extinct everywhere else.

Anatomy and Lifestyle

The best known stegosaur is *Stegosaurus* ("roofed reptile"), from the Late Jurassic of North America,

Stegosaur Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Reptilia
Order: Ornithischia
Suborder: Thyreophora
Geographical location: North America, Europe, China, India, and Africa
Habitat: Terrestrial habitats
Gestational period: Unknown
Life span: Unknown
Special anatomy: Large, quadrupedal dinosaurs in which the head was small, the back was covered by a double row of large vertical plates, and the tail bore large spikes

Image Not Available

and thus it is commonly used to typify the entire group. *Stegosaurus* had a small head with an unusually small brain, even for a dinosaur, and a narrow, horn-covered beak at the tip of the snout. The sides of the jaws were lined with leaf-shaped serrated teeth but these were not arranged in batteries and there is no evidence of the sophisticated grinding apparatus that was developed in some other herbivorous dinosaurs. However, *Stegosaurus* was a large animal and must have needed large quantities of plant food, so it is likely that it was a low-level browser that chopped up vegetation and then quickly passed it back to a large stomach, where it would have fermented, perhaps with the help of gastroliths (stomach stones) to further break it down.

The most distinctive feature of *Stegosaurus* is the row of vertical plates along the back. There has been some disagreement as to their relationship to each other, as they were set in soft tissue and not attached to the skeleton; however, it is generally agreed that they formed two parallel rows in which the plates were staggered. The plates are not optimally positioned for defense and it has been suggested that they were devices for thermoregulation, acting as radiators to gain or lose heat and help maintain a constant internal body temperature in animals that may have had an ectothermic metabolism (an internal temperature regulated by the ambient temperature, as in most modern reptiles). Experiments have shown that the plates were ideally shaped and positioned to do this. The surface of the plates is covered by fine grooves, indicating the presence of numerous blood vessels, and the plates themselves are hollow, implying that they were richly supplied with blood. Thus the animal could have flushed blood over the plates to cool itself if its internal temperature had risen too much, or to warm the blood by exposure to the sun if its internal temperature was dropping.

The proportions of the legs in *Stegosaurus* show that it was not a fast runner, and thus as a large and relatively slow-moving herbivore it would have needed some means of defense against predators. This would undoubtedly have been the spike-bearing tail. Two pairs of spines projected laterally from the tip of the tail and could have inflicted severe injuries on an attacking carnivorous dinosaur as the tail was lashed from side to side while the animal backed toward the attacker.

—David K. Elliott

See also: *Allosaurus*; *Apatosaurus*; *Archaeopteryx*; Dinosaurs; Evolution: Animal life; Extinction; Fossils; Hadrosaurs; Ichthyosaurs; Paleoecology; Paleontology; Prehistoric animals; Pterosaurs; Sauropods; *Triceratops*; *Tyrannosaurus*; Velociraptors.

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STORKS

Type of animal science: Classification
Fields of study: Anatomy, conservation biology, physiology, population biology, wildlife ecology

Storks are wetland birds that are physically striking in appearance and noted for their spectacular flight. They are found throughout the world, but their numbers have decreased dramatically due to habitat destruction by humans.

Principal Terms

FLEDGLING PERIOD: period after hatching, during which a nestling grows flight feathers and learns to fly

INDICATOR SPECIES: a species monitored by biologists as a means of ascertaining the health of the ecosystem in which it lives

NOMADIC: moving about from place to place according to the state of the habitat and food supply

SCAVENGER: an animal that feeds on the dead carcasses of other animals

THERMALS: rising currents of warm air

Storks are large wading birds that live near swamps, marshes, lakes, and rivers. There are nineteen species in the world. North America is home to two species, the wood stork of the southeastern United States and the jabiru of Mexico. Many species live in Africa, Asia, and Europe, and a few species also can be found in South America and Australia. The white stork is most commonly known. It summers in Europe, frequently nesting on rooftops, and is the source of the legends of storks delivering infants.

Physical Characteristics of Storks

Storks stand from 2.5 to 5 feet tall and weigh between five and thirteen pounds. The smallest species is the Abdim's stork. The saddlebill and the marabou stork are the largest. Storks have powerful wings and a wide wingspan. The marabou's wingspan is the greatest of all land birds, reaching nearly ten feet. Plumage can be white, gray, or black. Species with dark plumage often have iridescent shades of purple, green, or blue. Males and females look alike, but the male is larger.

Storks have long, slender legs that may be red, white, gray, or black. They have three long toes that are webbed at the base, and a shorter back toe. The strong beak is long and pointed and is straight or slightly curved.

Stork Behavior

Storks are carnivores and hunt for food in wetlands, along bodies of water, and in grassy plains. They feed on insects, worms, fish, frogs, reptiles, and small birds and mammals. The adjutant storks are scavengers, primarily seeking carrion. Many storks are tactile foragers, walking slowly through shallow water, groping with an open bill that snaps shut reflexively when it comes into contact with prey. Others are visual foragers, snatching insects or stirring the water to disturb prey, then seizing it with a thrust of the beak.

Storks do not vocalize. Instead, they communicate with bill clattering and snapping, rasping, and hissing. Nestlings make a high-pitched braying which decreases with age.

Storks fly with their necks stretched out. The legs dangle during takeoff, and then extend out behind in flight. Storks glide on thermals, soaring to high altitudes. They sometimes perform aerial acrobatics such as diving and flipping.

Some stork species migrate seasonally, others are nomadic, and some are nonmigratory. The availability of prey largely determines the migration and movement of stork colonies. Prey availability is in turn closely tied to climate and rainfall patterns. Storks will adapt the timing of migration and breeding and the choice of colony nesting site according to these climatic conditions, postponing or skipping a breeding cycle if food availability is low.

Excepting one or two species, storks live in colonies, building their nests of sticks, reeds, and vines in trees, on rooftops, or on the ground. Some mate for life; others may pair for just one season. Courtship begins with a color change of the birds' bill, face, legs, and skin. The male performs various aggressive, ritualized displays to attract the female, who then performs appeasement displays. Both members of the pair participate in nest building, incubation, and caring for nestlings. Clutch size is two to five eggs, and incubation averages thirty days. Parents feed the young by regurgitating food into the nest. The fledgling period varies from six weeks to four months.

Stork Facts

Classification:
Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Class: Aves
Order: Ciconiiformes (wading birds)
Suborder: Ciconiae (storks, ibises, spoonbills)
Family: Ciconiidae (storks)
Genus and species: Ten genera, one subgenus, and twenty-one species, including *Mycteria americana* (American wood stork), *M. cinerea* (milky stork), *M. ibis* (yellow-billed stork), *M. leucocephala* (painted stork); *Anastomus oscitans* (Asian open-bill stork); *A. lamelligerus* (African open-bill stork); *Ciconia nigra* (black stork), *C. abdimii* (Abdim's stork), *C. episcopus* (woolly-necked stork), *C stormi* (Storm's stork), *C. maguari* (Maguari stork), *C. ciconia* (white stork), *C. boyciana* (oriental white stork); *Ephippiorrhyncus asiaticus* (black-necked stork), *E. senegalensis* (saddle-bill stork); *Jabiru mycteria* (jabiru stork); *Leptoptilos javanicus* (lesser adjutant stork), *L. dubius* (greater adjutant stork), *L. crumeniferus* (marabou stork)

Geographical location: Every continent except Antarctica; most species are found in the Eastern Hemisphere
Habitat: Wetlands; some species require distinct wet and dry seasons
Gestational period: Incubation averages thirty days
Life span: Seven to thirty years, varying by species; longer in captivity
Special anatomy: Long, slender legs; long neck; long, pointed bill

Image Not Available

Conservation

Since 1950, the overall population of storks has declined by half, due to the destruction of wetland habitats from deforestation, drainage, farming and pesticide use. In 2000, the Storm's stork, greater adjutant, and oriental wood stork were listed as endangered by the International Union for Conservation of Nature and Natural Resources. The lesser adjutant, milky stork, black-necked stork, painted stork, and wood stork are considered vulnerable or near threatened. In the United States, the wood stork serves as an indicator species for the health of the Florida Everglades ecosystem. Solutions to the declining world stork populations include habitat improvement and protection, captive breeding and reintroduction of species, and artificial establishment of nesting and colony sites.

—*Barbara C. Beattie*

See also: Beaks and bills; Birds; Domestication; Feathers; Flight; Migration; Molting and shedding; Nesting; Respiration in birds; Wildlife management; Wings.

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SWAMPS AND MARSHES

Types of animal science: Ecology, geography
Fields of study: Conservation biology, ecology, environmental science, limnology, wildlife ecology

Swamps and marshes are shallow wetlands that are characterized by emergent vegetation and seasonal water level fluctuations. Swamps and marshes are among the most productive ecosystems on earth and often provide prime habitat for birds. Because swamps and marshes are often perceived as worthless, they have been extensively drained and their loss is of great concern to conservationists.

Principal Terms

CONSUMER FOOD CHAIN: a simplified description of the grazing and predator/prey relationships within an ecosystem
EMERGENT VEGETATION: aquatic vegetation that grows tall enough to be visible above the water
INVERTEBRATE: a simple animal lacking a backbone
PRIMARY CONSUMER: an organism that gets its nourishment from eating primary producers, which are mostly green plants and algae
PRIMARY PRODUCTIVITY: production of biomass mainly by green plants

Swamps and marshes differ from ponds and lakes in two primary ways: they are shallower, with seasonally fluctuating water levels, and they have little or no open water, being dominated by emergent vegetation. The predominant vegetation in marshes comprises grasses, sedges, and rushes. Marshes tend to have shallower water than swamps, and are more apt to dry out completely during the drier part of the year. The predominant vegetation in swamps comprises trees and shrubs. Not only is the water generally deeper in swamps, it is often more permanent, although water levels still tend to fluctuate seasonally.

Although swamps and marshes are usually thought of as freshwater wetlands, saline swamps and marshes also exist, either in desertlike environments where evaporation rates are high, or in coastal areas. Coastal swamps and marshes tend to fluctuate in depth and salinity as the tides change. Coastal swamps are often referred to as mangrove swamps or mangals. Coastal marshes are often called estuaries. Most of the following information will focus on freshwater swamps and marshes.

Insects and Other Invertebrates

The smallest of the invertebrates are primary consumers, who are at the base of the consumer food chain in wetlands. When algae is abundant in the water, primary consumers also proliferate. One of the most common of these is the water flea (*Daphnia*), which is just barely visible to the naked eye. When viewed under the microscope, the reason for its name becomes apparent, as it looks remarkably like a flea. Many species of water flea exist, varying greatly in size, head shape, swimming appendages, and other traits. Water fleas and other small invertebrates are preyed upon by larger invertebrates, tadpoles, and small fish.

The bulk of the invertebrates are insects, in either their adult or juvenile forms. Many flying insects, such as mosquitoes and dragonflies, spend their early life in the water. Dragonfly nymphs are especially vicious predators, preying upon almost anything small enough for them to grab in their strong jaws, including small fish. Adult dragonflies and their cousins, the damselflies, are commonly seen flying around marshes and swamps.

Other insects, such as water striders, backswimmers, water boatmen, and diving beetles, are also abundant in the still waters, making their entire lives in or on the water. Even a few spiders (which are arachnids, not insects) have adapted to the aquatic way of life, able to stay underwater for extended periods by trapping bubbles of air next to their bodies.

Another common invertebrate group is the shellfish. Freshwater clams live buried in the sediment and filter food out of the water, while mussels can form dense assemblages on rocks and other debris in the water. A few clams and mussels from tropical and semitropical parts of the world have inadvertently been introduced to some temperate wetlands with devastating effects. Snails can also be found in many marshes and swamps, where they feed on algae growing on rocks and on the submerged stems and leaves of plants.

Fish, Reptiles, and Amphibians

The occurrence of fish is most often associated with water depth. In shallow, seasonal marshes or swamps, fish are often absent. In deeper marshes and swamps, they can be abundant and provide food for other animals, especially birds. These fish can range from the unique, bottom-dwelling catfish to more active fish such as perch and bass. Many smaller, less noticeable species also occur, some of which are near extinction due to loss of unique habitat.

The most common reptile in marshes and swamps is the turtle. Most turtles are predators, although some feed primarily on plant material. The snapping turtle has a reputation for eating almost anything, plant or animal. Although turtles can be observed swimming in the water, they are most often seen sunning themselves on warm rocks just in reach of the water, where they can quickly escape from potential predators. Among the more dangerous reptiles of swamps and marshes are the alligators, crocodiles, and caimans. These are exclusively predatory, and although generally not very aggressive toward humans, they do attack on occasion. Snakes are also predators. Garter snakes grab their prey us-

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ing their mouth and gradually swallow it. The cottonmouth is a poisonous viper that injects venom into its prey to incapacitate it before swallowing. Although snakes are more often thought of as terrestrial, they are expert swimmers.

Amphibians include salamanders and frogs, both of which spend their early life entirely in the water, where their eggs are laid. Frog eggs develop into tadpoles with tails and no legs; as they develop, the tail disappears and legs start to grow. Salamander larvae have legs from the beginning and they never lose their tail. When young, frogs and salamanders feed mostly on algae and small invertebrates in the water. As adults, frogs typically eat insects, and salamanders eat a variety of invertebrates, including worms and grubs.

Birds and Mammals

Near the top of the food chain, a large variety of birds either live in swamps and marshes or come there to hunt. Common residents include ducks, geese, herons, and egrets. In these shallower waters, "puddling" ducks predominate, characterized by feeding behavior where they reach for vegetation on the bottom with only their rumps protruding from the surface. Herons and egrets frequently wade slowly and deliberately, searching for frogs or fish to quickly grab and eat. Many songbirds take advantage of the habitat; some, such as the marsh wren, even make their nests in the bullrushes near the margin of the water. Predatory birds such as hawks, eagles, falcons, owls, and osprey come to prey on other birds, snakes, fish, or smaller mammals.

Various mammals also take advantage of the aquatic bounty. Mink and otters freely swim in search of fish. Others, like raccoons, tend to hunt for food on the margins. Rodents of various kinds eat greens and seeds, abundant because of the water supply, and foxes and coyotes hunt the rodents. Other mammals, such as deer, come for the water, and sometimes eat the tender vegetation as well. Beaver may even be responsible for the development of a new swamp or marsh by building a dam across a creek.

Human Destruction of Swamps and Marshes

In spite of the great richness of life present in swamps and marshes, human society, in general, views these ecosystems as unsightly and useless. Consequently, many wetlands have been drained to make way for farmland, roads or other developments. Because so much has been lost, environmental laws in the United States now prohibit further wetland destruction, unless new wetlands are formed to replace those that are lost. These laws are a recognition of the ecological importance of swamps and marshes.

The primary productivity of swamps and marshes is only surpassed by tropical rain forests and algal beds and reefs. Shallow water and ample light allow rich plant and algae growth, which supports the rich variety of organisms found here. Swamps and marshes are especially important to migrating waterfowl, who need them for their abundant food supplies. As wetlands have been lost, waterfowl numbers have been reduced. Their high productivity also makes them important in absorbing excess carbon dioxide from the atmosphere, thus reducing global warming.

—*Bryan Ness*

See also: Ecosystems; Food chains and food webs; Forests, coniferous; Forests, deciduous; Habitats and biomes; Lakes and rivers; Marine biology; Rain forests; Tidepools and beaches.

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SWANS

Types of animal science: Anatomy, classification, reproduction
Fields of study: Anatomy, ornithology, zoology

Swans are the largest, most beautiful waterfowl. Some species were hunted almost to extinction for their feathers, before legislation protected them.

Principal Terms

COB: a male swan
CYGNET: a newly hatched swan
MANDIBLE: one of the two halves of a swan's bill
PEN: a female swan

Swans, the largest members of the waterfowl family of birds, have snow-white feathers and graceful necks. There are eight swan species, which inhabit rivers, lakes, and ponds on every continent except Antarctica. They eat both on land and in water; their diet consists of land plants and grasses, aquatic plants, fish, and invertebrates. Swans must dig much of their aquatic food from bottom mud, after dipping their necks far into the water to reach it.

Many American swans nest around the Arctic Ocean and Hudson Bay. In winter, they migrate in a V-formation to the Carolinas at airspeeds up to sixty miles per hour, filling the air with sounds ranging from deep bass notes to those like clarinets. Swans that live in more temperate climates, such as the Great Plains of the United States, do not migrate. Eastern hemisphere swans include European whistling swans and Bewick's swans. A scarlet-billed black swan inhabits Australia. The initial ugliness of cygnets, which only lasts for a

Swans are highly monogamous birds, forming pair-bonds that last their entire lives. (Corbis) year, was the inspiration for Hans Christian Andersen's fairy tale "The Ugly Duckling."

Physical Characteristics of Swans

Swans reach a maximum length (from beak to tail tip) of six feet, and weigh up to thirty-five pounds. Their plumage is usually white, white plus black, or rarely all black. Whooping (whooper), Bewick's, whistling, mute, and trumpeter swans are white. Black-necked swans have black areas on white bodies. Wingspans range from six to ten feet.

Swan necks are long and slender, usually held in a graceful S-curve. Trumpeters, whoopers, and whistlers, however, hold their necks straight upright. Swans have two short legs with huge, scale-covered, webbed feet. The tips of their strong bills are broad and flat, for optimum use in tearing underwater plants, a major part of their diet. Swans often feed by poking their heads underwater. They are not graceful on land, but fly, swim, and dive very well. All swans, including "mute" swans, hiss, bark, whistle, whoop, and cluck, especially when migrating.

The Lives of Swans

Swans form flocks to breed, nest, feed, and migrate. Depending on species, a flock has between a few dozen and thousands of individuals. Swans also form family units, comprising a set of parents with their offspring, within flocks. All swans choose mates for life. On mating, swans build nests from plants, twigs, and down, which they use over and over. Then the pens lay five to ten pale-colored eggs and incubate them until they hatch, after eighteen to thirty-nine days.

Cygnets, covered with gray to brown down, leave their nests a few days after hatching, following their parents to learn to swim and find food. Although the pen is usually responsible for the eggs, once the cygnets are born, the cob may feed and protect them. They fly for the first time at age four months. Most Northern Hemisphere swans breed yearly. Southern Hemisphere swans breed every two years. A swan is mature at age three or four and can live for twenty to thirty years in the wild or forty to fifty years in captivity.

Swan Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Class: Aves
Order: Anseriformes
Family: Anatidae (ducks, geese, and swans)
Tribe: Anserini
Genus and species: Three genera and twelve species, including *Cygnus columbianus* (whistling swan), *C. cygnus* (whooping swan), *C. bewickii* (Bewick's swan), *C. melancoryphus* (black-necked swan), *C. buccinator* (trumpeter swan), *C. olor* (mute swan); *Chenopis atrata* (black swan); *Coscoroba coscoroba* (Coscoroba swan)

Geographical location: Every continent except Antarctica

Habitat: Rivers, lakes, ponds, swamps, and moist forest areas

Gestational period: Incubation of twenty-five to forty-five days

Life span: Twenty to thirty years in the wild; forty to fifty years in captivity

Special anatomy: Long necks in S-curves or straight upright; short legs with scaled, webbed feet; broad, flat, strong bills

Swan Conservation

South Americans, Europeans, Asians, and North Americans hunted trumpeters and other swans almost to extinction by eating swan meat, and using their feathers for pens, hat decorations, and women's scarves. By the 1930's, many species were in trouble; for example, under one hundred trumpeter swans were alive at that time. Legislation and protective actions have enlarged swan populations by allowing them to increase by natural reproduction.

—*Sanford S. Singer*

See also: Beaks and bills; Birds; Feathers; Flight; Migration; Molting and shedding; Nesting; Respiration in birds; Wildlife management; Wings.

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SYMBIOSIS

Type of animal science: Ecology
Fields of study: Evolutionary science, immunology, invertebrate biology, zoology

All animals live in close association, or symbiosis, with other species. Most symbioses are based on nutritional interrelationships involving competition or cooperation. Some animals cannot survive without their symbiotic partners, while others are harmed or killed by them.

Principal Terms

- COMMENSALISM: symbiotic associations based chiefly on some form of food sharing, which may also involve shelter, protection, or cleaning
- HOST: by convention, the larger of two species involved in a symbiotic association
- INTERMEDIATE HOST: an animal species in which nonsexual developmental stages of some commensals and parasites occur
- MUTUALISM: a type of commensalism in which both symbiotes benefit from the association in terms of food, shelter, or protection
- PARASITE: a symbiote that must live in intimate contact with its host to survive; a parasite may be pathogenic or beneficial to the host
- PARASITE MIX: all the individuals and species of symbiotes living in a host concurrently
- RESERVOIR HOST: a host species other than the one of primary interest in a given research study
- SYMBIOSIS: all forms of evolved, nonaccidental, nontrivial, interspecies associations, excluding predator-prey relationships
- SYMBIOTE: a species involved in any form of symbiotic association with another species

Understanding the ways in which different species of animals interact in nature is one of the fundamental goals of biology. Predator-prey relationships, competition between species for limited resources, and symbiosis are the major forms of species interactions, and these have profoundly influenced the diversity and ecology of all forms of life. Significant advances have been made in understanding how organisms interact, but in studies of symbiosis (which literally means "living together") one finds the most complex, interesting, and important examples of both cooperation and exploitation known in the living world.

Symbiosis involves many types of dependent or interdependent associations between species. In contrast to predator-prey interactions, however, symbioses are seldom rapidly fatal to either of the associating species (symbiotes) and are often of long duration. With the exception of grazing animals that do not often entirely consume or destroy their plant "prey," most predators quickly kill and consume their prey. While a predator may share its prey with other individuals of the same species (clearly an example of "living together"), such intraspecific behavior is not considered to be a type of symbiosis. Fleas, some ticks, mites, mosquitoes, and other bloodsucking flies are viewed as micropredators rather than parasites.

All organisms are involved in some form of competition. The abundance and availability of environmental resources are finite, and competition for resources occurs both between members of the same species and between individuals and populations of different species. When the number of individuals in a population increases, the intensity of competition for limited food, water, shelter, space, and other resources necessary for survival and reproduction also increases. Thus, competition plays a major role in populations of free-living animals (those not inhabiting the body of other organisms) and in populations living on or in other animals. For example, both tapeworms and whales must compete for resources, and both have evolved habitat-specific adaptations to accomplish this goal. Whales compete with whales, fishes, and other predators for food; tapeworms compete with tapeworms and other symbiotes (such as roundworms) for food and space; and tapeworms and whales compete with each other for food in the whale's gut.

"Symbiosis" is a term used to describe nonaccidental, nonpredatory associations between species. When used by itself, the term "symbiosis" does not provide information on how or why species live together, or the biological consequences of their interactions. Recognizably different forms of symbioses all have one or more characteristics in common. All involve "living together"; most involve food sharing; many involve shelter; and some involve damage to one or both symbiotes.

Hosts and Symbiotes

Host species may be thought of as landlords. Hosts provide their symbiotes (also called symbionts) with transportation, shelter, protection, space, some form of nutrition, or some combination of these. Host species are generally larger and structurally more complex than their symbiotes, and different parts of a host's body (skin, gills, and gut, for example) may provide habitats for several different kinds of symbiotes at the same time. The three primary categories of symbiosis most commonly referred to in popular and scientific works are commensalism, mutualism, and parasitism.

Symbiotes that share a common food source are known as commensals (literally, "messmates"). In the usual definition of commensalism, one species (usually referred to as the commensal, although both species are commensals) is said to benefit from the relationship, while the other (usually referred to as the host) neither benefits nor is harmed by the other. Adult tapeworms which live in the intestinal tracts of vertebrate hosts provide a classic example of commensals. Adult tapeworms share the host's food, usually with little or no effect on otherwise healthy hosts. As in all species, however, too large a tapeworm population may result in excessive competition, lower fitness, or disease in both the host and the tapeworms. For example, the broad fish tapeworm of man, *Diphyllobothrium latum*, may cause a vitamin B12 deficiency and anemia in humans when the worm burden is high. In addition to tapeworms, many human symbiotes called "parasites" are, in fact, commensals.

External commensals (those living on the skin, fur, scales, or feathers of their hosts) are called epizoites. A good example of an epizoite is the fish louse (a distant relative of the copepod), which feeds on mucus of the skin and scales of fishes. Another type of commensalism is called phoresis (phoresy), which involves passive transportation of the commensal (phoront) by its host. Examples of phoreses include barnacles carried by whales and sea turtles, and remoras (sharksuckers), which, in the absence of sharks, may temporarily attach themselves to human swimmers. In inquilinism, the transported commensal (inquiline) shares, or more accurately, steals, food from the host, or may even eat parts of the host. Perhaps the best-known inquilines are the glass- or pearlfishes, which take refuge in the cloacae of sea cucumbers and often eat part of the host's respiratory system. A unique type of commensalism, known as symphilism, is found in certain ants and some other insects (hosts) which "farm" aphids (symphiles) and induce them to secrete a sugary substance which the ants eat.

Mutualism

The most diverse type of commensalism is mutualism. In some works, particularly those dealing with animal behavior, mutualism is used as a synonym of symbiosis; hence, the reader must use caution in order to determine an author's usage of these terms. As used here, mutualism is a special case of commensalism, a category of symbiosis. The relationship between mutuals may be obligatory on the part of one or both species, but it is always reciprocally beneficial, as the following examples illustrate. Some species of hermit crabs place sea anemones on their shells or claws (sea anemones are carnivores which possess stinging cells in their tentacles). Hermit crabs without anemones on their shells or claws may be more vulnerable to predators than those with an anemone partner. Hermit crabs, which shred their food in processing it, lose some of the scraps to the water, which the anemones intercept, and eat. Thus, the crab provides food to the anemone, which in turn protects its provider. Such relationships, which are species-specific, are probably the result of a long period of coevolution.

A different type of mutualism, but one having the same outcome as the crab-anemone example, is found in associations between certain clown fishes and sea anemones. Clown fishes appear to be fearless and vigorously attack intruders of any size (including scuba divers) that venture too close to "their" anemone. When threatened or attacked by predators, these small fishes dive into an anemone's stinging tentacles, where they find relative safety. Anemones apparently share in food captured by clown fishes, which have been observed to drop food on their host anemone's tentacles.

Cleaning symbiosis is another unique type of mutualism found in the marine environment. In this type of association, marine fishes and shrimp of several species "advertise" their presence by bright and distinctive color patterns or by conspicuous movements. Locations where this behavior occurs are called "cleaning stations." Instead of being consumed by predatory fishes, these carnivores approach the cleaner fish or shrimp, stop swimming, and sometimes assume unusual postures. Barracudas, groupers, and other predators often open their mouths and gill covers to permit the cleaners easy entrance and access to the teeth

Remoras attach themselves to larger fish for transport. (Digital Stock) and gills. Cleaners feed on epizoites, ectoparasites, and necrotic tissue that they find on host fishes, to the benefit of both species. Some studies have shown that removal of cleaning symbiotes from a coral reef results in a significant decrease in the health of resident fishes.

Parasitism

Parasitism is a category of symbiosis involving species associations that are very intimate and in which competitive interactions for resources may be both acute and costly. The extreme intimacy (rather than damage) between host and parasite is the chief difference between parasitism and other forms of symbiosis. Parasites often, but not always, live within the cells and tissues of their hosts, using them as a source of food. Some types of commensals also consume host tissue, but in such cases (pearl fishes and sea cucumbers, for example) significant damage to the host rarely occurs. Commensalism is associated with nutritional theft.

Some, but not all, parasites harm their hosts, by tissue destruction (consumption or mechanical damage) or toxic metabolic by-products (ammonia, for example). Commonly, however, damage to the host is primarily the result of the host's own immune response to the presence of the parasite in its body, cells, or tissues. In extreme cases, parasites may directly or indirectly cause the host's death. When the host dies, its parasites usually die as well. It follows that the vast majority of host-parasite relationships are sublethal. A number of parasites are actually beneficial or crucial to the survival of their hosts. The modern, and biologically reasonable, definition of parasitism as an intimate type of symbiosis, rather than an exclusively pathogenic association between species, promotes an ecological-evolutionary understanding of interspecies associations. Most nonmedical ecologists and symbiotologists agree that two distinct forms of intimate associations, or parasitisms (with many intermediate types), occur in nature. The most familiar are those involving decreased fitness in humans and in their domestic animals and crops.

Among animal parasites, malarial parasites, hookworms, trypanosomes, and schistosomes (blood flukes) cause death and disease in millions of people each year. The degree to which these parasites are pathogenic, however, is partly the result of preexisting conditions of ill health, malnutrition, other diseases, unsanitary living conditions, overcrowding, or lack of education and prevention. Parasites which frequently kill or prevent reproduction of their hosts do not survive in an evolutionary sense, because both the parasites and their hosts perish. Both members of intimate symbiotic relationships constantly adapt to their environments, and to each other. Over time, evolutionary selection pressures result in coadaptation (lessening of pathogenicity) or destruction or change in form of the symbiosis.

Nonpathogenic or beneficial host-parasite associations are among the most highly evolved of reciprocal interactions between species. The extreme degree of intimacy of the symbiotes (not lack of pathogenicity) distinguishes this type of parasitism from mutualism. Parasitic dinoflagellates (relatives of the algae that cause "red tides") are found in the tissues of all reef-building corals. These photosynthetic organisms use carbon dioxide and other waste products produced by corals. In turn, the dinoflagellates (*Symbiodinium microadriaticum*) provide their hosts with oxygen and nutrients that the corals cannot obtain or produce by themselves. Without parasitic dinoflagellates, reef-building corals starve to death. Similar host-parasite relationships occur in termites, which, without cellulose-digesting parasitic protozoans in their gut, would starve to death.

Studying Symbiosis

Early studies of symbiosis focused primarily on discovery and description of commensals and parasites found in humans and their domestic food animals. Malarial parasites and some of the important trematodes (flatworms known as flukes) and nematodes (roundworms) of humans were described by the ancient Greeks, and references to the guinea worm (*Dracunculus medinen-*

sis) are found in the Bible, where it is called "the fiery serpent." Some of the dietary conventions or laws observed in modern cultures have the side effect of preventing harmful symbioses, although it is still debated whether these proscriptions actually have their basis in early observations. It is widely known, for example, that pork products, if eaten at all, should never be consumed without thorough cooking. Swine are intermediate hosts for two very pathogenic human parasites, the trichina worm (the nematode *Trichinella spiralis*) and the bladderworm (the infective stage of the tapeworm *Taenia solium*). Much research in parasitology involves the description of symbiotes, particularly those of potential medical, veterinary, or agricultural importance.

The life cycles of many commensals and parasites are extremely complex and often involve two or more intermediate hosts living in different environments, as well as free-living developmental stages. Except for symbiotes of medical importance, relatively few complete life cycles have been worked out. Knowledge of life cycles remains as one of the most important areas of research in parasitology and is usually the phase of research following the description of new species.

Scientists have long recognized that "chemical warfare" (antibiotics, antihelminthics, insecticides) against microbial and animal parasites, and their insect and other vectors, provides only short-term solutions to the control or eradication of symbiotes of medical importance. Research attempts are being made to find ways of interrupting life cycles, sometimes with the use of parasites of other parasites. This research requires sophisticated ecological and biochemical knowledge of both the host-parasite relationship and the parasite mix. Studies of the parasite mix are ecological (parasite-parasite and host-parasite competition), immunological (host defense mechanisms and parasite avoidance strategies), and ethological (host and symbiote behavioral interactions) in nature. Investigators involved in this kind of research must be well trained in many of the biological disciplines, including epidemiology (the distribution and demographics of disease).

Immunology is the most promising modern research area in parasitology. Not only have specific diagnostic tests for the presence of cryptic (hidden or hard to find) parasites been developed, but also vaccines may be discovered that can protect people from such destructive protozoan diseases as malaria. Malaria has killed more humans than any other disease in history, and it currently causes the death of more than one million people, and lowers the quality of life for millions of others, each year.

The Interrelationship of Species

All species are involved in complex interrelationships with other species that live in or on their bodies, or with which they intimately interact behaviorally or ecologically. Such interactions may play a minor role in the life and well-being of one or both of the associates, or they may be necessary for the mutual survival of both. In relatively few symbiotic relationships, one or both species may suffer damage or death. Pathogenic associations are relatively rare, because disease or death of one symbiote generally results in corresponding disease or death of the other. Such relationships, which cannot persist over evolutionarily long periods of time, may nevertheless cause catastrophic loss of life in nonadapted host populations.

Domestic animals cannot live in some parts of the world, such as the central portion of Africa, because they have little or no resistance to parasites of wild species, which are the normal hosts and are not harmed. Native species have coadapted with the parasites. This situation presents a moral dilemma to humans. In the face of human needs for space and other resources, should native animals be displaced or killed? Or should human populations proactively slow their reproductive rates? History shows that humanity has often chosen to take the former course.

The common view that animals which live in other animals are degenerate creatures that take advantage of more deserving forms of life is understandable but inaccurate. Symbiotes are highly specialized animals that do not live cost-free, or always to the detriment of their hosts. Symbiotic relationships between species have vastly increased the diversity, complexity, and beauty of the living world.

—Sneed B. Collard

See also: Coevolution; Competition; Ecological niches; Ecology; Ecosystems; Evolution: Historical perspective; Habitats and biomes; Immune system; Invertebrates; Plant and animal interactions; Population growth; Predation.

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SYSTEMATICS

Type of animal science: Classification
Fields of study: Evolutionary science, systematics (taxonomy)

Systematics is the subdivision of biology that deals with the identification, naming, and classification of organisms and with understanding the evolutionary relationships among them. Systematics attempts to incorporate everything that is known about organisms in its effort to produce classification systems that may reveal the evolutionary relationships among various groups. The system of classification that has resulted from this discipline divides all organisms into five kingdoms: Monera, Protista, Fungi, Plantae, and Animalia.

Principal Terms

BINOMIAL NOMENCLATURE: the two-word system used for naming every individual species; the wolf, for example, is *Canis lupus*

EUKARYOTE: an organism whose cells have internal structures, such as a nucleus and a mitochondrion, separated from one another and from the rest of the cytoplasm by membranes

KINGDOM: the broadest category of organisms; the system currently used recognizes five kingdoms—Monera, Protista, Fungi, Animalia, and Plantae

NOMENCLATURE: the part of systematics that deals with establishing a valid name for a species, according to specific guidelines

PHYLUM (pl. PHYLA): the second-broadest category of classification; each kingdom is divided into phyla

PROKARYOTE: an organism that has no internal membranes in its cells; the only membrane in a prokaryote is the cell membrane

TAXON (pl. TAXA): the basic unit of taxonomy; any of the categories of classification to which an organism may be assigned

Systematics is concerned with the identification, naming, and classification of living organisms and with the relationships that exist among them. In its broadest sense, systematics gathers and summarizes everything that is known about organisms: their morphological, physiological, psychological, ecological, evolutionary, developmental, molecular, and genetic characteristics. The goal of the systematist is to develop a natural classification that will reveal evolutionary relationships among the various groups. A natural classification strives to show true evolutionary relationships. In this kind of system, organisms placed in a given category should share evolutionary origins. Although it is nearly impossible to be absolutely certain of the evolutionary ancestry of a group of organisms, one of the aims of classification is to approximate the natural relationships as closely as possible.

The earliest systems of classification, which go at least as far back as the ancient Greeks, grouped organisms into categories based on artificial standards. A system based on artificial criteria might, for example, use the length of the tail as the main standard to separate animals into different categories. Thus, under such a system, short-tailed animals such as elephants, pigs, and chihuahua dogs would be grouped together; horses, cats, and skunks would be in a separate group.

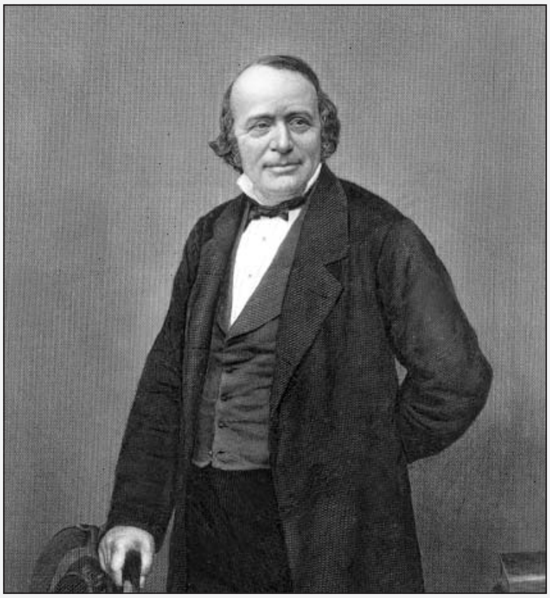
Binomial Nomenclature

The system of classification used by scientists today considers the species the basic unit of classifi-

Louis Agassiz

Born: May 28, 1807; Motier, Switzerland
Died: December 14, 1873; Cambridge, Massachusetts
Fields of study: Marine biology, paleontology, systematics (taxonomy)
Contribution: Agassiz's classification and description of fossil and living fish established his reputation as a major scientist. Later he vigorously opposed theories of evolution.

Jean Louis Rodolphe Agassiz studied at the universities of Zurich, Heidelberg, and Munich. His volume describing and classifying a collection of Brazilian fish earned him a Ph.D. from the University of Erlangen in 1829; the next year he received a doctor of medicine degree from Munich. In 1832, he went to Paris, where his work impressed the noted scientists Alexander von Humboldt and Georges Cuvier. Humboldt arranged a professorship for Agassiz at Neuchâtel, Switzerland. Cuvier gave Agassiz the material on fossil fish that he had collected.



Louis Agassiz made his name classifying fossil and living fish, but he is more widely known for his rejection of Darwin's theories of evolution. (Library of Congress)

Agassiz spent the next ten years studying fossil fish collections in museums and private collections across Europe, publishing his findings in a six-volume *Recherches sur les poissons fossiles* (1833-1843; research on fossil fish). Using the comparative methods taught by Cuvier, Agassiz carefully analyzed and classified more than seventeen thousand ancient fish. As a classifier, Agassiz meticulously distinguished between closely related forms, a procedure tending toward the multiplication of species. Convinced that an all-powerful deity had planned the entire range of creation, he rejected the idea that a hereditary connection extended from ancient to modern fish, insisting that each species represented a separate and special idea of God. While at Neuchâtel, he also published a series of papers describing how Ice Age glaciers had transformed the topography of Europe.

After Harvard University offered him a professorship of zoology and geology in 1847, Agassiz settled permanently in the United States. In 1859, he published his *Essay on Classification*, explaining his philosophy of nature, his belief in special creation, and his views on zoological classification. By that year, he had raised enough money to build a Museum of Comparative Zoology at Harvard. Agassiz planned to have the museum show the relationship of species, while insisting on the distinct and separate creation of each.

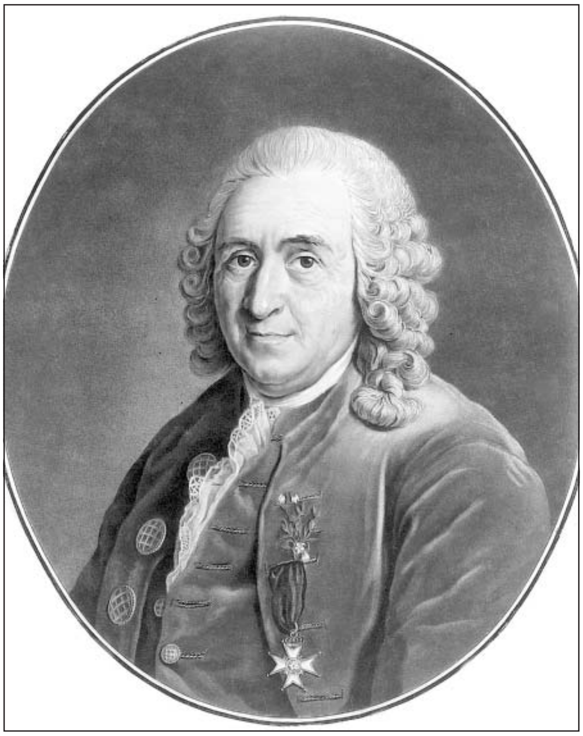
When Charles Darwin's *On the Origin of Species* appeared in 1859, Agassiz attacked it vigorously, calling the work untrue in its facts and unscientific in its methods. His rejection of Darwin attracted contemporary religious leaders uneasy with ideas that seemed to contradict those of the Bible. Younger scientists were less impressed by Agassiz's position, arguing that his concept of glacial periods supported Darwin's mechanism of change, and reading the geological order in which Agassiz showed species succeeding each other as evidence of an evolutionary progression. Agassiz's work on classification used paleontology, embryology, and geographical associations to demonstrate the true relationship of organisms. Agassiz believed this relationship had originated within the mind of God, but many of Agassiz's successors found it verification of an evolutionary sequence of change.

—Milton Berman

cation. To most individuals, the concept of a species is intuitively obvious. Dogs, cats, horses, cows, and pigs each constitute a separate, distinct group of organisms. Dogs breed with dogs to produce puppies, which in turn grow up and are able to have puppies of their own. These two concepts, as simple and obvious as they seem, form the cornerstone of the classification system in use today. This species concept was first introduced by the English naturalist John Ray in the late seventeenth century. Today, a species is usually defined as a population or group of populations of organisms that share similar characteristics and that, ideally, are capable of breeding to produce fertile offspring.

The earliest systematists were the ancient Greeks. Although many classification systems have been proposed over the centuries, the system used today to classify all living organisms is based on one developed in the eighteenth century by a Swedish scientist named Carolus Linnaeus. The beginning of modern classification is considered to date from the publication, in 1758, of the tenth edition of Linnaeus's book *Systema Naturae*. Linnaeus simplified all the previously existing systems of classifying living things and developed a two-word system for naming each organism. This two-word system, called binomial nomenclature, consists of two names ("binomial" simply means "two names") that are assigned to one, and only one, species. These two names are somewhat similar to a first and last name. For example, for the human species, the name is *Homo sapiens*, which means "wise man." *Homo*, the first word in the name, is similar to a last name, such as Jones. This is the name of the genus to which a species belongs. A genus may include a group of related species, as a family includes a group of related individuals. The second word, *sapiens*, is equivalent to a first name, such as Mary. This is the species name. The same two-word name is used for a given species in all languages, thus giving the system consistency and universality.

The names for a species are often in Latin or Greek. When words from a different language are used, Latin or Greek endings are added for consistency. Specific sets of rules must be followed in naming a species. For example, for naming animals, the rules used are outlined in the *International Code for Zoological Nomenclature*, known among zoologists as "the code." The code is published by the International Commission of Zoological Nomenclature. The Commission, in turn, answers to the International Union of Biological Sciences. Similar sets of rules have been outlined for scientists naming plants, bacteria, and viruses. The value of these specific sets of rules for naming organisms is that inconsistency is minimized.



Carolus Linnaeus gave his name to the Linnaean system of binomial nomenclature still used to identify species today. (Library of Congress)

Other examples of binomial species names are, for the grizzly bear, *Ursus horribilis* (meaning "horrible bear"), for the common earthworm, *Lumbricus terrestris* ("worm of the earth"), and for the housefly, *Musca domestica* ("fly of the house"). Sometimes species are named to honor a discoverer or to commemorate a famous personage, but

Carolus Linnaeus

Born: May 23, 1707; Råshult, Småland, Sweden
Died: January 10, 1778; Uppsala, Sweden
Fields of study: Entomology, ornithology, systematics (taxonomy), zoology
Contribution: Linnaeus, the most influential taxonomist of the eighteenth century, introduced the binomial system of nomenclature for the scientific naming of plant and animal species.

Carolus Linnaeus became interested in botany and the natural sciences as a youth. He attended the University of Lund and the University of Uppsala, where he received his degree in medicine. In 1730, Linnaeus was appointed lecturer in botany. Two years later, the Uppsala Academy of Sciences gave Linnaeus the opportunity to conduct an extensive field trip in wild and virtually unexplored regions of Lapland. In 1736, Linnaeus visited England and Paris, where he met many distinguished botanists, including Sir Hans Sloane, Johann Jakob Dillenius, and the three Jussieu brothers. Linnaeus completed the *Hortus Cliffortianus* while in Holland and then returned to Sweden. In 1738, he established a very successful medical practice in Stockholm. In 1741, he was appointed to the chair of medicine at Uppsala. One year later he accepted the chair of botany.

Linnaeus published the results of his exploration of Lapland in Amsterdam as the *Flora Lapponica* (1737). An English translation was published by Sir James Edward Smith as *Lachesis Lapponica* (1811). These publications brought Linnaeus to the attention of the scientific community, but his worldwide reputation was established by the *Systema Naturae, or The Three Kingdoms of Nature Systematically Proposed in Classes, Orders, Genera, and Species* (1735) and the *Genera Plantarum* (1737). The *Species Plantarum*, which provided a complete description of the specific names, was not published until 1753.

The first edition of the *Systema Naturae* contained the basic principles of the Linnaean system, although Linnaeus revised the text many times to accommodate new information and ideas. Plants and animals were grouped into species, genus, order, class, and kingdom. The international scientific community generally accepted the first edition of the *Species Plantarum* (1753) and the fifth edition of the *Genera Plantarum* (1754) as the starting point for naming flowering plants and ferns. Although the Linnaean classification system is based mainly on flower parts and is not natural, in the sense called for by Aristotle, it was useful and efficient in a period in which thousands of new plant species were being discovered. Using the binomial system, botanists could quickly place a new plant into a named category. The binary nomenclature standardized by Linnaeus became the universally accepted method of naming plants and animals. Indeed, the simplicity and success of the Linnaean system made it difficult for scientists to replace it when more natural systems were subsequently proposed.

Linnaeus thought that his work on the reproductive organs of plants was his major contribution to botany. His classification system organized plants into classes according to the number and character of the stamens; classes were divided into orders by the number and character of the pistils. Nevertheless, Linnaeus believed that the process of naming and classifying plants and animals was the most important aspect of biology and the essential foundation of science.

In 1761, Linnaeus was granted a Swedish patent of nobility, which entitled him to be called Carl von Linné. When Linnaeus died in 1778, he was buried with the honors proper to royalty, but his widow later sold his collections and books to Sir James Edward Smith. The Linnean Society of London acquired these materials in 1829.

—Lois N. Magner

occasionally the name may be based on some less serious criteria. For example, a scientist who identified a group of related beetles named them with words created by scrambling the letters in his mistress's name.

The System of Categories

The classification system in use today groups species into progressively broader categories, beginning with the species, the narrowest major category. Each of these categories is called a taxon;

there are seven major taxa. Organisms within each taxon are believed to share certain evolutionary ties. Related species are grouped within a genus (plural, genera), related genera are grouped in a family, families in orders, and orders in classes. One or more classes may then be grouped in a phylum (plural, phyla), and finally, related phyla are placed in a kingdom. Each of these seven major taxa may be further subdivided. Thus, when the human species is fully classified, it looks something like this:

Kingdom: Animalia (animals)
Subkingdom: Metazoa (animals composed of many cells)
Phylum: Chordata (contain a notochord, a dorsal, hollow nerve cord, and gills at some stage of the life cycle)
Subphylum: Vertebrata (jaws and paired limbs)
Superclass: Tetrapoda (two pairs of legs, lungs, a bony skeleton)
Class: Mammalia (hair, warm-blooded, nurse their young)
Subclass: Theria (young develop with a placenta or in a pouch)
Infraclass: Eutheria (placenta only)
Order: Primates (each limb has five fingers or toes with nails)
Suborder: Anthropoidea (upright, larger skull)
Superfamily: Hominoidea (no tail, no cheek pouches)
Family: Hominidae (large brain, flat face, small canine teeth)
Genus: Homo (even teeth, grinding molars)
Species: sapiens (toolmakers, thinkers, organizers, speakers)

The Whittaker System

Many different systems of classification have been developed since Linnaeus published *Systema Naturae*. As more information about species has been discovered and as more species have been identified, biologists have continually found it necessary to revise the classification systems. The most widely accepted scheme currently used was proposed by Robert H. Whittaker, of Cornell University, in 1969. The Whittaker system of classification divides all organisms into five kingdoms: Monera, Protista, Fungi, Plantae, and Animalia. Three criteria are used to determine where to place various types of organisms. Basically, to assign any group to the appropriate kingdom, the following three questions are asked, in this order: Is the organism a prokaryote or a eukaryote? Is the organism unicellular or multicellular? What is the organism's mode of nutrition? Although there are other systems of classification still in use, the simplicity and logic of the Whittaker system have contributed to its broad acceptance by biologists.

By applying these criteria, the five kingdoms can be derived easily. In response to the first criterion ("Is it a prokaryote or a eukaryote?"), all organisms that are considered prokaryotic are placed in the kingdom Monera. The Monera includes all bacteria, including the blue-green algae, or cyanobacteria. All monerans are prokaryotes—that is, the cells have no membrane-bound structures such as a nucleus, mitochondria, or chloroplasts.

All remaining organisms—the eukaryotes—are then classified according to the two remaining criteria. All eukaryote organisms that are unicellular (single-celled) are placed in the kingdom Protista. Protists are a very diverse group of organisms, united by their common unicellular organization. Examples of protists include amoeba, diatoms, *Paramecium*, *Toxoplasma*, and *Plasmodium*. Many of these, such as diatoms, are generally harmless and sometimes useful organisms. Others, such as *Toxoplasma* and *Plasmodium*, are termed pathogenic—that is, they can cause disease.

All remaining organisms are both eukaryotic and multicellular. These eukaryotes are now divided according to the third criterion, the organism's mode of nutrition. There are three basic modes of nutrition that an organism can use: absorptive, photosynthetic, and ingestive. In absorptive nutrition, the organism absorbs small molecules from the surrounding medium directly into the cell. These organisms have no digestive systems, and they need to live in an environment that will provide them with all the small organic molecules they need to survive. In a photosynthetic mode of nutrition, the organism converts the energy from the sun and carbon dioxide from the surroundings into usable nutrients. Finally, in ingestive nutrition, the organism engulfs or swallows food materials, then digests this food in specialized organs of the body.

Organisms whose mode of nutrition is absorptive are classified in the kingdom Fungi. The image of the kingdom Fungi generally elicits a negative response in humans—the first things that come to mind are often bread mold, spoiled potatoes, ringworm, and athlete's foot. Yet many members of the Fungi are beneficial. For example, penicillin was originally produced only from the fungus *Penicillium*. Many other antibiotics were originally discovered and commercially prepared from fungi. Other examples of useful fungi are the common mushroom used in cooking and those used in the preparation of blue cheeses.

The two remaining modes of nutrition are used to separate the remaining organisms. All eukaryotes using the photosynthetic mode of nutrition are grouped in the kingdom of Plantae (the plant kingdom). This kingdom includes the algae, mosses, ferns, liverworts, shrubs, and trees. Finally, eukaryotes that use ingestion as a way of obtaining nutrients are placed in the kingdom Animalia, or the animal kingdom. The animal kingdom includes the familiar animals such as dogs, pigs, cows, and elephants. Also included are some less obvious members, such as sponges, corals, jellyfish, and barnacles.

One might wonder how "natural" the five-kingdom system of classification is. Separating prokaryotes from eukaryotes is a fundamental, as well as evolutionary ancient, division. Although the other divisions are less clear, the consensus is that the Protista arose from the Monera and that the Protista in turn gave rise to each of the other kingdoms independently.

The Process of Classification

In practice, systematics may be subdivided into steps, or phases, through which the systematist takes a given species in the process of assigning it to its appropriate slot in a classification. These phases are taxonomy, nomenclature, and classification. Taxonomy (which means "the naming of taxa") is the phase of systematics that deals with the identification, differentiation, and naming of species. The process of identification and differentiation of a species involves making certain that the species is indeed different from all others and not merely a variation of a known species. This is often not an easy chore. Although some organisms can be differentiated quite easily, others are much more difficult. There are certainly differences between a husky and a miniature poodle, for example, yet they are members of the same species. Yet the timber wolf, which bears many physical similarities to the husky, is placed in a different, although related, species.

To accomplish the most accurate differentiation possible, the taxonomist draws on knowledge from many different disciplines in biology. Information from such different fields as molecular genetics and ecology may be used in establishing the differences between two groups.

Once a species is identified as new, it must be given a binomial name. The naming of species, or of any other taxa, is known as nomenclature. This is the legalistic phase of systematics. Once an organism is determined by a taxonomist to belong to a new species, a valid name for this new species must be established. In doing this, the careful scientist engages in extensive research to establish that the name assigned to a new species meets all the rules outlined for that particular group. When that research is completed, a description of the species is published in a scientific journal, such as the *Proceedings of the Biological Society of Washington*, or in a more specialized journal for that particular group (for example, *Crustaceana* for new species of crustaceans). Publishing information is an important part of the job of the systematist. One of the major goals of the systematists is to make cer-

John Ray

Born: November 29, 1627; Black Notley, Essex, England

Died: January 17, 1705; Black Notley, Essex, England

Fields of study: Environmental science, systematics (taxonomy)

Contribution: John Ray was the first naturalist to develop a taxonomic system applicable to both plants and animals that used species as its fundamental unit.

John Ray's father was the village blacksmith and his mother was an herbalist and healer. Her influence probably stimulated Ray's early interest in the medicinal virtues of plants. Ray (who also spelled his surname "Wray" until 1670) attended the grammar school in nearby Braintree. In 1644, he matriculated at St. Catherine's Hall, at the University of Cambridge, with the aid of a fund that had been established for needy scholars. He transferred to Trinity College in 1646.

Ray earned his bachelor's degree in 1648 and was elected to a fellowship at Trinity in 1649. Ray took holy orders in 1660, but he lost his fellowship in 1662 because, as a Puritan, he refused to subscribe to the Act of Uniformity, which required all clergy to take an oath of canonical obedience. Ray became totally dependent on the generosity of friends, who allowed him to spend the rest of his life studying natural history and writing numerous books. Ray was elected to the Royal Society in 1667.

In 1660, Ray published a catalog of the plants that grew in the vicinity of Cambridge. This led to studies of other areas in Britain. During an expedition to Wales and Cornwall in 1662, Ray entered into a partnership with his friend and pupil Francis Willughby (1635-1672). The two naturalists shared the goal of conducting a comprehensive study of the natural history of all living things. Ray agreed to catalog the plant kingdom while Willughby investigated the animal kingdom.

From 1663 to 1666, Ray and Willughby enhanced their knowledge of flora and fauna while touring the European continent. When they returned to England, they began composing a series of books describing the entire animal and plant kingdoms. Ray published a *Catalogus Plantarum Angliae* (a catalog of English plants) in 1670. Unfortunately Willughby died only two years later. Ray published *F. Willughbeii . . . Ornithologia* (1676; the ornithology of F. Willughby) and *F. Willughbeii . . . de Historia Piscium* (1685; history of the fishes), listing Willughby as the author, even though Ray had done much of the work. Ray's *Methodus Plantarum Nova* (1682; a new method of plant classification) established the taxonomic importance of the distinction between monocotyledons and dicotyledons.

Ray's most important contribution to botany was his three-volume *Historia Generalis Plantarum* (1686-1704; a general history of plants). In this work Ray established the species as the ultimate unit of taxonomy. Ray suggested that a breeding test could be used to determine whether plant specimens were members of the same species. Urging naturalists to aspire to a more sophisticated and natural system, he attempted to incorporate all structural characteristics, including internal anatomy, into his taxonomic system. Although Ray's system of taxonomy was not truly natural, it did approach that goal more closely than a strictly artificial system like that of Carolus Linnaeus.

Another example of Ray's cataloging tendencies was his *Collection of English Proverbs Digested into a Convenient Method for the Speedy Finding Any One upon Occasion* (1670), an early example of folklore research which was probably intended to assist clergymen in the writing of their sermons. This book was still forming the basis of English proverb collections into the late nineteenth century. Ray's work in the fields of natural history and folklore illustrates the permeable boundaries between disciplines of his age.

In the 1690's, Ray published several books on religion. This was not really a departure from his scientific work because Ray always believed that his taxonomic studies reflected the order and purpose inherent in God's design. *The Wisdom of God Manifested in the Works of the Creation* (1691) was Ray's most popular and influential book. Indeed, the period between the publication of *The Wisdom of God* and *On the Origin of Species* (1859) saw the flowering of an approach to science known as natural theology, largely based on Ray's work.

—Lois N. Magner

tain that the newly organized knowledge is available to all biologists.

The classification phase of systematics involves the assigning of organisms to specific taxa. Classification provides a filing system that allows the logical grouping of species. Like the process of identification and differentiation of a species, classification requires an extensive knowledge of biology. The systematist involved in classification takes into account virtually everything known about a given species in order to arrive at the most logical, natural classification. Because of the breadth of knowledge required in their field, some biologists involved in systematics feel that theirs is the ultimate synthesizing branch of biology.

Humans are almost instinctive sorters and classifiers, tending to sort everything into groupings, classes, or types. These are mostly groupings of convenience: Information is easier to store, retrieve, and exchange in this way. Thus, people may be classified as short or tall, heavy or thin, blonde, redhead, or brunette. Biologists classify living things for similar reasons—that is, to facilitate the exchange of information. The classification of organisms also satisfies the curiosity of biologists to know how many different kinds of organisms are found on earth. Of the estimated 10 million species living on earth, only about 1.5 million have been identified. Finally, and most important, classifying organisms by their similarities gives scientists insights into their relationships to one another, as well as their relationship to extinct groups of organisms.

—*Alina C. Lopo*

See also: Amphibians; Arthropods; Birds; Chordates, lower; Evolution: Historical perspective; Fish; Insects; Invertebrates; Mammals; Reptiles; Vertebrates.

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TAILS

Types of animal science: Anatomy, evolution, physiology
Fields of study: Anatomy, conservation biology, developmental biology, entomology, evolutionary science, herpetology, invertebrate biology

The tail is a prolongation of the animal body that serves the animal as a means of defense, locomotion, stabilization, or ornament.

Principal Terms

ARBOREAL: living in trees
BURROWING INSECTIVORE: an insect-eating animal that usually lives in nests formed by digging holes or tunnels in the ground
INVERTEBRATE: animals without backbones, such as insects, frogs, and snakes
PREHENSILE TAILS: tails that are adapted for seizing and holding
VERTEBRATE: animals with backbones, such as mammals
VISCERA: any internal body organ, such as intestines or entrails

The tail is the prolongation of the backbone, beyond the trunk of the body, of any animal, insect, or fish. The tail of the vertebrate is composed of flesh and bone but does not contain any viscera. For many aquatic animals (such as fish and amphibians) as well as animals that use water as part of their living environment (such as crocodiles, otters, and whales), the tail is fundamental to their locomotive ability. Squirrels and other arboreal animals use the tail to keep balance and as a rudder when they jump from branch to branch, while others, such as the spider monkey and the chameleon, use the tail as an extra limb to increase their mobility through the branches of the rain forest. The tail may also be used as a means of defense for porcupines, as a warning signal in rattlesnakes, as a hunting weapon in alligators and scorpions, an ornamental sexual attractant in peacocks, or even a communication tool for dogs. Most birds do not carry a tail; instead, the prolongation has been fused into the short pygostyle bone, which serves as the holder of tail feathers and assists the birds in flying.

The shape, morphology, and structure of the tail vary according to the nature and behavior of the specific animal. Burrowing insectivores, like all other burrowing animals, usually have no tail. In contrast, climbing and running species have very large tails. Slow-moving animals, such as hedgehogs, have short tails, while chameleons have coiled tails.

Tails in Invertebrates

A number of lizards have thick tails that are covered by large, spiny, hard scales. The tail is often used as a defensive measure against predators such as snakes, especially when the head and body of the lizard are wedged between rocks. Moreover, lizards are capable of shedding their tails, which wriggle in a way that may confuse their predator, thus giving them enough time to escape. Each vertebra of such a tail has a fracture line along which it splits when the tail muscles contract. A unique lizard is the Solomon Islands skink, whose prehensile tail muscles are bound both to the vertebrae and to a fibrous sheath of collagen located under the skin, thus creating a much stronger and more flexible tail. Stimulation of the nerve contraction in the severed position keeps the tail moving for several seconds after severing occurs. Normally the tail splits off in one place, but in a few lizard species, such as the glass snakes

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(*Ophisaurus*), tails may be broken in more than one place. The stump usually heals very quickly and a new tail regenerates, although it is not as long and not as elaborate as the original. Bioengineers in the late 1990's conducted research trying to isolate the gene that is responsible for the regeneration of the severed tails.

Amphibians such as tadpoles and salamanders also lose and, in many cases, regenerate their tail, which has a spinal cord. Tadpole tails have a stiff rod for support, called the notochord, while the salamander's tail has a backbone with vertebrae. No tail is regenerated in the salamander if the spinal cord is severed, unlike the tadpoles, where the tail is reformed regardless of the fate of the severed spinal cord.

Tails in invertebrates are used in characteristic, unique ways among the different animals. Iguanas use their tails like large oars to swim in water, while tucking its legs close to its body. When threatened, the armadillo lizard puts its tail in its mouth, rolls over, and assumes the shape of a tight ball. Day geckos use their tails as a means of support while jumping from tree to tree to avoid their main predator, the falcon. The skink has a very short tail, whose shape is very close to that of its head. This confuses its enemies, since they do not know the direction the skink is going to take while escaping.

Tails in Vertebrates

The squirrel owes its name to its tail. The name is derived from the Greek word *skia* (meaning "shadow") and *oura* ("tail"), indicating that the tail is large enough to shade the rest of the animal body. Unlike the bat, which is the only mammal that truly flies, the flying squirrel is the only vertebrate that glides. Using its strong and sturdy back feet to jump from the top of a tree, it flattens its tail and spreads the loose folds of the skin so that it can glide in air. Just before landing, the gray squirrel lowers its tail first, then quickly lifts it and lands on its hind feet. When in danger, the red squirrel attempts to scare its predator by flicking its tail while using a series of noises, such as whistling, chattering, and chirping, and stomping its hind feet.

Other nonmammals, such as snakes, crocodiles, and turtles, may lose their tails to predators or to accidents, although not voluntarily. In fact, some snakes, such as the African python *Calabaria* and the oriental venomous *Maticora*, wave their thick, colored tails toward their enemy while retreating slowly. Both male and female diamondback rattlesnakes have the ability to rattle their tail ninety times per second. During the motion, the sonic muscles pump calcium out of the myoplasm fifty times faster than the locomotor muscles do. As a result, the filaments in the sonic muscles release each other and get ready for the next contraction much more quickly than the locomotor muscles.

Parrots (Psittaciformes) are the most popular birds that possess colorful and widely variable tails. In some species the tail is short, square, or rounded; in others it is long and pointed, but no parrots have forked tails. Birds that fly long distances tend to have longer tails, sometimes longer than the total length of their body. Climbing parrots usually possess rounded wings and blunt tails.

Long, elaborate tails are considered by evolutionists as unusual ornaments to win mates and use in elaborate courtship rituals. Wildlife scientists believe that the more attention-getting displays also give an indication of which bird will make a good parent. In agreement with Charles Darwin's theory of sexual selection, fe-

Tail Evolution

Various discoveries in Africa and Pakistan in the 1980's and 1990's have provided evidence that supports Charles Darwin's evolutionary idea that land animals may have the ability to evolve into aquatic animals, such as whales. The findings suggest that whales were actually land-dwelling mammals, once upon a time. The very well-preserved fossil whale, *Ambulocetus natans*, had a long mammalian tail, in addition to feet and legs. This is in strong disagreement with the creationist idea that discounts any possible slow transformation of a land mammal to an aquatic species. This observation also supports the principle that some anatomical features may either evolve or become atrophic as evolution progresses.

Recent evidence indicates that Ediacarans may have been the ancestors of modern life forms. These species emerged about six hundred million years ago and were the first large, complex life species. Although basic organs such as eyes, mouths, heads, and tails did not appear to be part of the original anatomy, paleontologists suggest that Ediacarans survived well into the Cambrian period, when evolution started taking place, and all the above organs slowly emerged and developed with time. The prehistoric ancestors of sturgeons, the largest and longest lived fish, appear to have been similar to sharks in appearance, with submarine-like bodies, strongly upturned heterocercal tails, and pronounced flattened snouts. Fossils of *Anomalocaris*, a large aquatic Cambrian predator, found in China and the Burgess Shale of North America, have provided concrete evidence that they must have had fanlike tails, which were used effectively while swimming.

Although fundamental, tails in several species, such as in stingrays, are not necessary for the animal to survive. Even the human being is believed to have had a tail, which with time has proven unnecessary. In the case of elephants, the trunk is much more useful than the tail. Adjustment to the environment has been established by experimental results conducted by Alan Harvey, who studied the development of baby crabs that were made to grow in and out of a shell. The tails of the latter grew to be symmetrical, while those in the shell became more asymmetrical, because their left sides had more room to grow than the right sides.

male animals of some species develop a preference for armaments that now have purely ornamental function, while others show preference for a certain trait which males eventually have to adopt if they are to mate. Male swallows that have long tails have a much higher degree of paternity and produce more biological offspring as compared to similar birds that are short tailed, indicating a distinct positive correlation between male tail length and paternity in this species.

The function of the heterocercal tail in shark locomotion has been given two explanations. The first one suggests that as a result of the lift created by beating the tail, the net force acting on the tail is directed dorsally and anteriorly. In the so-called Thomson's model, the tail generates a net force directed through the shark's center of gravity.

Sea animals use their tails in peculiar ways. In the depths of the species-rich Amazon River, electric fish and catfish predominate. Among the unusual incidents observed, electric fish appear to eat the tails of other fish. Eels plant their tails in burrows they dug in the sand underwater and let their bodies wave in the current, while waiting for food, such as drifting tiny crustaceans, fish eggs, and plankton, to reach them.

—Soraya Ghayourmanesh

See also: Anatomy; Beaks and bills; Bone and cartilage; Brain; Circulatory systems of invertebrates; Circulatory systems of vertebrates; Claws, nails, and hooves; Digestive tract; Ears; Endoskeletons; Exoskeletons; Eyes; Fins and flippers; Immune system; Kidneys and other excretory structures; Lungs, gills, and tracheas; Muscles in invertebrates; Muscles in vertebrates; Nervous systems of vertebrates; Noses; Physiology; Reproductive system of female mammals; Reproductive system of male mammals; Respiratory system; Sense organs; Skin; Teeth, fangs, and tusks; Tentacles; Wings.

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TASMANIAN DEVILS

Types of animal science: Anatomy, classification
Fields of study: Anatomy, developmental biology, ecology, evolutionary science, physiology, zoology

The Tasmanian devil is the world's largest carnivorous marsupial. It is now found only on the island of Tasmania, where it is reasonably common throughout the island and is strictly protected. Its noisy and screechy sounds make it seem much more ferocious than its size might indicate.

Principal Terms

ADAPTIVE RADIATION: the process by which many species evolve from a single ancestral species in adapting to new habitats

DINGO: the wild dog brought to Australia by the aborigines

MARSUPIAL: primitive mammals in which the young are born alive but in a very immature state

MARSUPIUM: the pouch in which the immature young remain attached to nipples until they complete their development

PLACENTAL MAMMAL: a mammal that possesses a placenta, an organ used to nourish the developing embryo

The Tasmanian devil belongs to a primitive group of mammals, the marsupials, which are found today primarily in Australia, Tasmania, New Guinea, southern Mexico, Central America, and South America. The name "marsupials" refers to the animal's marsupium, the pouchlike structure to which the immature young move after they are born, becoming attached for several months as they complete their development. The well-known pouch of kangaroos is the classic example of a marsupium, although it should be noted that a few marsupials do not have pouches and in some, including the Tasmanian devil, the pouch opens downward. During their long geological separation from the rest of the world, marsupials in Australia and South America underwent adaptive radiation, which produced an enormous diversity of forms as species became adapted to various habitats. As a result, many marsupials resemble placental mammals although they are not closely related. Thus, there are marsupials that resemble flying squirrels, moles, woodchucks, cats, and dogs. The Tasmanian devil, although a marsupial, has many similarities in structure and behavior to a dog.

Physical Characteristics

The devil belongs to a family of marsupials known as the Dasyuridae, which are found in Tasmania, Australia, New Guinea, and some nearby islands. The group includes the Tasmanian wolf or tiger, the numbat or banded anteater, and shrewlike, catlike, and ratlike forms. The Tasmanian devil is distinctive even within this distinctive group of marsupials. It received its name, "The Devil," from the early European settlers to Tasmania, who were awed by its fierce behavior and loud vocalizations. The devil actually is a stocky but short-limbed animal, doglike in shape, and only weighs between 4.5 and 12 kilograms, standing only about 30 centimeters tall. Its dark, mostly black color also contributes to its "evil" reputation. The animal does have a voracious appetite. It has a large head and very powerful jaws with long canine teeth. The devil is the largest carnivorous marsupial, extremely strong for its size; it can feed on animals larger than itself, including small kangaroos. It usually rests during the day and seeks food at night. Its food is varied and may include amphibians, lizards, rodents, insects, and poultry. The devil may prey on live animals or may feed on carrion. Its nightly movements may cover distances up to ten miles or more. The legs are short and the animal usually moves along slowly, although it is capable of running quickly for short distances.

Early Life

As is true of all marsupials, the young are born alive after a relatively short gestation period—about three weeks. Breeding usually takes place in early spring. The newborns travel from the birth canal to the pouch, which is backward-opening in this species, and attach themselves to a nipple, where they remain secure for about four months.

For the next several months, the young will venture outside of the pouch at times and, finally, become weaned and independent by the end of the year. Breeding usually commences between the second and third year. Reproduction is somewhat limited, as the mother has only four nipples and usually more than four young are born. It is not unusual for only two young to survive to weaning.

The Tasmanian devil has had a persecuted history, especially with the advent of European settlers. Its fierce appearance, loud screeches, and occasional predation on domestic livestock and poultry caused it to be hunted, trapped, and poisoned to the point of near extinction. Its value in cleaning up carcasses was not appreciated. The Tasmanian devil finally became protected by law in 1941. Going from outlaw to icon, the Tasmanian devil was selected as the symbol of the Tasmanian National Parks and Wildlife Service.

—*Donald J. Nash*

See also: Fauna: Australia; Kangaroos; Marsupials; Opossums; Reproduction; Reproductive systems of female mammals.

The Tasmanian devil is a doglike marsupial. Its name derives not from its appearance, but from its fierce nature and loud cries. (Courtesy of Talune Wildlife Park)

Tasmanian Devil Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Subclass: Theria
Order: Marsupiala
Family: Dasyuridae
Genus and species: Sarcophilus harrisii
Geographical location: Tasmania, but formerly was also found in Australia
Habitat: From coastal areas to the mountains, in shrubs and forests
Gestational period: Twenty-one days, then remains in marsupium for five to six months
Life span: Between six and eight years
Special anatomy: A powerfully built, solid animal, with a large head, short tail, and marsupium

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TEETH, FANGS, AND TUSKS

Type of animal science: Anatomy
Fields of study: Anatomy, conservation biology, developmental biology, entomology, herpetology, invertebrate biology

Teeth, fangs, and tusks are hard, resistant structures found in the jaws of vertebrates. Teeth are used primarily for catching and chewing food, while fangs and tusks are specialized for defense.

Principal Terms

ELAPIDS: a snake classification which includes cobras and rattlesnakes that have short, fixed front fangs

HETERODONT: having two or more types of teeth, such as molars and incisors

HOMODONT: having teeth all of the same type

INCISOR TEETH: teeth that are located in the front of the mouth and whose function is to tear, hold, and cut the prey

TOXIN: any substance, such as the venom in snakes or spiders, that is toxic to an animal

VIPERIDAE: poisonous terrestrial or semiaquatic snakes

VIPERS: a snake classification that includes copperheads and rattlesnakes, which have long, movable front fangs

Teeth, fangs, and tusks are found in vertebrates, and are used for obtaining and masticating food and for defense. Fangs and tusks are elongated canine or incisor teeth, which serve to deliver venom (fangs) or as defensive weapons (tusks). Tusks, which are made of ivory, have been valued for making jewelry and decorative objects, which has led to the endangerment of the elephants and walruses that carry them.

Teeth

Teeth are hard, resistant structures that are found on the jaws, as well as in or around the mouth and pharynx of vertebrates. Teeth were formed through the evolution of bony structures found in primitive fish. A tooth consists of a crown and one or more roots. The crown is the visible, functional part, while the root is attached to the tooth-bearing bone. However, many living organisms, such as birds, turtles, whales, and many insects, do not have teeth.

Although the teeth of many vertebrates have been adapted for special uses, their function is to catch and masticate food and defend against predators or enemies, as well as other specific purposes. Rodents and rabbits, for instance, have curved incisors that are deeply embedded in the jaws and grow longer with age. Several types of apes have enlarged canines for defense, while the sawfish, which is the only animal with teeth completely outside its mouth, uses its teeth to attack its prey. All perissodactyls, a group of herbivorous animal species characterized by an odd number of toes on the hind foot, including horses, rhinoceroses, and tapirs, have evolved specialized forms of teeth that are adapted for grinding. Generally, lizards are insectivores and have sharp tricuspid teeth that are adapted for grabbing and holding. Mollusk and crustacean feeders, such as the caiman lizard, have blunt, rounded teeth along the jaw margin or on the palate.

Tooth-bearing animals may be heterodont or homodont. Most mammals are heterodont and carry two or more types of teeth, such as the incisors and the molars. The purpose of the incisors is to tear and bite into the food, while the molars crush and grind the food. Cats do not have flat-crowned crushing teeth; instead only the stabbing and anchoring canine teeth cut up the food, which is then swallowed. In the case of elephants, the upper second incisors have developed into ivory tusks, which are the longest and heaviest teeth in any living animal. On the other hand, fish and most reptiles are homodonts—their teeth are all of about the same size, and their purpose is to catch prey. This is the main reason why their teeth are regularly replaced during their life span.

Snakes have teeth that curve back toward the throat. Thus, as soon as the prey is caught, it is pushed into the throat. In poisonous snakes, teeth called fangs have a canal through which the poison (venom), normally stored in glands that are in the roof of the mouth, may be ejected.

Fangs

Fangs are long, pointed teeth used by many animals as a means of self-defense, for securing their prey, or other reasons. Many snakes use their hollow fangs as hypodermic needles to puncture their victim and, in the case of a venomous snake, to inject toxic venom. Because of the snake's muscular elasticity, the fang tips at penetration average 112 percent further apart than their bases at rest. The wound resulting from penetration of the flesh is called a snakebite. A nonvenomous snakebite is usually similar to a puncture wound which, when untreated, may become infected and in extreme cases may cause gangrene. That of a venomous snake is much more serious and there is a potentially lethal effect, which depends on several factors such as the size of the victim, the bite location, the quantity of venom that has been injected, the speed of venom absorption into the victim's blood circulation, and the speed with which first aid and the antidote are given.

Several venomous snakes, such as the ringhals and the black necked cobra (types of African cobras), have the ability to spit. A fine stream of venom is forced out of each fang which, instead of having to go through a straight canal that ends in a long opening, is forced through a different canal that turns sharply forward to a small round opening on the front surface. Contraction of the muscle that surrounds the poison gland leads to the spitting of the venom, which is harmful to human eyes unless washed quickly. Front-fanged snakes include pit vipers such as rattlesnakes, fixed-fanged snakes such as brownsnakes and cobras, seasnakes, and true vipers (Viperidae). All have hollow, tubelike fangs created by the extension of the dentine across the anterior seam. Evolutionary herpetologists have postulated that this anterior seam may have been open several tens of thousands of years ago.

Only poisonous snakes possess fangs and venom glands, which are considered to be an evolutionary result of salivary glands found in primitive fish. Poisonous snakes bite the victim with their fangs and proceed to inject the venom in the wound in their effort to kill their prey. The venom contains toxins, which are chemical compounds that have the potential of attacking the blood and the nervous system with lethal consequences. The proteinaceous enzymes that are found in the venom are also used to digest the eaten animal. These snakes are generally subdivided into vipers and elapids. Vipers, which include copperheads and rattlesnakes, have long, movable front fangs, while elapids, such as cobras and rattlesnakes, have short front fangs that are fixed. Occasionally some venomous snakes have a fang on the upper jaw in the rear of the mouth, which makes them less harmful to large animals since the venom injection occurs at a much slower pace. The devouring or swallowing of the prey usually takes place only after the venom has taken full effect and the animal is dead. Generally, small snakes embed their fangs in the prey for a longer duration than larger snakes.

The analysis and determination of the composition of the hard dental tissues of the Viperidae has been conducted using classical microscopy, scanning electron microscopy, transmission electron microscopy, X-ray diffraction, and infrared spectroscopy. The results have shown a thin, calcified outer layer, composed of very small needle-like crystals that are randomly distributed. The calcified outer layer contains pores and collagen fibers that are incompletely mineralized, especially in the wall of the poison canal. Chemical analysis of the dentine has indicated a poorly mineralized apatite with a high level of carbonate content.

All six species that belong to the marine fish classified under the genus *Chauliodus* (order Salminoformes) are called viperfish. They are all small in size, the largest being the Pacific viperfish (*C. macouni*), which is no more than one foot long. They are characterized by their long fangs, which protrude from the upper and lower jaws and are used to securely grab their prey. The tigerfish of the Zambezi river, with its two rows of long and very sharp teeth, has been seen as more fearsome than the true piranha or the mako shark.

Tusks

Evolutionary theories suggest that the tusks of both the walrus and the wild boar are enlarged canine teeth, while in the case of the pig, the lower incisor has been modified with time into an organ that is used for digging purposes. In male Indian elephants and African elephants of both sexes, the tusk is the upper incisor, which continues to grow throughout their lifetime. The female Indian elephant has either no tusks or very small ones. Male Ceylonese elephants, found in Sri Lanka, generally have no tusks, while Sumatran elephants, found in Indonesia, bear the longest tusks. Elephant tusks from Africa are typically six feet long, conical at the end, and weigh approximately fifty pounds each. Indian elephants have slightly smaller tusks. Each tusk from the largest pair, recorded and exhibited at the British Museum, is twelve feet long, has a barrel circumference of eighteen inches and weighs close to 150 pounds.

Studies by Raman Sukumar, an ecologist at the Indian Institute of Science in Bangalore, and Milind Watve, a microbiologist, indicate that male Asian elephants with longer tusks are prone to

Elephant tusks evolved from the upper incisors, whereas walrus and boar tusks are enlarged canine teeth. A genetic link has been shown between the length of a male elephant's tusks and his resistance to parasites, which increases his genetic fitness. (Digital Stock) host many fewer parasites. This is in agreement with the theory of the evolutionary biologist William D. Hamilton, of the University of Oxford, who proposed in 1982 that males that carry genes resistant to parasites have the ability to be healthier and therefore live longer. At the same time, these species develop secondary sexual characteristics which enable females to select males that will produce better offspring.

Anatomically, the tusk is composed of several layers, the innermost of which grows the latest. One third of the tusk is embedded in the bone sockets of the elephant's skull. At the beginning, the head end of the tusk has a hollow cavity that becomes almost fully solid with aging. Only a narrow nerve channel runs through the center of the tusk to its end.

Ivory is a type of dentin that is the major component of the elephant tusk and is desirable worldwide for its beauty and durability. There are generally two types of ivory, soft and hard. The ivory isolated from the tusks from East African elephants is soft, while that found in the West African elephants is hard. Hard ivory is usually darker in color and is straighter than the soft type, which has a fibrous internal texture, is less brittle, and is a more opaque white. The demand for ivory has led to a large number of elephant slaughtering incidents and a dangerous decline of the African elephant population, beginning in the late nineteenth century and continuing up to the twenty-first. The discovery by archaeologists in the early 1980's of tusk material in a Greek ship that was sunk around 1400 B.C.E. revealed that ivory was a trade commodity even during the Bronze Age.

Elephants belong to the order Proboscidea, whose early ancestors were not larger than the average pig. It is believed that during the process of evolution, the lower jaw elongated beyond the upper and eventually turned into tusks. As a result, the nose and upper lips developed into an elongated cover to the projecting lower jaw. During the Eocene Epoch (between fifty-four and forty million years ago) the upper tusks were lost, and a downward-hooked, tusk-tipped mandible developed. The mandible and its tusks became more shovel-like during the Miocene era (twenty-six to seven million years ago). It is believed that the tusks assumed a cylindrical shape not very much later. It appears that tusks were also part of the anatomy of the woolly mammoth, as seen in the specimen that died about twenty thousand years ago and was discovered in a Siberian excavation in the 1990's.

—*Soraya Ghayourmanesh*

See also: Anatomy; Beaks and bills; Bone and cartilage; Brain; Circulatory systems of invertebrates; Circulatory systems of vertebrates; Claws, nails, and hooves; Digestive tract; Ears; Endoskeletons; Exoskeletons; Eyes; Fins and flippers; Immune system; Kidneys and other excretory structures; Lungs, gills, and tracheas; Muscles in invertebrates; Muscles in vertebrates; Nervous systems of vertebrates; Noses; Physiology; Reproductive system of female mammals; Reproductive system of male mammals; Respiratory system; Sense organs; Skin; Tails; Tentacles; Wings.

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TENTACLES

Types of animal science: Anatomy, classification
Fields of study: Anatomy, invertebrate biology, marine biology

A tentacle is a slender, leglike or armlike protrusion from the body of an animal. It is used for protection, as an organ of touch, or to capture food.

Principal Terms

BUD: protuberance used in asexual reproduction
BUDDING: bud development into a complete organism
CARRION: dead animals
FUNNEL: an opening in a cephalopod mantle, providing oxygen and propulsion
GAMETE: sperm or an egg
NEMATOCYST: poison sting cell
RADULA: tonguelike, toothed organ that grinds food and drills holes in shells of prey

Tentacles are slender, leglike or armlike protrusions from the body of a living organism. They are used for protection, as organs of touch, or to capture food. They are often seen in coelenterates, an animal phylum that includes jellyfish, anemones, and coral polyps. The name *coelenterate* comes from the Latin for "hollow intestine."

Coelenterates are hollow tissue sacs with two layers of cells in their walls. The cells carry out digestion, excretion, and reproduction. There is one body opening, a mouth. Food enters it, is digested, and used by the cells. Wastes also leave through the mouth, surrounded by long, slender sense organs called tentacles, which also grab food and pull it into the mouth.

Box Jellyfish: Poison Tentacles

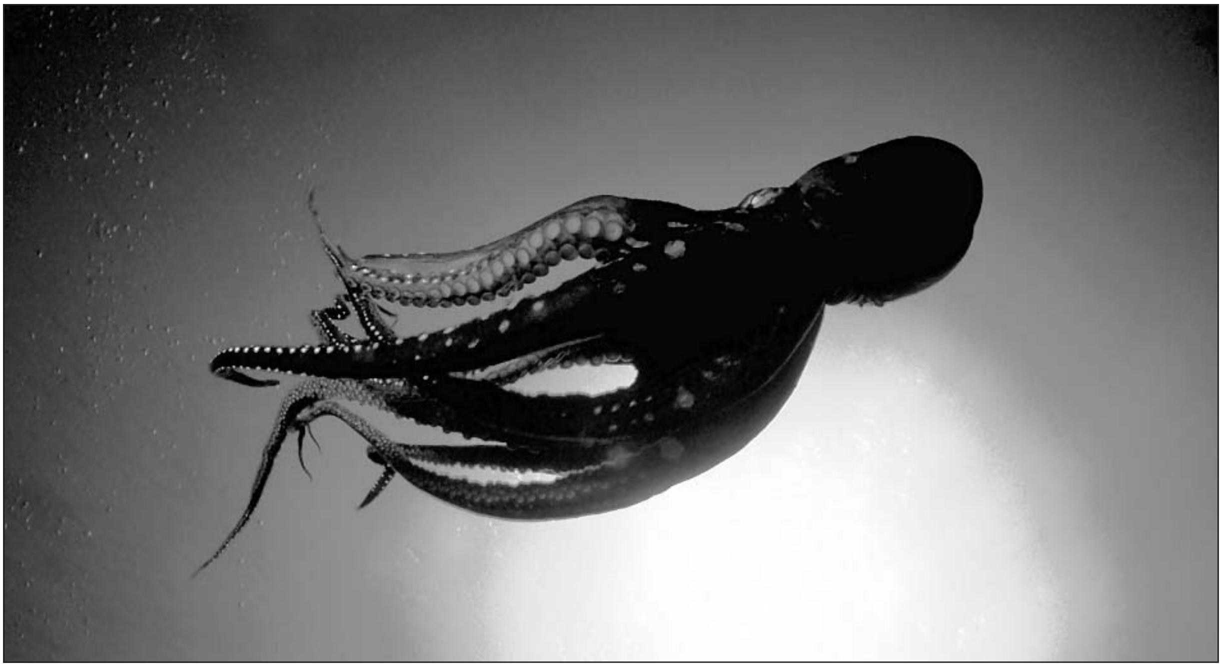
Box jellyfish (*Chironex fleckeri*), native to Australia's north coast and Southeast Asian coastlines, are the most poisonous creatures on earth. They get their name from their box-shaped, translucent bodies, which are approximate 1.25 feet wide. Sixty tentacles, up to 15 feet long and 0.25 inches in diameter, hang from the box.

The box holds an eye and a mouth. Prey—plankton, small fish, and shrimp—are caught in tentacles and pulled into the mouth. Tentacles hold huge numbers of sting cells called nematocysts. When something comes in contact with the tentacles, the nematocysts inject a poison which paralyzes and kills their prey, and can cause extreme pain and even death to large animals or humans. Severe stings will kill within four to six minutes after a human is stung.

Worm and Mollusk Tentacles

Some worms have tentacles. For example, sandworms (family Nereidae) inhabit shallow ocean waters worldwide. Most live in sand or mud burrows. They have colorful bodies ranging from one inch to three feet long and are in the same phylum as earthworms. A sandworm body has several hundred segments. Each segment has two muscular parapodia, both attached to bundles of bristly chaetae. The first segment of a sandworm holds two light-sensitive tentacles, four eyes, and two sensory palps. The second segment has eight more tentacles called cirri. The palps and cirri help sandworms find crustaceans, small fish carrion, and other prey.

Many cephalopods have tentacles. For example, the nautilus (family Nautilidae) is found in South Pacific and Indian oceans. All nautilids have soft bodies with spiral, brown and white shells.



Octopuses have suckers on their tentacles which are used to catch, hold, and explore objects around them. (Digital Stock)

Their mouths have beaks and radulas (toothed tongues) to eat carrion and crustaceans on ocean bottoms. Around the nautilid mouth are almost one hundred short tentacles that are used to sense objects, feed, and move. At one side of the arms, an opening called a funnel allows water to enter and carry oxygen to gills. A nautilid can also spray a jet of water from the funnel, to swim.

Octopus and Squid Tentacles

Octopuses (family Octopodidae) have eight slender, flexible tentacles. On the underside of each arm is a row of suckers. Sensors in suckers serve in defense, detect prey, capture it, and identify its texture, shape, and taste. Arms join at their bases into a bulb-shaped head/body.

An octopus squeezes water out of the mantle cavity and moves its tentacles to swim. It captures mollusk and crab prey by wrapping tentacles around them and using its suckers to tear them to pieces. In the center of the arm juncture is its mouth, which has a radula and a beak to continue shredding prey.

The giant squid (*Architeuthis harveyi*) inhabits the Atlantic Ocean depths. Its torpedo-shaped body is up to sixteen feet in diameter and twenty-five feet long from head to tail. This cephalopod tapers toward its posterior and has at the tail end two fins for swimming and steering. Two eyes provide excellent vision. In front of the eyes are eight round, elongated tentacles with suckers and hooks on their undersides. Two longer tentacles lack suckers and hooks, except at the tip. The tentacles are thirty-six feet long, and from tail to tentacle tip giant squid often exceed sixty feet in length. They are earth's largest invertebrates. Squid hide near the ocean bottom and ambush or pursue prey. The two long tentacles are shot forward to seize their victims, which are passed along to the mouth. A beak in the mouth crushes and tears up prey.

Squid and octopus are eaten by humans worldwide. Nautilids, sandworms, and related organisms help maintain the balance of nature, eating carrion and helping to keep the ocean clean. Other tentacled organisms are eaten by fish that humans use as food. On the other hand, squid and octopuses eat food fish and crabs, competing with humans, and jellyfish can kill via the nematocysts in their tentacles.

—*Sanford S. Singer*

See also: Anatomy; Circulatory systems of invertebrates; Digestive tract; Eyes; Fins and flippers; Invertebrates; Jellyfish; Marine animals; Marine biology; Mollusks; Muscles in invertebrates; Octopuses and squid; Physiology; Poisonous animals; Sense organs; Skin; Worms, segmented.

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TERMITES

Types of animal science: Behavior, classification
Fields of study: Anatomy, entomology, invertebrate biology, physiology

Termites are cellulose-eating social insects that live in colonies of hundreds to millions of individual members produced by a single king and queen. Termites are highly beneficial to the ecosystem because they break down dead plant material, but some species can become serious pests when they colonize manmade wooden structures.

Principal Terms

ALATES: recently molted winged adult termites
CARTON: cardboardlike material composed of wood fragments, saliva, and fecal matter, used for constructing termite nests
CELLULOSE: fibrous polysaccharide that chiefly constitutes the cell walls of plants
PHEROMONE: chemical substance produced by an animal that usually elicits certain behavioral responses in other animals of the same species
PROTOZOAN: mobile, one-celled animal
REPRODUCTIVES: sexually mature male and female
SYMBIOTIC: having a mutually beneficial relationship

Termite fossils date from about 130 million years ago, but they probably evolved much earlier from a primitive, wood-eating, roachlike ancestor. There are about 1,900 termite species divided among six families. Five of the families are considered primitive or lower termites because, like their primitive wood-eating roach relatives, they harbor symbiotic protozoa in the hindgut that digest cellulose. Without these protozoans, the termites would starve to death. The higher termite family, Termitidae, is the largest family, containing about 75 percent of all termite species. Higher termites may be able to digest cellulose themselves, or bacteria in the gut may secrete enzymes to aid in digestion.

Caste System and Nests

Termites are notable for their highly organized societies. Because most termites are effectively deaf and blind, they communicate through touch, smell, and taste. Most species are divided into castes of reproductives, workers, and soldiers. Normally, there is only one reproducing pair, the primary reproductives, or queen and king. Secondary reproductives are present, too, in case the queen or king dies.

The sterile workers and soldiers are of both sexes. Workers care for the eggs and nymphs, provide food for the nymphs, soldiers, and reproductives, and construct, repair, and maintain the nest. Soldiers have evolved modified heads and jaws for defending the nest. The heads are large and hard with powerful, scissorlike mandibles or long, tubular snouts that squirt sticky chemicals. Some soldiers have both formidable jaws and chemical weapons.

Termites are vulnerable to desiccation, changes in temperature, and hungry ants, birds, aardvarks, and other predators. They maintain a moist, temperature-controlled, safe environment by constructing nests. Dry-wood termites never touch the soil but nest in the wood they feed upon, gnawing out tunnels and chambers inside living tree trunks and branches, rotting logs, or furniture and wooden buildings. Subterranean termites must maintain contact with the soil for food sources such as grass and humus or for moisture.

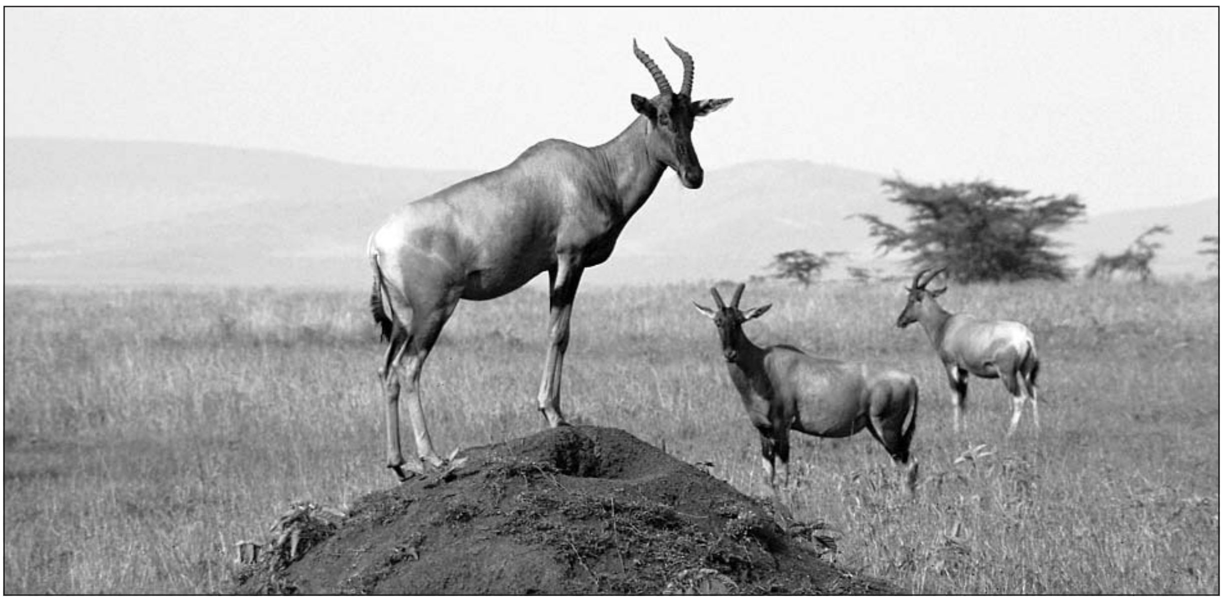
Termite Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Arthropoda
Subphylum: Uniramia
Class: Insecta
Subclass: Pterygota
Order: Isoptera (termites)
Geographical location: Every continent except Antarctica
Habitat: Majority of species inhabit tropical rain forests but many live in temperate and subtropical zones, deserts, or mountains up to an altitude of 2,500 meters (8,200 feet)
Gestational period: Varies but averages approximately two weeks
Life span: The primary queen and king may live to seventy years, although ten or twenty years is more common; workers and soldiers live from two to five years
Special anatomy: Isoptera means "equal wings"—adult reproductives have two oval-shaped pairs of overlapping wings of nearly equal length; small to medium-sized, very soft, usually light-colored bodies; thorax fused with the abdomen; workers have specialized mouthparts for chewing wood, while soldiers' mouthparts have been modified for fighting; except for reproductives, termites usually lack eyes

Many species are master builders, constructing elaborate nests of carton in trees with covered runways leading to the ground or mounds in the soil complete with ventilation shafts, towering chimneys up to 9 meters (29.5 feet) high, and even fungus gardens to supplement their cellulose diet. Although the architecture varies widely, most nests provide an inner chamber for the egg-laying queen and her king, and areas for brood chambers and food storage.

Life Cycle

Unlike insects such as butterflies, termites undergo incomplete or gradual metamorphosis. From the time they hatch, immature termites looks like pale, wingless, miniature versions of adults. To allow for growth, these nymphs molt periodically, shedding and then eating their outer skin. All nymphs start out the same. The correct balance among the castes appears to be maintained by bodily secretions



Termites, like ants, create large mounds for their colonies to live in. (Digital Stock) containing hormones that are transferred by licking, but the mechanism is not yet understood.

New colonies are usually formed when alates swarm during certain seasons. Workers prepare by digging tunnels to the surface, with exit holes and sometimes launching platforms. Once the alates leave, soldiers prevent them from returning. They are weak fliers and usually descend within a few hundred meters of the original nest. Wings are shed after landing. Females attract males by raising the abdomen and emitting a pheromone. Before mating, pairs locate a likely site for a nest and seal the entrance with fecal matter. The first batch of eggs is usually small. The king and queen take care of the eggs until there are enough older nymphs to take over. After a few years, the queen's ovaries and abdomen increase in size, and her egg laying accelerates. She may grow to 11 centimeters (4.3 inches) long and produce up to 36,000 eggs per day.

—Sue Tarjan

See also: Arthropods; Bees; Communication; Digestion; Digestive tract; Home building; Insect societies; Insects; Metamorphosis; Nesting; Wasps and hornets.

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TERRITORIALITY AND AGGRESSION

Type of animal science: Ethology
Fields of study: Ethology, invertebrate biology, zoology

Aggressive behavior and territoriality are common features of animals. Territories may differ in function across species, but general trends occur. Territoriality is best viewed as a means by which individuals maximize their own reproductive success rather than as a mechanism of population regulation.

Principal Terms

ADAPTIVE FUNCTION: the reason that a characteristic evolved by means of natural selection

CONSPECIFICS: members of the same species

DOMINANCE HIERARCHY: a social system, usually determined by aggressive interactions, in which individuals can be ranked in terms of their access to resources or mates

HOME RANGE: an area that an animal frequently uses but does not defend

POPULATION REGULATION: long-term stability of population size at a level that prohibits overexploitation of resources

RESOURCE-HOLDING POTENTIAL: the ability of an individual to control a needed resource relative to other members of the same species

STRATEGY: a behavioral action that exists because natural selection favored it in the past (rather than because an individual has consciously decided to do it)

TERRITORIALITY: the active defense of an area that is required for survival and/or reproduction

Any field or forest inhabited by animals contains countless invisible lines that demarcate territories of individuals of many different species. Humans are oblivious to these boundaries yet have quick perception of human property lines; other animals are equally oblivious to human demarcations. Most organisms, in fact, appear to attend only to the territorial claims made by members of their own species. If separate maps of individual territories could be obtained for each species in the same habitat and superimposed on one another, the resulting hodgepodge of boundaries would show little consensus on the value of particular areas. Yet basic similarities exist in why and how different species are territorial.

Causes of Territoriality

The existence of aggression and territorial behavior in nature hardly comes as a surprise. Even casual observations at a backyard bird feeder reveal that species that are commonly perceived as friendly can be highly aggressive. The observation of birds at feeders can lead to interesting questions concerning territorial behavior. For example, bird feeders usually contain much more food than any one bird could eat: Why, then, are aggressive interactions so common? Moreover, individuals attack conspecifics more often than birds of other species, even when all are eating the same type of seeds.

Aggressive defense of superabundant resources is not expected to occur in nature; however, bird feeders are not a natural phenomenon. Perhaps the aggressive encounters that can be observed are merely artifacts of birds trying to forage in a crowded, novel situation, or perhaps bird feeders intensify aggressive interactions that occur less frequently and less conspicuously in nature. While the degree to which aggression observed at feeders mirrors reality is open to question, the observation of a greater intensity of interactions between conspecifics definitely reflects a natural phenomenon. Members of the same species are usually more serious competitors than are members of different species because they exploit exactly the same resources; members of different species might only share a few types of resources. Despite the ecological novelty of artificial feeders, noting which individuals win and lose in such an encounter can provide valuable information on the resource-holding potential of individuals that differ in various physical attributes such as body size, bill size, or even sex. For organisms that live in dense or remote habitats, this type of information can often be obtained only by observations at artificial feeding stations.

Territorial defense can be accomplished by visual and vocal displays, chemical signals, or physical encounters. The sequence of behaviors that an individual uses is usually predictable. The first line of defense may involve vocal advertisement of territory ownership. One function of bird song is to inform potential rivals that certain areas in the habitat are taken. If song threats do not deter competitors, visual displays may be employed. If visual displays are also ineffective, then residents may chase intruders and, if necessary, attack them. This sequence of behaviors is common in territorial interactions because vocal and visual displays are energetically cheaper than fighting and involve less risk of injury to the territory owner.

It may be less obvious why fighting is a necessary component in territorial interactions for both territory owners and intruders. Without the threat of bodily injury, there is no cost to intruders that steal the resources of another individual. This would severely hamper an owner's ability to control an area. On the other hand, if intruders never physically challenge territory owners, then it would pay for all territory owners to exaggerate their ability to defend a resource. Thus, physical aggression may be essential. Animals do not frequently kill their opponents, however, so there must be something that limits violence. Various species of animals possess formidable weapons, such as large canine teeth or antlers, that are quite capable of inflicting mortal wounds. Furthermore, a dead opponent will never challenge again. Yet fights to the death are rare in nature. When they do occur, some novel circumstance is usually involved, such as a barrier that prohibits escape of the losing individual. Restraint in normal use of weapons, however, probably does not indicate compassion among combatants. Fights to the death may simply be too costly, because they would increase the chance that a victor would suffer some injury from a loser's last desperate attempts to survive.

Functions of Territory

Territories can serve various functions, depending on the species. For some, the area defended is only a site where males display for mates; for others, it is a place where parents build a nest and raise their offspring; for others, it may be an all-purpose area where an owner can have exclusive access to food, nesting sites, shelter from the elements, and refuge from predators. These different territorial functions affect the area's size and the length of time an area is defended. Territories used as display sites may be only a few meters across, even for large mammal species. Territorial nest sites may be smaller still, such as the densely packed nest sites guarded by parents of many colonial seabirds. All-purpose territories are typically large relative to the body size of the organism. For example, some passerine birds defend areas that may be several hundred meters across. Although all three types of territories may be as ephemeral as the breeding season, it is not uncommon for all-purpose territories to be defended year around.

The abundance and spatial distribution of needed resources determine the economic feasibility of territoriality. On one extreme, if all required resources are present in excess throughout the habitat, territory holders should not have a reproductive advantage over nonterritory holders. At the other extreme, if critical resources are so rare that enormous areas would have to be defended, territory holders might again have no reproductive advantage over nonterritory holders. If needed resources, however, are neither superabundant nor extremely rare and are somewhat clumped in the habitat, territoriality might pay off. That is, territorial individuals might produce more offspring than nonterritorial individuals.

Studies of territoriality raise more questions than biologists can answer. Researchers investigate how large an area an individual defends and whether both sexes are equally territorial. They seek to determine whether the territories of different individuals vary according to quality. The density of conspecifics may influence territoriality; on the other hand, territoriality itself may serve to regulate population size, although evidence suggests that this is an incidental effect.

All-purpose territories vary considerably in size, depending on the resource requirements of the individuals involved and the pattern of temporal variation in resource abundance. In some organisms, individuals only defend enough area to supply their "minimum daily requirements." In others, individuals defend a somewhat larger area—one that could still support them even when resource levels drop. In others, individuals defend territories that vary in size depending on current resource levels. For example, pied wagtails (European songbirds) defend linear territories along riverbanks that are about six hundred meters long during the winter. The emerging aquatic insects they consume are a renewable resource, but renewal rates vary considerably during the season. Rather than adjusting territory size to match the current levels of prey abundance in the habitat, wagtails maintain constant territory boundaries. This inflexibility persists even though territories that extend for only three hundred meters could adequately support an individual for about one-third of the season. In contrast, the territory size of an Australian honey eater varies widely during the winter. Nectar productivity of the flowers visited by honey eaters varies considerably during the season. By adjusting territory size to match changing resource levels, individual birds obtain a relatively constant amount of energy each day (about eighteen kilocalories).

Territorial Roles

In some species, only males are territorial. In other species, both sexes defend territories, but males defend larger territories than females do. In some mammals in which both sexes are territorial, males are aggressive only to other males, and females are only aggressive to other females. In these species, male territories are sufficiently large to encompass the territories of several females. Presumably, these males have increased sexual access to the females within their territories. Perhaps the most curious example of sex-specific territorial behavior is observed in a number of coral reef fish, in which all individuals in the population are initially female and not territorial. As the individuals grow older and larger, some develop into males. Once male, they engage in territorial behavior.

Within a species, significant variation in territory quality exists among individuals. Studies on numerous species have demonstrated a relationship between territory quality and an individual's resource-holding potential. For example, larger individuals tend to control prime locations more often than smaller individuals. In addition, possession of higher-quality territories often results in increased reproductive success. For some species, this occurs because individuals with better territories obtain mates sooner or obtain more mates than individuals with poorer territories. In other species, possession of superior territories increases the survival chances of the owner.

As the density of conspecifics increases, the ability of individuals to control territories decreases. In some species, the territorial system may break down completely, with all individuals scrambling for their share of needed resources in a chaotic fashion. In other species, the territorial system is replaced by a dominance hierarchy. All competitors may remain in the area, but their access to resources is determined by their rank in the hierarchy. For example, elephant seal males can successfully defend areas containing from eighty to a hundred females from other males. Very dense clusters of females, however (two hundred or more), attract too many males for one male to monopolize. When this happens, one male—usually the largest male—dominates the rest and maintains disproportionate access to females.

Territoriality undeniably has an adaptive function: to increase the survival and reproductive success of individuals. Territoriality can also have several possible incidental effects, one of which was once considered to be an adaptive function: serving as a means of population regulation. The reasoning behind this hypothesis is simple. The number of territories in a habitat would limit the number of reproducing individuals in a population and would thereby prevent overpopulation that could cause a population crash. Support for this hypothesis would include demonstration that a significant number of nonbreeding adults exist in a population. Indeed, for several species, experimental removal of territory owners has revealed that "surplus" individuals quickly fill the artificially created vacancies. In most of the species studied, however, these surplus individuals are primarily males. Population growth can be curbed only by limiting the number of breeding females, not the number of breeding males. Furthermore, the population regulation argument assumes that some individuals abstain from reproduction for the good of the population. If such a population did exist, a mutant individual that never abstained from reproducing would quickly spread, and its descendants would predominate in future generations.

Territoriality in the Field

Territoriality is typically investigated in the field using an observational approach. Initial information collected includes assessing the amount of area used by each individual, how much of that area is defended from conspecifics, and exactly what is being defended. It is relatively easy to discern the spatial utilization of animals. For many species, all that is required is capturing each individual, marking it for field identification, and

While many animals engage in aggressive behavior and may wound each other severely, fights to the death are rare in nature. (Digital Stock) watching its movements. For species that range long distances, such as hawks or large mammals, and species that are nocturnal, radio telemetry is frequently used. This methodology requires putting radio transmitters on the individuals to be followed and using hand-held antennas, or antennas attached to cars or airplanes, to monitor movements. For fossorial species (animals that are adapted for digging), animal movements are often determined by repeated trapping. This method involves placing numerous baited live traps above the ground in a predetermined grid.

Knowing the spatial utilization of an animal does not document territoriality. Many types of animals repeatedly use the same regions in the habitat but do not defend these areas from conspecifics. Such "home ranges" may or may not contain areas that are defended (that is, territories). Territorial defense can be readily documented for some animals by simply observing individual interactions. These data often need to be supplemented by experiments. Behavioral interactions might only occur in part of the organism's living space because neighbors do not surround it. For these individuals, researchers play tape-recorded territorial vocalizations or place taxidermy mounts of conspecifics in different locations and note the response of the territory holder. For other species, such as fossorial rodents, direct estimates of territory size cannot be obtained because aggressive interactions cannot be observed; as a result, territory boundaries must be inferred from trapping information. Regions in which only the same individual is repeatedly trapped are likely to be areas that the individual defends. This is an indirect method, however, and can be likened to watching the shadow of an organism and guessing what it is doing.

It is often difficult to determine exactly what an animal is defending in an all-purpose territory where organisms use many different types of resources. Which resource, that is, constitutes the "reason" for territorial defense? On the other hand, several resources may contribute in some complex way. For many species these things simply are not known. This uncertainty also complicates estimates of territory quality. For example, red-winged blackbirds in North America have been particularly well studied for several decades by different investigators in various parts of the species range. Males defend areas in marshes (or sometimes fields), and some males obtain significantly more mates than others. Biologists think that males defend resources that are crucial for female reproduction. Some males may be more successful at mating than others because of variation in territory quality. Yet the large number of studies done on this species has not yielded a consensus on what the important resources are, whether food, nest sites, or something else.

Theoretical investigations of territorial behavior often employ optimality theory and game theory approaches. Optimality theory considers the benefits and costs of territorial defense for an individual. Benefits and costs might be measured simply as the number of calories gained and lost, respectively. Alternatively, benefits might be measured as the number of young produced during any one season; costs might be measured as the reduction in number of future young attributable to current energy expenditures and risks of injury. For territorial behavior to evolve by means of natural selection, the benefits of territorial behavior to the individual must exceed its costs.

Game theory analyses compare the relative success of individuals using alternative behaviors (or "strategies"). For example, two opposing strategies might be "defend resources from intruders" and "steal resources as they are encountered." In the simplest case, if some individuals only defend and other individuals only steal resources, the question would be which type of individual would leave the most offspring. Yet defenders interact with other defenders as well as with thieves, and the converse holds for thieves. By considering the results of interactions within and between these two types of individuals, a game theory analysis can predict the conditions under which one strategy would "win" or "lose" and how the success of each type of individual would vary as the frequency of the other increases in the population. A complete understanding of territoriality involves not only empirical approaches in the field but also the development of testable theoretical models. Considerable advances have been made recently merging these two methodologies. Future investigations will no doubt include experimental control over resource levels that will allow definitive tests of predictions of alternative theoretical models.

Territoriality and Aggression

The importance of investigating any biological phenomenon might be measured by its contribution to understanding nature in general and humankind in particular. By these criteria, aggression and territoriality may be among the most important topics that could ever be studied. Among animals in general, some species are highly aggressive in defending their living space, and others ignore or tolerate conspecifics in a nearly utopian manner. Some animals are territorial during only part of the annual cycle, and some only in specific areas that they inhabit; others remain aggressive at any time and in any place. Thus, a main goal for researchers is to unravel the ecological and evolutionary conditions that favor aggressive behavior and territoriality.

Aggression and territorial behavior appear to have evolved in various organisms because, in the past, aggressive and territorial individuals outreproduced nonaggressive and nonterritorial ones. An implicit assumption of behavioral biologists is that animals other than humans do not interact aggressively because of conscious reasoning, nor are they consciously aware of the long-term consequences of aggressive acts. Should these consequences be detrimental, natural selection will eliminate the individuals involved, even if this means total extinction of the species. Humans are different. They are consciously aware of their actions and of the consequences of such actions. They need only use conscious reasoning and biological knowledge of aggressive behavior to create conditions that can reduce conflict between individuals and groups.

—Richard D. Howard

See also: Adaptations and their mechanisms; Communication; Competition; Ecology; Emotions; Ethology; Instincts; Mammalian social systems; Mating; Pheromones; Population fluctuations; Reproduction.

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THERMOREGULATION

Type of animal science: Physiology
Fields of study: Biophysics, physiology

Temperature regulation in animals is a process that may utilize either environmental or physiological sources of heat to maintain conditions conducive to life. By learning about temperature regulation, scientists have gained insights into interactions between animals and their environments or between the functional components of their bodies.

Principal Terms

CONVECTION: a transfer of heat from one substance to another with which it is in contact

COUNTERCURRENT MECHANISM: a heat exchange system in which heat is passed from fluid moving in

ECTOTHERM: an animal that regulates its body temperature using external (environmental) sources of heat or means of cooling

ENDOTHERM: an animal that regulates its body temperature using internal (physiological) sources of heat or means of cooling

HELIOTHERM: an animal that uses heat from the sun to regulate its body temperature

HOMEOSTASIS: the maintenance by an animal of a constant internal environment

HOMEOTHERM: an animal that strives to maintain a constant body temperature independent of that of its environment

OPTIMUM TEMPERATURE: the narrow temperature range within which the metabolic activity of an animal is most efficient

POIKILOTHERM: an animal that does not regulate its body temperature, which will be the same as that of its environment

THERMOGENESIS: the generation of heat in endotherms by shivering or increased oxidation of fats

Body-temperature regulation by animals is essential for life. The maintenance of life relies on the sum of all chemical reactions or metabolic activity in an organism. These reactions are facilitated by catalysts, substances not directly involved in a reaction as either a product or reagent but essential for accelerating the process or allowing the reaction to proceed under conditions compatible with life. For example, a reaction that, in a test tube, might require exceedingly high temperatures will proceed, if catalyzed, at normal body temperatures. Biological catalysts are complex proteins called enzymes. These are fragile molecules and are quite temperature-sensitive. If exposed to excessively high or low temperatures, they will be denatured and lose their functional properties.

Homeostasis is the maintenance of a constant internal environment, one suitable for proper enzymatic activity. Homeostatic mechanisms involve three components: a sensor (or receptor) that reacts to changes in environmental conditions, a coordinator (or integrator) that responds to information from the sensor, and one or more effectors (activated by the coordinator), which elicit appropriate, regulatory responses.

Temperature sensors are scattered throughout the bodies of most animals, but those specifically associated with temperature regulation in vertebrates (animals with backbones) are found in the hypothalamic region of the brain. Coordinators are found within the brain (or its equivalent in simpler animals), again in the hypothalamus of more advanced types. Effectors may be any structure capable of affecting temperature.

Animals generally function at temperatures between 4 and 40 degrees Celsius. Peak metabolic efficiencies, however, exist over a much narrower range, called the optimum temperature. This temperature varies by the animal and its habitat. Optimum temperatures often approach lethal limits, the highest temperature an animal can tolerate. This necessitates precise control of temperature in order to avoid exceeding those limits. Within lower temperature ranges, some animals can alter metabolic requirements in order to adapt to changing temperatures without sacrificing efficiency. This process, which involves complex biochemical and cellular adjustments, is called "temperature compensation." Animals that utilize metabolic mechanisms to maintain constant, relatively high body temperatures are often referred to as being "warm-blooded." Others, whose body temperatures are not regulated or are regulated primarily by behavioral means, are called "cold-blooded." That these terms are imprecise and irrelevant becomes obvious when one considers that the temperature of a desert-dwelling "cold-blooded" lizard or insect may often exceed that of any bird or mammal. On the other hand, the core temperature of some hibernating mammals may be reduced to being anything but "warm."

Most invertebrates (animals lacking backbones) as well as many fishes, amphibians, and some reptiles, do not regulate body temperatures; they are called poikilotherms. They monitor environmental conditions, attempt to seek out areas where temperatures are suitable, and avoid those where they are not. Their temperatures are essentially identical to environmental temperatures. If excessively high temperatures are unavoidable for more than short periods, death may occur. Low temperatures are seldom fatal (unless below freezing) but will result in diminution of metabolic functions, causing the animal to become torpid, or inactive. Since these animals are vulnerable, they will seek shelter, which is why insects, for example, are rarely encountered during colder months.

Ectotherms

Animals that regulate body temperatures fall into two categories. Those that utilize environmental sources of heat are called ectotherms (animals that "heat" their bodies using external sources). Those that utilize physiological temperature control mechanisms are called endotherms (animals that "heat" their bodies using internal sources). Since endotherms (birds and mammals) strive to keep temperatures constant, they may also be called homeotherms (animals that maintain constant temperatures). All regulators must invest considerable energy in the process. To minimize that expenditure, they utilize microhabitats in which regulatory mechanisms are not necessary. Ectotherms use behavior, enhanced by physical or physiological mechanisms, to take advantage of environmental conditions. A principal source of heat for most ectotherms is sunlight; temperature regulators that rely on the sun are called heliotherms (animals that "heat" their bodies using the sun). Lizards from temperate zones (areas with moderate and/or seasonal climates) are the most efficient ectotherms and may serve as models to illustrate the process. Tropical species, which live in constant, warm environments, tend to be poor regulators.

Sunlight and heat may be assimilated directly by basking lizards or indirectly by convection from sun-heated surfaces. Basking occurs when an animal exposes itself to sunlight by seeking unshaded perches. Position and posture are critical. Lizards will orient themselves in order to expose the greatest amount of surface to the sun. This involves a position in which the animal is broadside to the sun. Surface area is further enhanced by flattening the body dorsoventrally (top to bottom). Similarly, animals may absorb heat from the substrate. Lizards flatten themselves against a warm surface to maximize the area through which heat is assimilated. Area is critical in elevating temperatures, either by basking or convection, but does not increase proportionately with volume as animals increase in size. Thus, large ectotherms require disproportionately more energy and time to raise their temperatures than animals with similar proportions but smaller dimensions. This explains why the first animals to emerge in the spring or early morning tend to be small. Also, since dark colors absorb more radiation (heat and light), cold animals will stimulate pigment cells and are invariably much darker than those at optimum temperatures. That these mechanisms work effectively is illustrated by observations of active lizards at near-freezing temperatures at high elevations in the Andes of South America. When these lizards are captured, body temperatures of 31 degrees Celsius are recorded. In another study, lizards active at –4 degrees Celsius have been found to have body temperatures above 10 degrees Celsius. Some investigators have observed lizards, buried in sand during the night, emerging slowly, exposing only their heads. Since many lizards have large blood sinuses in their heads, it has been suggested that they can raise their body temperatures while minimizing exposure to predators. It is unlikely that this is effective, as heat gained would be rapidly lost to the substrate by convection. Only if the ground were warmer than air and only until body temperature reached that of the ground would this mechanism be operative.

In ectotherms, cooling is a much more difficult proposition. Without access to a source of "cold," ectotherms can do little more than minimize heat absorption. Coloration is lighter to increase reflection, orientation is toward the sun, posture involves lateral (side-to-side) compression, and animals will "tiptoe," lifting themselves away from warm substrates. If these are inadequate, animals must seek shelter. Many desert-dwelling lizards exhibit activity cycles that peak twice each day (morning and evening) to avoid cold nights and hot midday periods.

Endotherms

Endotherms use physiological effectors to raise or lower temperatures. If cold, they will generate heat (thermogenesis) by rapid muscular contractions (shivering) or increased oxidation of fats. Simultaneously, devices minimizing heat loss will be implemented. These include lowered ventilation (breathing) rates; since inhaled air is warmed during passage through the respiratory tract, heat is lost with each expiration. Also, superficial blood vessels narrow (vasoconstriction), reducing flow of warm blood to the skin, from which heat is lost by convection. Attempts to insulate skin are illustrated by "goose bumps." Though ineffective in sparsely haired humans, this reaction to cold is quite effective in mammals with thick body hair or fur. Muscles attached to hair follicles contract and draw hairs into an upright position, and the ends droop, trapping dead air between matted ends and skin. A fine undercoat in many species enhances the process. Dead air is an excellent barrier to heat flow. A similar device affecting feathers exists in birds.

When hot, endotherms keep muscular activity to a minimum, increase ventilation rates (panting), and expand superficial blood vessels (vasodilation). Rates of heat dissipation in some mammals are enhanced by sweating. Sweating and panting rely on evaporative cooling, the same principle involved in using radiators to prevent hot automobile engines from overheating. Endotherms adapted to hot climates produce concentrated urine and dry feces to conserve water, since much is lost in cooling.

Many of these mechanisms are surface-area related. Consequently, endotherms in hot climates, especially large species with relatively poor surface-to-volume ratios, often possess structures, such as elephant's ears, to increase area through which heat may be dissipated. On the other hand, endotherms occupying cold habitats are designed to minimize exposed surfaces. For example, arctic hares have short ears and limbs compared to the otherwise similar jackrabbits of warmer climes. In addition, cold-adapted endotherms may decrease rates of heat loss from poorly insulated appendages by means of countercurrent mechanisms. Heat from blood in arteries flowing into a limb is passed to venous blood returning to the body. This minimizes the amount of heat carried into a limb, whose surface-to-volume ratio is very high. It also functions to warm the returning blood, which prevents cooling of the body core. The appendages themselves are very cold; portions may even be at below-freezing temperatures. Actual freezing is prevented by special fats in the extremities.

Studying Thermoregulation

Specific methods vary according to the subject, approach, and discipline in question. Anatomy (study of structure), using both micro- and macroscopic methods, often centers on surface-related phenomena. For example, studies investigating the vascularization (blood supply) of whale flukes, whose physiology is difficult to study, have indicated that these are quite capable of dissipating heat and have led to the knowledge that these animals, even in cold water, because of their large size and poor surface-to-volume ratios, have potential problems with overheating. The role of blubber was reevaluated in this light and is now recognized as being one of fat storage with little to do with insulation. Furthermore, with new technologies in electron microscopy, anatomists have been able to describe, often for the first time, the complex structural components of organs (and even cells) that are active in thermoregulation.

Physiological studies of function are of two major types. One involves measurements of activity under different thermal regimes; for example, patterns of locomotion or digestion (involving specifically neural and muscular or neural, muscular, and glandular entities, respectively) may be observed at different temperatures. Often, these include observations of performance on treadmills or of rates at which food items are processed in controlled laboratory settings. On a different scale, metabolic activity itself might be linked to temperature by measuring rates of oxygen consumption in special metabolic chambers or utilization rates of products necessary for particular chemical reactions. These types of investigations have led to the determination of optimum and lethal temperatures in many species.

A second type of physiological study deals with actual thermoregulation. The ability to monitor body temperatures continuously, even in small animals, by means of radiotelemetry has made possible whole series of experiments in which animals' thermal responses to induced or natural conditions can be evaluated. Investigations of this type have provided insights into, for example, adaptive hypothermia (significantly reduced body temperatures) in small endotherms such as bats and hummingbirds. These species drastically reduce their core temperatures when inactive in order to conserve energy otherwise rapidly lost as heat through their relatively large surface areas.

Since laboratory work often fails to simulate natural conditions adequately, observations of animals in nature have been instituted. These seek to evaluate thermoregulation in the contexts of ethology (the study of behavior) and ecology (the study of organisms' relationships with their environments). These types of studies frequently entail prolonged observations until patterns of behavior or habitat use emerge and can be quantified and evaluated. The use of rapid-reading thermometers or implanted radiothermisters facilitates understanding of the often-subtle modifications in thermoregulatory behavior or microhabitat use characteristic of many animals. Relating recorded temperatures to changes in posture, position, orientation, activity level, and ambient temperatures of substrate and air has, for example, led to an appreciation of how efficiently some ectotherms regulate temperature and the complexity of the mechanisms involved.

Applications of Thermoregulation Research

Long restricted by concepts of "warm-blooded" versus "cold-blooded" animals, investigators did not begin in-depth explorations of thermoregulation until the twentieth century. Most early efforts grew out of medical studies dealing with dynamics of human temperature regulation, especially in the context of pathological states associated with fever or trauma-induced hypothermia. Monitoring these conditions led to an appreciation of how complex temperature regulation is and how many of the body's systems are involved. These studies, in turn, led to investigations of similar mechanisms in animals. Initially, most dealt with laboratory animals, but pioneering investigations into thermoregulation by animals in natural habitats soon opened whole new vistas. These studies were subsequently extended to "cold-blooded" species, which in turn led to an appreciation of how effective behavioral temperature regulation could be. In the 1970's, suggestions that at least some dinosaurs may have been homeotherms stimulated further interest in this field of study.

Most heat exchange with the environment occurs through skin or respiratory systems; muscular systems generate heat as a by-product of contraction; digestive and urinary systems regulate elimination of wastes, which influences retention or loss of heat-bearing water; cardiovascular systems transport heat; and nervous and endocrine systems regulate the entire complex. In addition, all cells require a proper thermal environment and may affect heat production by altering rates of oxidative metabolism. Therefore, a more complete understanding of thermoregulation has enhanced scientists' awareness of both normal and pathological functions in most body systems. Specific medical applications of these studies include induced hypothermia during surgery-related trauma and treatment of accident-related hypothermia using mechanisms first observed under natural conditions in animals.

Studies of temperature-regulating mechanisms, both behavioral and physiological, have also provided insights into relationships between animals and their environments. Thermoregulatory needs have been used to explain behavioral and ecological phenomena for which causative agents were previously unknown. From a practical perspective, this knowledge is useful in developing management tools to sustain disrupted or endangered ecosystems. Appropriate techniques must be developed with a thorough knowledge of the dynamics in any given system, and this must be based on biological criteria rather than human perceptions. For example, reforested areas have often been managed as crops, with all the attendant problems of monocultures (areas cultivated for plants of only one species). Among these is the lack of biodiversity (variety of life-forms). When efforts began to take into consideration microhabitat requirements, often related to temperature regulation, varieties of plants—many with little or no commercial value in themselves—were planted. This resulted in managed areas becoming capable of supporting many different species.

Finally, a more complete knowledge of structures related to thermoregulation has been applied by paleontologists (scientists who study fossils) to the study of dinosaurs. Long thought to be "sluggish," lizardlike ectotherms, dinosaurs are now thought by many investigators to have been more like mammals and birds in their physiological capabilities. This image is more in tune with their domination of the earth for some hundred million years.

—Robert Powell

See also: Cold-blooded animals; Ethology; Habitats and biomes; Kidneys and other excretory structures; Metabolic rates; Osmoregulation; Warm-blooded animals; Water balance in vertebrates.

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TIDEPOOLS AND BEACHES

Type of animal science: Geography
Fields of study: Marine biology, oceanography, zoology

Beaches are muddy, sandy, or pebbly shores of oceans or lakes. They protect these bodies of water and are esthetically pleasing recreation sites. Tidepools are pools of sea water left behind when tides ebb. Their presence is due to beach and coast topography.

Principal Terms

BACKSHORE: the horizontal beach part farthest from the ocean

BARRIER ISLANDS: islands seaward of estuaries, parallel to the shore and separated from it by a lagoon

DELTA: an accumulation of sediment at a river mouth

ESTUARY: a stream-fed bay

FORESHORE: the sloping beach part closest to the ocean, which is continually altered by waves, tides, and longshore currents

INTERTIDAL FLAT: a beach part located in shallow water just seaward of the foreshore, made of mud and/or sand, holding burrowing animals

LONGSHORE CURRENT: a current parallel to a seashore, from shoreline through breakers, created by waves approaching the coast at a small angle to the shore

TIDE: the regular rise and fall of sea level due to gravitational fields of the moon and sun

TIDEPOOL: a pool of water originally or permanently composed of water left behind at ebb tide

The term "beach" indicates the muddy, sandy, or pebbly shore of a body of water such as an ocean or lake. Most beaches are located around earth's seacoasts. They are composed of mud, sand, and pebbles, sediments that accumulate in arrangements and forms dependent on coastal actions, sediment sources, and rates of sediment deposition. There are three main beach types: sediment strips edging rocky coasts; borders of sediment accumulations along rivers; and sediment regions parallel to coasts and associated with barrier islands.

At most times a beach has a seaward, sloping foreshore lacking vegetation and a landward, horizontal backshore that can hold some hardy plants. Near the land's end, waves rise and break along the foreshore. Sediment is moved both along this shore and perpendicular to it. During storms, waves erode beaches, moving sediment back into oceans. This temporarily leaves only foreshore. In the ensuing calm, waves move sediment landward again and rebuild the beaches.

Due to very rapid changes in wave sizes, the appearance and sediment types of a foreshore often change significantly from day to day. Backshores, normally unaffected by waves, are altered most by winds. There are also variations in beach form along and perpendicular to the beach shoreline. Most common are undulating foreshores that vary from beach to beach and time to time. Beach sands in areas having mild climates are mostly quartz and feldspar. In tropical regions, beaches are often made of calcium-containing remains of marine organisms.

Natural Forces and Beaches

Beaches develop along coastlines due to natural processes including waves, longshore currents, tides, climate, and gravity. Waves, in their contin-

Currents That Affect Beaches

Longshore currents are those parallel to a sea shore and extending from the shoreline through the breakers. They occur because waves approach coasts at a small angle and bend in the shallows. The speed of a longshore current is related to wave size and angle of approach to a shore. During quiet weather, longshore currents move at under half a mile per hour, but during storms they can move ten to twelve times that speed. The combined actions of waves and longshore currents transport a lot of sediment along shallows bordering a shore. Longshore currents move in either direction along a beach, depending on the direction of wave approach, itself a result of wind direction. Thus, waves suspend sediment and longshore currents transport it along beaches.

Tides, the regular rise and fall of sea level due to the gravitational fields of the moon and the sun, cause daily changes in ocean levels of one to fifty feet. Tidal currents transport large amounts of sediment and erode rock, and tidal rise and fall distributes wave energy across shores by changing water depth. In estuaries, tides create the speeds needed to move sand. On open coasts, that is, on beaches, tides do not move the water fast enough for sediment transfer. However, the rise and fall of tides along open coasts indirectly affect sediment movement, because their landward movement or retreat causes shorelines to move. This changes the region where waves and longshore currents operate. Beach slope is also crucial, with gently sloped beaches having the largest shoreline changes during tide cycles.

ual beachward motion, vary in size at different coastal areas and different times. They interact with the ocean bottom as they move into shallows, suspending sediment and moving it landward. Large waves suspend sediment from deeper water and move larger sediment particles than small waves. For example, small waves only move sand, while large waves can even move boulders. During storms, large waves return beach sediment to deep water. Waves also erode coastal bedrock by abrasion from their suspended pebbles and larger rock fragments.

The important effects of climate on beach development begin with rainfall, which creates runoff streams, transports sediment to seacoasts, and causes differences in the volume and types of sediment sent to coasts in different world areas. Temperature is also quite important because it causes weathering of coastal sediment and rock. This is most extensive in cold areas, where water freezes in rock cracks, causing their fragmentation. Wind action is also important because of its relation to wave size. Coasts with fairly constant, strong winds have high-energy waves. Onshore winds around the earth's coasts produce sand dunes wherever sediment is available and can accumulate. Gravity acts indirectly in wind and wave production, and directly in the down-slope movement of sediment.

Most beaches cannot support large plants, though some hardy plants are found on their backshores. Near beach waterlines, organic matter such as decaying seaweed can be found. However, a bit further seaward, mud and sand flats (intertidal flats) hold burrowing animals including worms, clams, mussels, and burrowing shrimp. The worms ingest sediment and eat the organic matter it holds. Other burrowing organisms, such as clams, use tubes to reach into the water above them to filter out food when they are covered by the tide. Crustaceans and starfish also use intertidal flats to seek prey.

Intertidal flats are important feeding grounds for wading birds such as sandpipers, terns, and plovers. In temperate climates these birds remain all year. Hundreds of thousands of them also make seasonal migrations to specific beaches located between their summer and winter habitats. During such migrations the birds rely on intertidal flats for food along the way. For example, hundreds of thousands of sandpipers stop, each July and August, on the intertidal flats of Canada's Bay of Fundy, each eating tens of thousands of burrowing shrimps before they migrate to South America.

Tidepools

Tidepools are pools of various types and sizes originally or permanently composed of water left behind by the ocean when the tides go out. Their presence is due to the topography of beaches and coasts. Some tidepools occupy beach crevices or fissures with seaward ends open to the sea and landward ends abutting cliffs, caves, or boulders. Others occur in rocky basins with high rims on the seaward side. The rims hold back water when the tide ebbs. Seaweed lines a tidepool's walls or bottoms. Sponges, hydroids, anemones, sea slugs, insects, mussels, fishes, jellyfish, and starfish live in many of the pools, either temporarily or permanently.

Fish and jellyfish may become temporary tidepool residents when swept into them by tides. Almost as suddenly these visitors, who enter the pools to seek prey, leave with one of the next few tidal cycles. Permanent tidepool inhabitants include seaweeds. The seaweed species depend on the position on the beach of a given tidepool, the acidity or alkalinity of the pool, and its salt content. Tidepools high on a beach contain only plants. This is because they are almost entirely isolated from the sea and so their temperatures are too high to allow animal survival. Even plants may have some trouble living in such pools.

Lower on the beach, tidepools provide far more stable conditions because they are connected to the ocean, filling and only partly emptying during tidal cycles, so both plants and animals live in them. Yet they, too, are affected by the duration of the ocean's presence or absence, and the inhabitants of a pool in the middle of the foreshore are very different from those of low-foreshore pools, which are separated from the sea only very briefly.

Other Types of Beach Sites

Beaches form along depositional coasts, that is, wherever sediment accumulates due to longshore currents, waves, and tides. Locations other than long, open coastal areas are associated with river deltas, estuaries, lagoons, and barrier islands. Deltas are accumulations of sediment at river mouths. They vary in size and shape. However, all require that more sediment is deposited at a river mouth than is carried into the ocean, and that shallow sites are available for sediment accumulation. Delta size is proportional to the size of the river involved and delta shape is dictated by the strengths of the river, tide, and waves. Deltas can be river-dominated (such as the Mississippi River Delta) when waves and tides do not affect water discharge or accretions of sediment. Such deltas are irregularly shaped. A wave-dominated delta experiences sediment erosion that simplifies and smoothes its edges. Tide-dominated deltas are funnel shaped.

Waves may erode coastal bedrock and eventually destroy beach habitats altogether. (Corbis)

Irregularly shaped depositional coasts are rich in stream-fed bays, or estuaries. They receive a lot of sediment due to coastal runoff. Seaward of estuaries are sandy barrier islands that parallel the shoreline, formed by waves and longshore currents. The islands are separated from the mainland by lagoons, which are long, narrow bodies of water. Barrier islands contain well-developed beaches, dunes, and tidal flats on their landward sides.

Beaches are very important land features. They serve to protect coastlines from storms and erosion. In addition, they are ecologically important, serving as homes, in intertidal flats and tidepools, for useful and sometimes rare flora and fauna.

—Sanford S. Singer

See also: Ecosystems; Food chains and food webs; Habitats and biomes; Lakes and rivers; Marine biology.

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TIGERS

Type of animal science: Classification
Fields of study: Anatomy, conservation biology, genetics, zoology

Tigers are carnivorous mammals which are the largest members of the Felidae family. They are an endangered species in all their habitats, and three species became extinct in the twentieth century.

Principal Terms

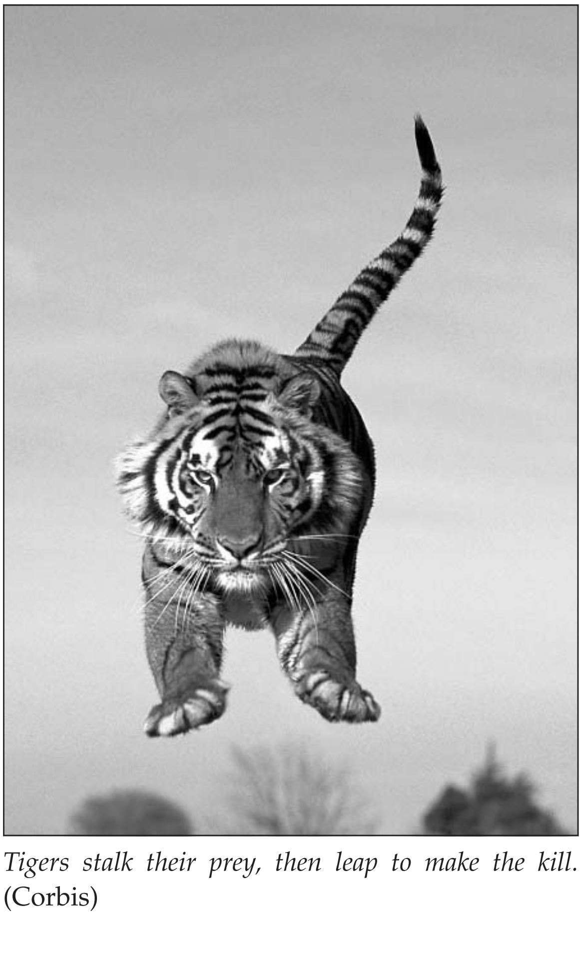
ALLELES: alternate forms of genes
DIGITIGRADE: walks on toes
FLEMEN: lip movement when cats detect an unusual scent
PUGMARKS: pawprints
SAGGITAL: bony skull top

The first tigers were members of the Felidae family of big cats that lived in northern Asia during the Late Pleistocene epoch. They migrated south and east and evolved into specific types of larger tigers according to their habitats. The ancient saber-tooth tigers were not ancestors of modern tigers. Three of the eight tiger subspecies, Bali, Caspian, and Javan, became extinct during the twentieth century.

Anatomy

Tigers range in weight according to their subspecies and gender. Sumatran male tigers are the lightest, weighing 110 kilograms (250 pounds). Females weigh approximately twenty kilograms less. Siberian male tigers weigh as much as 225 kilograms (500 pounds). The heaviest known tiger weighed 465 kilograms (1,025 pounds). From head to the base of the tail, tigers measure from 1.4 to 2.8 meters (4.5 to 9 feet) long, and their tails are from 90 to 120 centimeters (3 to 4 feet). They use their tails to balance and to communicate.

Tiger skulls have a big saggital crest which anchors a large jaw muscle. Tigers' vertebra and joints are flexible. Their hind legs are longer than their front legs, providing impulsion and assisting leaping when they are chasing game. They have five toes on their front paws and four toes on their hind paws. Each toe has a retractable claw which is 80 to 100 millimeters (3 to 4 inches) long and helps them restrain prey and climb trees.



Tigers stalk their prey, then leap to make the kill. (Corbis)

Mature tigers have thirty teeth. The canine teeth are 75 to 90 millimeters (2.5 to 3 inches) long. Tigers have triangular, erect ears set atop broad skulls, with their eyes positioned on the front of their face. Tigers' eyes have reflecting retinas which enable excellent night vision. Tigers' sense of smell is also acute; they can distinguish different animals by smell and exhibit the flemen response.

Tigers have nineteen pairs of chromosomes, which determine genetic patterns. Their coats are colored shades of orange, with black or brown stripes of varying widths and lengths and white accents around the eyes, ruffs, and other body parts. Rarely, Bengal tigers with the two necessary alleles are born with a white foundation coat and blue eyes. They are not albinos or a separate subspecies. Tigers' stripes vary according to subspecies, with Sumatran tigers having the most and Siberian tigers having the fewest. Each tiger's stripes are unique and function as camouflage. Fur thickness varies with seasonal changes and geography. Siberian tigers have almost twice the number of hairs per square centimeter than Sumatran tigers.

Tiger Facts

Classification:
Kingdom: Animalia
Subkingdom: Metazoa
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Subclass: Eutheria
Order: Carnivora
Suborder: Feloidea
Family: Felidae
Genus and species: Panthera tigris
Subspecies: P. t. tigris (Bengal), *P. t. altaica* (Siberian), *P. t. amoyensis* (South Chinese), *P. t. balica* (Balinese), *P. t. corbetti* (Indochinese), *P. t. sondaica* (Javan), *P. t. sumatrae* (Sumatran), *P. t. virgata* (Caspian)
Geographical location: Asia, specifically India, Thailand, Manchuria, China, and Indonesia
Habitat: Jungles, forests, tundra, mountains, and swamps
Gestational period: 3.5 to 4 months
Life span: Up to fifteen years in the wild, up to twenty years in captivity
Special anatomy: Sharp canine teeth, saggital crest

Behavior

Tigers are solitary, preferring to hunt alone. A male tiger's territory averages twenty-six to seventy-eight square kilometers (ten to thirty square miles), depending on the availability of prey. Some Siberian tigers roam territories of 1,036 square kilometers (400 square miles). Tigers' territories often overlap, with several females sharing territorial space with one male. Tigers scratch on trees, leave fecal droppings, and spray urine to mark their territory. Male tigers occasionally fight. Tigers have several vocalizations to communicate aggression and receptiveness to other tigers.

Females attain sexual maturity at age three and males at age four. After a four-month gestation, females have litters of two to five cubs which are born blind and are vulnerable to predators such as pythons. The cubs drink their mother's milk for two months, then feed at her kills until they are about two to three years old and capable of hunting alone.

Tigers can catch and kill prey as large as 160 to 900 kilograms (440 to 2,000 pounds). They stalk and ambush ungulates, knocking prey to the ground and biting the neck or throat to sever the spinal cord or suffocate the animal. Tigers can consume twenty to twenty-five kilograms (sixty to seventy pounds) of meat daily. They drag carcasses into vegetated areas and gorge on a kill, then fast. Tigers also eat termites and snakes. Some tigers, especially in the Sunderbans river delta of India and Bangladesh, have attacked and killed humans.

Conservation

Adult tigers are hunted by poachers for their hides, bones, teeth, and body parts or for sale to exotic pet traders. Much of their jungle habitat has been destroyed during wars or for agricultural use. As a result, only about five thousand to seven thousand tigers are alive in the wild. Authorities estimate that an equivalent number are kept as exotic pets in North America and in zoos, sanctuaries, and circuses. Tiger censuses have been taken by counting pugmarks in known tiger habitats.

In captivity, tiger hybrids include ligers, the hybrid of lion fathers and tiger mothers, and tigons, produced by tiger fathers and lioness mothers. Conservation breeding programs are aspiring to preserve and increase the tiger population.

—Elizabeth D. Schafer

See also: Breeding programs; Cats; Cheetahs; Endangered species; Fauna: Asia; Jaguars; Leopards; Lions; Mountain lions; Wildlife management.

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TOOL USE

Type of animal science: Behavior
Field of study: Ethology

Tools extend an animal's ability to interact with or modify its environment. Most of these interactions involve obtaining food, but animals are known to use tools in many different ways.

Principal Terms

ECHOLOCATION: the ability of animals to locate objects at a distance by emitting sound waves which bounce off an object and then return to the animal for analysis

ECTOPARASITE: a parasite, such as a tick, that lives on the external surface of the host

ETHOLOGY: the study of an animal's behavior in its natural habitat

INSIGHT LEARNING: using past experiences to adapt and to solve new problems

PHEROMONE: a hormone produced by an animal and then released into the environment

PREDATOR: an organism that kills and eats another organism, generally of a different species

PRIMATES: a group of mammals including apes, chimpanzees, monkeys, humans, lemurs, and tarsiers

In general, a tool is considered to be something which is not an integral part of an animal's body but is used by the animal to accomplish a specific task. For example, a lobster may use its claw to crack open shells; however, since the claw is a normal appendage of the lobster, it is not considered to be a tool. When humans use a similar object, a nutcracker, to open shells, the nutcracker serves as a tool. It is difficult to define tools accurately. Examples of tools acceptable under the definition of one scientist may not meet the criteria set down by another investigator. Some scientists expand the definition of tool use to include specialized structures some animals use to extend their capability to locate and capture prey. These capabilities might include echolocation or sonar, electromagnetic fields, and specialized cells used for feeding such as the cnidocytes used by jelly fish. Other scientists consider products produced by an organism to be used to capture food as tools. Under this definition, a spider's web can be considered to be a tool.

Quite often, objects taken directly from the environment, such as stones or sticks, are used as tools without further modification by the animal. Other times, the object may be modified by actions such as stripping the leaves from a stick prior to use. Tools allow the user to complete a task more easily or to accomplish a task that may not have been possible without the advantage provided by the tool. The size, shape, and even texture of tools varies across the animal kingdom. Some animals use trees as tools and others use grains of sand. Some fish use spurts of water as tools. In addition to capturing or obtaining food, tools are also used in grooming, for defense, or even as protection from the elements. Thus, animals that use tools are actively interacting with and even modifying their environment.

Sticks and Stones Used as Tools

Many different species of animals, including insects, fish, birds, mammals, and primates, are known to use tools in some way during their everyday activities. While many different types of tools are used in the animal kingdom, the stick is a common and readily available tool. The use of sticks as tools has been well documented in non-human primates, such as chimpanzees, apes, and orangutans. Primates often use insight to solve a problem using tools and the young learn to use tools from either observing or being taught by the adults. A classic example of insight learning leading to multiple tool use in chimpanzees was shown by Wolfgang Köhler, an early twentieth century psychologist. Chimpanzees held in captivity were offered food that had been placed beyond their normal reach. When boxes and sticks were added in the enclosure, the chimpanzees stacked the boxes, climbed them, and then used the sticks to knock down bananas that were hanging overhead. If one stick was not long enough, they would connect them together.

Orangutans and chimpanzees will strip the leaves from a stick and then use it to probe into the nest of insects such as ants or termites. When the stick is removed from the nest, the insects crawling over it can be eaten. Leaves themselves have been used by chimpanzees to gather water for drinking. Birds, too, use sticks to probe for insects and to remove them from crevices in the bark of trees. Some birds, the Galápagos woodpecker finch for example, will use their bill to trim and modify the twig before using it as a probe. Pacific island crows use their beaks to modify sticks as well as leaves before using them as probes. In the absence of sticks or leaves, some animals will use cactus spines as probes. Elephants use trees and sticks in various ways. They will rub against a tree or they may pick up a stick with their trunk to scratch. They have been observed to use tree trunks as levers and to use sticks to remove ectoparasites. When monkeys throw sticks and rocks, they are using these objects as tools for defense.

Stones are another common tool. Sea otters use stones in two different ways. Some otters will carry stones with them when they dive and use the stone as a hammer to free a tightly adhered abalone from a rock. While floating along the surface on their backs, otters use stones to crack open the shells of abalone or of bivalves such as clams, mussels, or oysters, which they also pluck from under the water. Otters may use bottles floating in the water to crack shells. Birds use stones in a similar way. Egyptian vultures pick up stones in their beaks and use them in a pecking fashion, like a hammer, to crack open an ostrich egg. If this method fails, they will fly at the egg while clasping the stone in their talons. Mongooses also use rocks to crack eggs. Other birds, such as eagles, gulls, and crows, drop shelled animals such as turtles onto the rocks to crack their shells. Vultures are known to drop bones of prey onto rocks to crack them open and expose the marrow. Chimpanzees use stones to crack open nuts, analogous to humans using a hammer and anvil. Even spiders use stones as tools. The trap-door spider, *Stanwellia nebulosa*, uses a stone as a defensive tool. If forced to retreat when being attacked, the spider uses a stone to close off its burrow behind it.

Using Traps to Catch Prey

Traps are one example of animals using a tool to ambush and capture prey. When a predator is an ambusher, it lies in wait for another animal to happen upon its territory, and then the predator strikes. This technique has been especially perfected by the ant lion. The ant lion is the larval form of hundreds of species of insects in the order Neuroptera, family Myrmeleontidae. Using a series of circular and backward body movements combined with a quick side-to-side motion of the head, the ant lion digs into sandy soil, forming an inverted, cone-shaped impression. When an ant or a small insect crawls along the margin of the cone or happens to fall over the edge, the ant lion vigorously begins to throw grains of sand out of the bottom of the pit. This causes the prey to fall deeper into the pit and into the grasp of the ant lion's two large mandibles. The ant lion thus has used the method of tossing sand grains as a tool to capture food. Natural selection will favor the gene pool of those individuals with the greatest ability to move and throw quantities of sand quickly.

Sea otters use stones as tools to open tasty clams and mussels. (PhotoDisc)

Other Tools

In Japan, one species of crow uses a very different tool, a car. It has been reported that these crows use cars as nut crackers by placing the nut on the road and, after a car has run over it, retrieving the nut meat. If the car should miss hitting the shell, the crow may try again.

Humans are not the only species to use tools for fishing. Some green herons are known to drop objects into the water to attract fish looking for food. The herons then consume the curious fish. The archer fish uses jets of water shot from its mouth to knock insects off overhanging branches and into the water. Some scientists do not view this as a tool because the water passes along a specialized region of the mouth. However, it is similar to using a bow and arrow to subdue prey from a distance. Octopuses use water shot from their siphon system as a broom to clean the exoskeletons of eaten invertebrates from its den. An octopus may also use the jet of water to modify the size of the den. Another group of animals that uses a form of liquid tool belongs to the spider family, Scytodidae. These spiders shoot sticky material from modified venom glands to entangle their prey.

Spiders use their webs as tools in various ways. Those species of spiders that construct webs make them with silk produced from modified appendages called spinnerets. Webs are used to ambush animals that happen to enter into them. Some spiders strum their webs and use them as tools for communicating. Others may spin a long single strand of silk that they use as a drag line to find their way back or as a safety line to catch themselves. In some species, young spiders make silk parachutes which trap the air currents and allow them to be dispersed far from the nest. Spiders of the genus *Mastophora* spin a single thread, on the end of which is a sticky globule. By suspending the thread from one leg, the spider uses the web to "fish" for male moths, which are attracted to the sticky globule containing chemicals similar to the pheromones produced by female moths to lure males for mating.

The jellyfish and the hydra, two members of the phylum Cnidaria, have specialized cells, cnidocytes, concentrated on the surface of their tentacles. Inside these cells is an organelle, the nematocyst, which contains a thread. The nematocyst is stimulated to discharge when prey are near to it. This thread may have a barb on its tip that will penetrate the body surface of the prey, or it may be a lasso that wraps around the prey. The prey is then pulled into the digestive cavity of the cnidarian.

Sonar

Bats and dolphins are two good examples of animals that use echolocation to locate prey. Since sound waves can travel over great distances, the prey can be well beyond the predator's immediate area. The objects do not need to be large in order to be detected. Bats are able to locate mosquitoes. By analyzing the sound waves returning after bouncing off an object, the bat knows which objects are moving and which are stationary. The moving objects represent potential prey. Some potential prey, moths, have evolved a way to detect that they are being tracked by a bat. Thus, they are able to take evasive action and seek shelter near a stationary object such as a tree, or by landing on the ground. In a similar manner, dolphins use a series of high-frequency clicks to track fish. However, the fish, unlike the moths, are often not aware that they are being followed.

—Robert W. Yost

See also: Beaks and bills; Displays; Ethology; Grooming; Intelligence; Learning.

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TRICERATOPS

Types of animal science: Classification, evolution
Fields of study: Anatomy, ecology, evolutionary science, paleontology, systematics (taxonomy)

Triceratops *was a quadrupedal, three-horned herbivore that lived in the western United States at the end of the Cretaceous period and had an ecological role similar to that of the rhinoceros today.*

Principal Terms

DENTAL BATTERY: unit of teeth in the upper and lower jaws consisting of the cutting teeth and the rows of replacements below them

FRILL: elaborate crest at the back of the skull that was used for visual display but not for protection

OCCIPITAL CONDYLE: ball-shaped bone that connected the back of the skull to the fused upper vertebrae of the spine

PREDENTARY BONE: keeled and pointed bone that terminated the lower jaw

ROSTRAL BONE: keeled and pointed bone that terminated the upper jaw

STEGOSAURS: quadrupedal, herbivorous dinosaurs with vertical bony plates arranged along their backbones

Triceratops became the first genus of horned dinosaur known to science when its skull was described by Othniel C. Marsh in 1889. The remains of its horns were originally attributed to the high-horned bison (*Bison alticornis*), and its occipetal condyle was originally named *Ceratops montanus*. In his preliminary description of the skull, Marsh named its owner *Ceratops horridus* and felt it was related to the stegosaurs. After the skull had been cleaned, Marsh changed the name to *Triceratops horridus*. Thirteen species of *Triceratops* have been described, but only one (or possibly two) species actually occurred in nature. *Triceratops* lived in western North America at the end of the Cretaceous, between 68 and 65 million years ago.

Characteristics

The most characteristic feature of the animal was its large, V-shaped head which terminated in an elongate frill. The skull can be more than 6 feet long (2.2 meters). Only whales have larger skulls. The frill allowed an animal to recognize members of the same species as well as members of the opposite sex. Since *Triceratops* had color vision, the frill was probably pigmented, and its ornamentation was designed for visual display and not for protection or to serve as a point of attachment for the jaw muscles. The head bore three horns that functioned in display, ritual combat, and protection from predators. One short horn arose over the nose, and two others, the longest, arose over the eyes. Males had large, erect horns while females had smaller, somewhat forward-pointing horns. The large number of skulls that have been found indicates that *Triceratops* was an abundant, gregarious species.

No complete skeletons are known. A composite, presumably female, skeleton on display at the Science Museum of Minnesota is 26 feet (7.9 meters) long and 9 feet, 7 inches (2.9 meters) high. With a weight of 8.5 metric tons (9.4 tons), *Triceratops* was three times heavier than a rhinoceros. The shin bone (fibia) was notably shorter than the thigh bone (femur). The size relationship between these two bones is the reverse of what is seen in animals that are fast runners. Evidence from ceratopsian trackways and the anatomy of its shoulder (the hind legs were located directly below the hips while the forelimbs sprawled out-

Image Not Available

ward and were not located below the shoulders) also indicates that *Triceratops* was rather slow. Its running speed has been estimated at about 4.2 kilometers per hour (2.6 miles per hour).

—*Gary E. Dolph*

See also: *Allosaurus*; *Apatosaurus*; *Archaeopteryx*; Dinosaurs; Evolution: Animal life; Extinction; Fossils; Hadrosaurs; Ichthyosaurs; Paleoecology; Paleontology; Prehistoric animals; Pterosaurs; Sauropods; Stegosaurs; *Tyrannosaurus*; Velociraptors.

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Triceratops Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Reptilia
Subclass: Dinosauria
Order: Ornithischia (bird-hipped dinosaurs)
Suborder: Ceratopsia (beaked dinosaurs)
Family: Ceratopsidae (horned dinosaurs)
Subfamily: Chasmosaurinae (horned dinosaurs with long frills)
Genus and species: Triceratops horridus
Note: A number of competing classification schemes exist and will probably continue to do so in the future.

Geographical location: All large, horned, frilled dinosaurs were confined to western North America from present-day Denver, Colorado, to southern Alberta, Canada, between the western interior seaway to the east and the forming Rockies to the west

Habitat: Restricted to the arid, coastal, lowland plain

Gestational period: Although no eggs have been found, *Triceratops* must have been an egg layer; the frequency of egg laying, the time it took for the eggs to hatch, and the reproductive life span of the adults are unknown

Life span: Based on mammalian models, sexual maturity would be reached after ten years and the life span was probably in excess of one hundred years

Special anatomy: Rostral and predentary bones combined to give the snout its parrotlike appearance in side view; the occipital condyle projected off the back of the skull and gave the head a high degree of movement; each tooth had two roots, with the crown of each lower tooth in the dental battery fitting into the notch formed by the two roots of the tooth above it

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TUNDRA

Types of animal science: Ecology, geography
Fields of study: Ecology, environmental science, ethology, ornithology, wildlife ecology, zoology

The tundra, a characteristically treeless area of shrubs and patchy grass, lies above 60 degrees north latitude and covers about 10 percent of the earth's surface. It is inhabited by large numbers of a small variety of animals.

Principal Terms

CONIFEROUS FOREST: great northern forests, mostly evergreen, that end where the tundra begins
HERBIVORES: plant-eating animals
LICHENS: organisms formed by algae and fungi that are a source of food for tundra animals
MIGRATORY ANIMALS: animals that move from one place to another for feeding or breeding
PERMAFROST: a permanently frozen layer below the earth's surface
TEMPERATE REGION: a mild climatic area between the Tropic of Cancer and the Arctic Circle

From March to September, the tundra, which covers about one-tenth of the earth's surface, is warmed by sunshine, with the sun visible for days or weeks. Over much of the tundra, from September to March the sun does not rise at all, with temperatures of –40 to –50 degrees Fahrenheit common during the dark months.

Basically, two kinds of tundra exist: the Arctic tundra, which follows the coniferous forest belt and covers the northernmost landmass of Europe, Asia, North America, Greenland, and Iceland; and alpine tundra, found on mountain slopes above the tree line in temperate areas.

Permafrost is a consistent feature of the Arctic tundra, as well as of the poorly developed tundra of the Antarctic. The summer thaw in the Arctic tundra extends to a depth of six to twelve inches, with most plant root depth and burrowing of animals limited to this thawable area. The tundra permafrost retards drainage, thereby causing boggy, saturated lowland during the summer thaw. Alpine tundra is drier because of drainage.

Year-Round Inhabitants

Some hardy animals have learned to cope with the cold. Musk oxen, bulky animals with shaggy protective coats of hair, live along the shores of the Arctic Ocean and in other desolate areas of the tundra, where darkness continues for months and the temperature never rises above zero. These herbivores do not seek shelter even in the coldest weather, but search for frozen twigs or grass beneath the snow. Also capable of enduring the cold winter is the arctic fox, whose thick coat of fur turns white in winter and provides camouflage from his enemies. Foxes feed on arctic hares, birds, and lemmings, small rodents that dig beneath the snow. Lemmings remain active all winter, living under the snow and feeding upon grass and roots. Frequently, they reproduce under the snow.

Ptarmigans spend winters on the tundra, having feathers on their feet to aid traveling in the snow. Living in the driest areas of the tundra, they eat berries and tender leaves in the summer and rely on frozen vegetation during the winter. Their feathers turn white in winter, helping camouflage them from their fiercest enemy, the snowy owl. The owl, a bird of prey, moves southward into the forest in winter when the food supply becomes scarce in the tundra. Owls feed upon lemmings, small birds, insects, and arctic hares that are twice their size.

Some alpine mammals, such as marmots and ground squirrels, hibernate, eating large amounts of vegetation in summer and early fall before hibernation begins. Other small animals, including rabbits, forage as they can for winter feeding. Foxes range over alpine tundra in winter.

Migratory Inhabitants

As summer approaches and the days slowly grow longer and warmer, the frozen tundra begins to sprout grass, leaves, and wildflowers. The plants which have adapted to the tundra's short growing season and shallow topsoil above the permafrost are unusually small and provide food for animals. Huge herds of caribou migrate north from the forest to roam across the tundra, feasting on tender, young vegetation. The tundra wolf, or arctic wolf, a strong, fast animal endowed with exceptional hearing, vision, sense of smell, and endurance, follows the caribou into the tundra. Living and hunting in family groups or packs, the wolves feed off young, sick, and old members of the caribou herd.

After hibernating in the forest for the winter, grizzly bears move north to enjoy the berries and plants of the summer. These blond-colored bears also eat fish, lemmings, and carrion (remains left over by other animals). Polar bears, who prefer to eat meat, live near the Arctic Ocean to enjoy the seals, walruses, and fish. Occasionally, they move inland and devour berries, carrion, and other tundra animals.

Many birds also move north from the warm southern areas to feed, nest, and raise their young. Swans, ducks, and geese converge on the ponds, while gulls and terns occupy the tundra's beaches, and falcons and eagles soar at great heights above the tundra seeking their prey. In summer on the tundra, birds hatch as food becomes plentiful. As new vegetation is abundant and fish are plentiful in ponds and lakes, there are large numbers of insects on the tundra. Butterflies, moths, and bees abound, and flies and mosquitoes swarm after the caribou herds, providing food for the birds and fish.

Alpine animals, such as mountain sheep, ibex, wildcats, and many birds, who are not equipped for year-round alpine life, migrate south into more temperate forest environments in winter, returning to higher regions in the summer.

—Mary Hurd

See also: Chaparral; Ecosystems; Food chains and food webs; Forests, coniferous; Forests, deciduous; Grasslands and prairies; Habitats and biomes; Lakes and rivers; Marine biology; Mountains; Rain forests; Savannas; Tidepools and beaches.

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TURTLES AND TORTOISES

Types of animal science: Classification, evolution
Fields of study: Evolutionary science, herpetology, systematics (taxonomy)

Turtles are reptiles with shells that enclose the major body as well as the girdles to which limbs are attached. Shells not only define turtles, but determine by their structure what lifestyle is available to a particular species.

Principal Terms

AMNIOTE: animals with eggs in which embryos develop within fluid-filled membranes (the amnion), allowing eggs to be laid on land; amniotes include reptiles, birds, and mammals

BRIDGE: the portion of the shell that connects the carapace to the plastron

CARAPACE: the portion of the shell that covers a turtle's back (dorsum)

CLADE: a group of animals and their common ancestor

PLASTRON: the portion of the shell that protects a turtle's belly (venter)

Turtles, tortoises, and terrapins are all turtles. The term "tortoise" is used for terrestrial turtles with high-domed shells and elephantine hindlimbs, whereas the term "terrapin" is used properly for some highly aquatic turtles (genus *Malaclemys*) of eastern North America, although it frequently is used in error for American box turtles in the genus *Terrapene*.

Turtles are easily recognized and distinguished from all other vertebrates by their shells. Shells are composed of a dorsal carapace and a ventral plastron. These are usually rigidly connected on the sides by bridges. Shells are composed of bony plates that form within the skin. These are fused to underlying vertebrae and ribs. Most shells have a covering of horny plates made of keratin, a protein which, in other vertebrates, forms scales, hair, nails, claws, or horns. In some turtles, the plates of bone and keratin are reduced or absent, and the shell is covered by leathery skin. Many turtles have one or more hinges in their shells, usually in the plastron. These allow the shell to completely enclose the withdrawn head, limbs, and tail. The plastron of males in many species is indented to accommodate the female's shell during mating.

Turtle Lifestyles

Shell shape largely determines the lifestyle of its owner. Terrestrial (land-dwelling) turtles such as box turtles (*Testudo*) and tortoises (*Geochelone*) have high-domed shells. These reduce surface area through which water is lost and also are difficult for predators to grasp and break. Most aquatic and all marine turtles have relatively flat, streamlined shells for ease in swimming. However, African pancake tortoises (*Malacochersus*) have flat shells that allow them to hide in rocky crevices, and some bottom-dwelling aquatic turtles, such as the mud turtles (*Kinosternon*) of the southeastern United States, have high-domed shells. Snapping turtles in the genera *Chelydra* and *Macrochelys* have rough shells on which algae grow. This camouflages these turtles as they wait to ambush prey.

Limbs also provide clues to lifestyles. Aquatic turtles have webbed feet, and sea turtles have forelimbs modified into flippers that allow them to "fly" through water. In contrast, terrestrial turtles often have spadelike feet for digging and/or columnlike limbs to support them as they walk. Regardless of shape or function, the girdles to which the limbs attach are enclosed by the ribs and shell. Turtles are the only vertebrates with this skeletal arrangement.

Other anatomical modifications include nostrils on top of the snout or at the very tip of a long proboscis; these allow aquatic turtles to breathe at the surface with minimal exposure. Modern turtles, like modern birds, lack teeth. Instead, they have horny beaks of keratin variously shaped to cut leaves, tear flesh, or crush the shells of snails or clams. Because the shell prevents expansion and contraction of the thorax when breathing, turtles compress or expand the lungs by altering the location of other internal organs to which the lungs are attached. Shells limit mobility to a great extent; consequently, turtles have long and flexible necks. These allow them to reach up to browse or down to graze, or to quickly extend their necks in order to ambush quicker prey. In addition, neck vertebrae are modified to allow the head to be withdrawn into the shell, either by pulling it straight back while the neck assumes an S-shape (cryptodiran turtles) or by laying it to the side under the overhanging lip of the carapace (pleurodiran or sideneck turtles).

Turtle Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata (vertebral column and braincase)
Class: Reptilia
Order: Chelonia (turtles), consisting of twelve families, with fifty-two genera and about 260 species

Geographical location: Worldwide

Habitat: Terrestrial, aquatic, and marine habitats, except at high latitudes

Gestational period: Varies according to temperature

Life span: Turtles live longer than other vertebrates, with some small species living fifty years and larger forms up to two hundred years

Special anatomy: The only vertebrates with shells; lack teeth and instead have a horny beak; neck vertebrae are modified to allow the head to be extended or retracted from the shell; lungs are compressed and expanded by altering the position of other, attached internal organs

Some Types of Turtles

Alligator snapping turtles (*Macrochelys temminckii*), from the southern United States, may exceed three hundred pounds. These bottom-dwellers rest motionless with their mouths open, waving a wormlike projection on the tongue to lure unsuspecting fish.

Sideneck turtles (families Chelidae and Pelomedusidae), of the Southern Hemisphere, include the matamata (*Chelus fimbriatus*), a bottom-dweller that uses its long neck as a snorkel and to ambush small fish attracted to flaps of skin that act as lures, and the large Amazonian river turtles (*Podocnemis expansa*), whose nesting behavior is much like that of sea turtles.

Sea turtles (families Cheloniidae and Dermochelyidae) nest on beaches and flee to the sea immediately after hatching; males never return to land and females do so only to lay eggs. The leatherback (*Dermochelys coriacea*) is the largest living turtle; specimens with shells eight feet long and weighing over a ton have been taken.

Giant tortoises (*Geochelone elephantopus*) from the Galápagos Islands were collected by the thousands by nineteenth century whalers heading for Antarctic waters; stored upside down, they provided fresh meat for months. Populations on many islands were extirpated.

Turtles are the only vertebrates that have shells. (Digital Stock)

Origins and Future of Turtles

Fossil turtles are known from the Jurassic. Most systematists (biologists who study evolutionary relationships) group turtles with some extinct relatives in a clade called the Parareptilia. Although turtles traditionally have been considered reptiles, many experts now place them a separate vertebrate class. Regardless, the ancestors of turtles arose from the first amniotes before the ancestors of other reptiles. This and their many unique features justify placing turtles into their own class.

Unlike many reptiles, turtles are perceived positively by most people. Nevertheless, many species are threatened or endangered. Habitat destruction and alteration are responsible in most cases. Aquatic habitats are drained or polluted and nesting sites, especially beaches, are developed, rendering them unusable by turtles. Many species are exploited as food, either as eggs or adults, and others are killed for their shells or body parts, which are thought by some cultures to have medicinal or aphrodisiac qualities. Exotic predators, such as rats and dogs, dig up nests and kill adults. Hundreds of thousands of wild-caught turtles die each year in the pet trade, much of it illegal. Many species become roadkills when they migrate to new habitats or breeding sites. Only a few species are formally protected in at least some parts of their ranges, and several, including the sea turtles, may be nearing extinction in spite of efforts to conserve them.

—Robert Powell

See also: Beaks and bills; Endangered species; Fins and flippers; Lakes and rivers; Lungs, gills, and tracheas; Marine animals; Reptiles; Shells.

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TYRANNOSAURUS

Type of animal science: Classification
Fields of study: Archaeology, evolutionary science, paleontology

The largest terrestrial carnivore, Tyrannosaurus *appeared late in the Cretaceous era that ended some sixty-five million years ago.*

> **Principal Terms**
>
> CARNIVORES: meat eaters
>
> FIBULA: the smaller of two bones between the knee and ankle
>
> JURASSIC ERA: dating from 135 to 190 million years ago
>
> PALEONTOLOGIST: a scientist who studies fossils
>
> TRIASSIC ERA: dating from 190 to 225 million years ago

Dinosaurs have a 175 million-year history beginning in the Permian period and extending through the Triassic and Jurassic periods to the Cretaceous, the last period in the Mesozoic era, which lasted 160 million years and ended 65 million years ago. *Tyrannosaurus* dates to the latter part of the Cretaceous period, which ceased when a great deal of life on earth disappeared for reasons that are not fully known, although it is speculated that a huge meteor crashed into earth, causing a heavy cloud to hang over the planet long enough to kill most vegetation.

No land animal weighing over about fifty-five pounds survived whatever catastrophe caused the sudden end of an era when huge animals roved the earth. *Tyrannosaurus*, the largest terrestrial carnivore, was almost forty feet long. *Tyrannosaurus* had a huge head, a large mouth, and menacing teeth.

Physical Characteristics and Habitat

An adult *Tyrannosaurus* standing upright would have been as tall as a four-story building, but *Tyrannosaurus* did not stand erect. Its hind legs provided sturdy underpinnings, whereas its arms were short and weaker than its legs. They could be used defensively when necessary. Fossil footprint evidence substantiates that *Tyrannosaurus* has feet over three feet long.

This dinosaur depended on its hind legs for most of its locomotion, although it used its arms minimally when it walked. Bulky in the midsection, its long tail aided its balance. Its long neck supported a huge head with a large mouth and seven-inch-long serrated teeth. Adults weighed about seven tons.

Most of the extant remains of *Tyrannosaurus* have been found in the United States, mostly in the South Dakota, Montana, and Wyoming Badlands. The first three *Tyrannosaurus rex* remains were found in Montana and Wyoming in the early 1900's. This area was also inhabited by duck-billed dinosaurs, much smaller animals than *Tyrannosaurus*, who were often eaten by their larger counterparts.

During the late Cretaceous period, the area in which *Tyrannosaurus* remains were found was warmer than it currently is. It is known from fossil remains that its climate resembled the current climate of the southern states. The area was rich in such plant life as ferns, palm trees, redwoods, and flowering plants, which contributed to the diet of dinosaurs. The preserved contents of *Tyrannosaurus* stomachs reveal that they ate many of these plants.

Most of the animals that coexisted with dinosaurs were small, seldom exceeding the size of a domestic cat. Birds were abundant, as were such insects as spiders and beetles. Opossums existed in large numbers, and the waterways of the ancient landscape were filled with fish and turtles, all of which became part of the *Tyrannosaurus* diet. One thing is clear: For a period of 150 million years, dinosaurs ruled the earth. They were the largest, most complex organisms in existence, and *Tyrannosaurus* was preeminent among dinosaurs.

Tyrannosaurus rex lived closer to the beginnings of human existence than it did to the time when the earliest dinosaurs roved the earth. Some paleontologists believe that it was descended from a species of carnivores in Mongolia that migrated from Asia to North America over a formation that once bridged the Bering Straits, but has since disappeared. The Badlands are the richest depository in the United States discovered to date of dinosaur remains.

Tyrannosaurus Facts

Classification:
Kingdom: Animal
Subkingdom: Bilateria
Phylum: Craniata
Subphylum: Tetrads
Class: Protheria
Order: Saurischia
Suborders: Theropoda (four-toed bipeds), Sauropodomorpha (lizard-footed, five toes), Carnosaurus (large predators)
Geographical location: Every continent except Antarctica
Habitat: Land
Gestational period: Unknown; presumably two to three years
Life span: Unknown; presumably over fifty years
Special anatomy: Strong hind legs, with arms weaker than the legs; two fingers on each hand; large head; sharp, serrated teeth

The Largest *Tyrannosaurus rex* Ever Found

Peter Larson, an independent collector of fossils who knew a great deal about paleontology, unearthed the skeleton of Sue, the largest and most perfect *Tyrannosaurus* skeleton ever found. Painstakingly cleaned and reassembled, it is dramatically displayed in Chicago's Field Museum.

Sue was discovered by Sue Hendrickson in August of 1990, when she noticed three large dinosaur vertebrae and a femur protruding from a cliff in the Badlands of South Dakota. These items obviously belonged to *Tyrannosaurus* because the vertebrae were concave from the disk, unlike the straight vertebrae of duck-billed dinosaurs.

With Larson's help, Hendrickson determined that because part of its skull was damaged, Sue died in some sort of conflict. Sue had suffered a fractured fibula that healed but that must have left her defenseless for some time. Contents of its stomach indicated that Sue's last meal was a duck-billed dinosaur.

—R. Baird Shuman

Image Not Available

See also: *Allosaurus*; *Apatosaurus*; *Archaeopteryx*; Dinosaurs; Evolution: Animal life; Extinction; Fossils; Hadrosaurs; Ichthyosaurs; Paleoecology; Paleontology; Prehistoric animals; Pterosaurs; Sauropods; Stegosaurs; *Triceratops*; Velociraptors.

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UNGULATES

Types of animal science: Anatomy, classification, ecology
Fields of study: Anatomy, zoology

Ungulates are herbivorous, hoofed mammals. Those having an odd number of toes are perissodactyls (such as horses), while those with an even number of toes are artiodactyls (such as cattle). Elephants (proboscids) and rabbitlike hyraxes are also ungulates.

Principal Terms

ANTLERS: branched, temporary horns made of solid bone, shed and regrown yearly
CARNIVORE: any animal that eats only the flesh of other animals
GESTATION: the term of pregnancy
HERBIVORE: an animal that eats only plants
NOCTURNAL: active at night
OMNIVORE: an animal that eats both plants and other animals
TRUE HORNS: straight, permanent, hollow bone horns

Ungulates are the hoofed mammals, belonging to the phylum Chordata. The word "ungulate" comes from Latin *ungula*, meaning "hoof." Ungulates are a large group of dissimilar vertebrate animals, grouped together because their outermost toe joints are encased in hooves. There are four ungulate orders. Those ungulates having an odd number of toes belong to the order Perissodactyla. This includes horses (one-toed), rhinoceroses (three-toed), and tapirs (four-toed on the front feet and three-toed on the back feet). Entirely even-toed ungulates belong to the order Artiodactyla. This includes pigs (four-toed) and two-toed ruminants such as camels, giraffes, antelope, deer, cattle, sheep, and goats.

The two other orders are Proboscidea (elephants) and Hyracoidea (rabbitlike hyraxes). The size extremes among ungulates range from the seven-ton male African elephant to the rabbit-sized dik-dik antelope. Most ungulates are herbivores. Ungulates are also the only mammals with horns or antlers, although not all of them have this bony headgear. They are native to all earth's continents except Australia.

Wild Ungulates

Antelope, elephants, hippopotamuses (hippos), and deer are some common wild ungulates. Horses, sheep, goats, cattle, and pigs are mostly domestic ungulates. Ungulate appearance varies widely, but there are common physical and digestive characteristics. Most are artiodactyls, which walk on two toes. Their ancestors had five toes, but evolution deleted the first toe and made the second and fifth toes vestigial. The third and fourth toes provide support, and end in protective hoofs. Hippopotamuses, unique among artiodactyls, have four toes of equal dimensions.

Most ungulates are herbivorous ruminants. They eat only plants, and have specialized digestive tracts with three or four chambers in their stomachs. They chew and swallow vegetation, which, after partial digestion, is regurgitated, chewed again, and reenters the stomach for more digestion. This leads to maximum nutrient uptake from vegetable food. Ungulates usually lack upper incisor and canine teeth. They have hard pads in their upper jaws, which help the lower teeth to grind food.

Deer and antelope are swift-running, hoofed ruminants. Male deer have solid, branched antlers (temporary horns) made of bone, which are shed and regrown yearly. Antelope of both genders have unbranched, permanent, hollow bone horns (true horns). Deer inhabit Asia, Europe, the Americas, and North Africa. Antelope inhabit Africa, Asia, and Europe. Both deer and antelope live in woods, prairies, marshes, mountains, and tundra. Their sizes range from huge moose and elands to rabbit-sized species. Deer and antelope eat twigs, leaves, bark, and grass. The largest antelope are ox-sized.

Giraffes and hippos are very unusual African ungulates. Giraffes live south of the Sahara desert. They have very long legs and necks. Males are over sixteen feet tall and both sexes have short horns. Their flexible tongues and upper lips pull leaves—their main food source—from trees. The two-ton animals can go months without drinking, getting most of their water from the leaves they eat. The three- to four-ton hippos walk on all four toes of each foot. They have short legs, large heads, no horns, small eyes and ears, and nostrils that close underwater. Hippos have long, sharp incisors and canines in both jaws. A hippo can be fifteen feet long and five feet high at the shoulder. They spend most of their time submerged, eating aquatic plants.

Brazilian tapirs inhabit South American forests from Colombia and Venezuela to Paraguay and Brazil. They look a bit like elephants and pigs, but are related to horses. The tapirs have stout bodies and short necks and legs, well adapted for pushing through dense forests, and have short, rigid manes, which protect them from predators. Each tapir has a short trunk with a flexible "finger" at its tip. Like elephants, they use the finger to pull leaves into the mouth. They are dark brown to reddish colored, about 6 feet long, 2.5 feet tall at shoulder height, and weigh up to six hundred pounds. Tapirs are nocturnal herbivores, spending much of the night eating grass, grasses, aquatic vegetation, leaves, buds, soft twigs, fruits,

Zebras are perissodactyl ungulates, walking on only one hoofed toe. (Corbis) and plant shoots. The tapirs roam the forest and can climb river banks and mountains. Excellent swimmers, they spend a lot of time in the water, eating and cooling off.

Domesticated Ungulates

Bovids—cattle—are domesticated ungulates. Most have true horns. Bovid horns are spiral, straight, tall, or grow from the sides of the head and then up. Most are herbivorous ruminants. Cattle are raised to provide meat, milk, and leather. Modern cattle come from European, African, and Asian imports. Breeding modern cattle began in mid-eighteenth century Europe; today there are three hundred breeds. Dairy cattle such as Holsteins make milk, and beef cattle such as Angus yield meat.

Sheep and goats are also domesticated, ruminant ungulates. Sheep were domesticated eleven thousand years ago from Asiatic mouflons. They have paired, spiral true horns, largest in males. Adults reach lengths of five feet and weights from 250 to 450 pounds. The eight hundred domesticated breeds provide wool for clothing, meat, and milk. Goats, closely related to sheep, have shorter tails, different horn shape, and beards. They eat grass, leaves, and branches. Numerous breeds are domesticated for meat and milk. Angora goats yield silky mohair. Goat milk is as nutritious as cow milk.

The horse, donkey, zebra (HDZ) family are perissodactyls. They live in habitats ranging from grassland to desert. They eat grasses, bark, leaves, buds, fruits, and roots, spending most of their waking hours foraging and eating. Wild specimens inhabit East Africa and the Near East. Domesticated horses and donkeys are used for food, meat, and leather. Zebras are too savage to domesticate.

Members of the HDZ family lack horns. They have long heads and necks, slender legs, manes on their necks, and long tails. They have good wide-angle day and night vision and a keen sense of smell. The smallest family members are African wild donkeys, 4 feet tall, 6.5 feet long, and weighing nearly five hundred pounds. The largest, Grevy's zebras, are five feet tall, nine feet long, and weigh up to nine hundred pounds. Zebras have black or brown and white, vertically striped coats. The other HDZ family members are brown, black, gray, white, and mixtures of these colors.

The Lifestyles of Ungulates

The lifestyles of ungulates are very different. Many of them are very sociable and live in large herds, including many bovids, horses, deer, antelope, and zebras. In other cases, the animals live in smaller family groups, or are solitary, coming together only to breed.

Wild donkeys and horses live in herds made up of a male and his mates. Young stay in the herd until two or four years old for females and males, respectively. Males then join other bachelors until winning a herd. Females join other herds. Goats and sheep are also herd animals. Young goats, sheep, and cattle join herds or live in solitary fashion after they are weaned.

Moose are quite different. Males are solitary until they fight for mates and breed in the fall. A successful male often leads several females and babies all winter. In the spring he returns to the solitary life. Giraffes and male elephants are solitary. Female elephants and young form herds whose members breed with visiting males, protect each other, and raise young.

Ungulates are of great importance to humans and to the world. First of all, in the wild state they are food for many carnivores and omnivores. Domesticated, they provide meat, milk, hides, and sinew for human use. Furthermore, elephants, horses, and reindeer have long been used as beasts of burden. In addition, ungulates are biologically important because as herbivores, they prevent overgrowth of all sorts of plants by eating them.

—*Sanford S. Singer*

See also: Antelope; Cattle, buffalo, and bison; Deer; Donkeys and mules; Elephants; Elk; Giraffes; Goats; Hippopotamuses; Horns and antlers; Horses and zebras; Moose; Pigs; Reindeer; Ruminants; Sheep.

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URBAN AND SUBURBAN WILDLIFE

Types of animal science: Behavior, ecology
Fields of study: Ecology, ethology, wildlife ecology

The global increase in the human population growth and density has seen a simultaneous increase in the growth of urban and suburban areas throughout the world. As urban habitats and their suburban extensions have become more common, the wildlife of these human landscapes has become the focus of attention and study.

Principal Terms

ANTHROPOGENIC: originating from human sources, such as aerosols and other pollutants

BIODIVERSITY: variety of life found in a community or ecosystem; includes both species richness and the relative number of individuals of each species

EXOTICS: organisms, usually animals, that have been deliberately or inadvertently introduced into a new habitat, such as monk parakeets in New England, or brown snakes on Guam

FERAL ANIMALS: domestic animals that have reverted to a wild or semiwild condition, such as cats, dogs, or caged birds that have been released or escaped and now survive in the wild

MORPHOLOGY: development, structure, and function of form in organisms

OPEN SPACE: natural or partly natural areas in and around cities and suburbs, such as woodlots, greenbelts, parks, and cemeteries

URBAN WILDLIFE: generally the nondomestic invertebrates and vertebrates of urban, suburban, and urbanizing areas; may include domestic animals that have escaped and are subsequently feral

Animals and plants of cities and suburbs are categorized as urban wildlife. As cities and suburbs grow ever larger and displace natural habitats, many city and suburban landscapes have become more attractive for certain kinds of wildlife, or at least urban wildlife has become more noticeable. Urban wildlife consists of an eclectic and unlikely mix of escaped pets (mostly exotics and caged birds), feral animals, furtive and temporary intruders from adjacent natural habitats, and species whose natural ecology and behavior enables them to fit within human-modified landscapes and tolerate living in close proximity to humans.

Urban landscapes present a seemingly stark and forbidding environment for wildlife. The horizontal pavement of streets and sidewalks is punctuated by rising angles and arches of concrete and steel which in turn are topped by wood and metal rooftops. Overhead, a maze of telephone, power, and cable lines limits vertical movement, while vehicle and foot traffic pose a constant threat to surface movement. All of these edifices and connecting corridors and lines result in a complex, vertically structured environment within which some animals find difficult to maneuver yet to which other animals quickly adapt. In addition to monotonous and often dangerous structural diversity, urban wildlife is subject to elevated and often almost continuous noise and disturbance and is constantly exposed to an enormous variety of residential wastes (garbage, litter, excess water, salts, sewage), vehicular pollutants (lubricants, greases, gasoline, hydrocarbons, nitrogen oxides), and chemical wastes (pesticides, paints, lead, mercury, contaminants).

Despite the forbidding features offered by urban habitats, a surprising variety of wildlife manages to exist on a more-or-less permanent status. In fact, some kinds of wildlife can be found even in the midst of the most degraded forms of urban blight. *Ailthanthus*, which is also commonly called tree-of-heaven, is but one of many opportunistic trees and shrubs that can take root and grow given a bare minimum of soil and nutrients. A simple linear crack in the pavement of a sidewalk, a little-used roadway, an unused parking area or vacant lot can trap enough windswept dirt to offer a growing substrate for *Ailanthus* and similar hardy plants. Each *Ailanthus*, in turn, provides food and shelter for equally tough and adaptable wildlife, ranging from the variety of invertebrates that colonize and feed upon *Ailanthus* to birds and mammals that take shelter or find food in its branches and foliage. Similarly, every invading sprig of grass, wildflower, shrub, or tree, however large or small, creates its own suite of microhabitats which, in turn, offer colonization opportunities for other plants and animals, the whole ultimately contributing to an overall increase in urban biodiversity.

Characteristics of Urban Wildlife

Ailthanthus is an example of those plants and animals able to tolerate the most extreme urban conditions, but in reality most urban wildlife derives a number of benefits by living within the confines of cities and suburbs. Far from being homogenous expanses of concrete, most urban centers are a patchwork of different habitats—residential, commercial, and industrial buildings, warehouses, power stations, vacant lots, detached gardens, rooftop gardens, and alleyways—that each offers innumerable opportunities for wildlife. Many urban areas also have a number of limited access areas that animals are quick to adopt for shelter and breeding places; these include fenced-in lots and boarded-up buildings, along with a rabbit warren of underground tunnels, ducts, steam and water pipes, basements, and access ways.

City lights extend foraging time and opportunities, allowing wildlife to hunt for food not only throughout the day but also during much of the night, as needed. Urban nooks and crannies offer an extensive variety of microhabitats that differ fundamentally in size, microclimate, and other structural features. These microhabitats serve primarily as shelters and breeding sites for city wildlife. Many birds, such as house sparrows (*Passer domesticus*) and Eurasian starlings (*Sturnis vulgaris*) nest in innumerable crevices, cracks, nooks, niches, and sheltered rooftops. Pigeons (*Columbia livia*) and starlings hide in sheltered enclaves offered by bridge abutments and supports, archways, and other edifices.

The most adaptable wildlife are quick to find and take advantage of subtle advantages offered in urban habitats: Many birds cluster around chimneys and roof reflectors or in shelters afforded by lee sides of rooftops during harsh cold and windstorms. Others are equally quick to obtain warmth by sitting on poles, rooftops, or other elevated perches to orient toward sunlight, while at ground level animals gather near gratings, vents, and underground heating pipes.

Urban wildlife quickly concentrates in areas where potential food is made available, for instance, during trash pickup, then just as quickly disperses to find new food sources. Most urban wildlife forage opportunistically as scavengers, specializing in finding and consuming all bits of discarded food, raiding trash cans, and concentrating at waste collection and disposal centers. Thus, the rubbish dumps, found in or immediately adjacent to every city of the world, attract an amazing diversity of small mammals and birds. Feeding on the scavenged food of urban areas and bird feeders is much more efficient because it requires less energy to find or catch and is usually available throughout the year.

Because of the need to find and exploit temporary food resources, some of the most successful urban animals forage in loose groupings or flocks—the more eyes, the more searching, and the more feeding opportunities can be identified and exploited. Solitary and nonsocial species often do less well in urban environments simply because they lack the collective power of the group to find food and shelter, and avoid enemies.

The availability of a year-round food supply—however tenuous and temporary—along with the presence of an enormous variety of safe shelters and breeding sites promotes a higher life expectancy, which partly or mostly balances the higher vehicle-related death rates to which urban wildlife is continuously subject.

Parks and open space provide the only true refuges of natural habitats set deep within urban and suburban landscapes. Such open-space habitats function as ecological islands in a sea of urbanism. Most are necessarily managed habitats rather than entirely natural and, like the urban environment that surrounds them, are usually subject to constant disturbance from adjacent traffic, noise, and other forms of pollution. Economically, since most open-space parks are set aside and maintained for a variety of recreational purposes rather than as natural habitats, the wildlife that colonizes these unnatural natural habitats must have an unusually high tolerance for human presence and recreational activities of all kinds.

Sources and Types of Urban Wildlife

For some urban wildlife, the urban landscape is merely a manmade version of their natural environment. Thus, for pigeons the ledges, cracks, and crevices of buildings and bridges represent an urban version of the cracks and crevices of cliffs and rock outcrops that they use for roosting and nesting in the native habitats. Similarly, the short-eared owls (*Asio flammeus*) and snowy owls (*Nyctea scandiaca*) that show up in winter to stand as silent sentinels at airports, golf courses, and other open areas are simply substituting these managed short-grass habitats for the tundra habitats preferred by snowy owls and the coastal marshes hunted by short-eared owls. Their summer replacements include a host of grassland nesting species such as grasshopper sparrows, kildeer, and upland sandpipers, which all find these managed habitats to be ideal substitutes for the native grasslands which they displaced or replaced.

Many bird inhabitants of urban and suburban environments are exotics which were deliberately or inadvertently introduced into urban areas. Certainly the three birds with the widest urban distribution in North America, the pigeon or rock dove, European starling, and house sparrow or English sparrow, all fit within this category. The introduction of the European starling into North American cities and suburbs resulted from the dedicated efforts of the American Acclimitization Society of the late 1800's. The goal of this society was the successful introduction of all birds mentioned in the works of Shakespeare into North America. Unfortunately for North Americans, the character of Hotspur in *Henry IV* makes brief note of the starling, so the society repeatedly attempted to introduce the starling into Central Park until they were finally successful. Since then, the starling has become the scourge of cities and suburbs throughout much of North America and the rest of the civilized world. Starlings damage and despoil crops, and dirty buildings with their droppings.

The association between house sparrows and urban centers is apparently very old. Evidence suggests that they abandoned their migratory ways to become permanent occupants of some of the earliest settlements along the Nile and Fertile Crescent, a trend that has continued to this day. Sparrows and starlings both share certain characteristics that enable them effectively to exploit urban and suburban habitats; both are aggressive colonizers and competitors, able to feed opportunistically on grains, crops, discarded bits of garbage, and other food supplies.

Avian occupants also include an increasing diversity of released caged pets. Thus, urban locales in Florida, Southern California, and along the Gulf Coast support an ever increasing diversity of parakeets, parrots, finches, and lovebirds, all stemming from caged pet birds either deliberately released or lost as escapees.

Feral animals, mostly dogs (Canidae) and cats (Felidae), represent another important source and component of urban wildlife. Feral dogs revert to primal adaptive behaviors, gathering in loose packs that usually forage and take shelter together, but have limited success because almost all cities in developed countries have ongoing measures to control and remove them whenever found. Feral cats are often more successful because they are secretive, mostly nocturnal, and can clearly better exploit available urban food sources. The role of other feral animals as urban wildlife, mostly escaped pets, is not well known.

Humans and Urban Wildlife

The attitude of urban dwellers toward urban wildlife varies greatly. For many humans, urban wildlife offers a welcome respite from their otherwise dreary and mundane surroundings. Urban wildlife in all of its forms and colors can be aesthetically attractive, even beautiful, and is also compellingly interesting. For example, the nesting of a pair of red-tailed hawks (*Buteo jamaicensis*) in New York City's Central Park sparked a remarkable interest in birdwatching in the city and a heightened awareness of exactly how exciting wildlife watching can actually be. All facets of the pair's courtship and nesting were watched and reported in newsprint, novellas, and even a book, *Red-Tails in Love*. Other animals, while not nearly as large, conspicuous, and glamorous in their color and disposition, also elicit interest. Urban wildlife adds lively color and contrast to the otherwise monotonous gray and grime of streets and sidewalks. Part of the attraction is that urban birds are usually already sufficiently tolerant to be semitame in spirit, easily seen and observed, and, in some instances, easily attracted. Strategically placed bird feeders and bird houses also attract these birds.

Public attitude toward urban predators varies considerably. Some people find them attractive and interesting and even put out food for them. Others consider them pests or potentially dangerous and avoid them. During rabies outbreaks or public scares, most urban wildlife is targeted by various control programs to remove unwanted animals.

Suburban Wildlife Habitats

The vast sprawl of suburbs across the landscape offers many types of wildlife yet another habitat opportunity to exploit, either as residences or as temporary components of the search for food or shelter. Like urban areas, suburbs offer a range of differing habitats. The simplest suburbs are merely extensions of urban row houses with minimal yardscapes, but there is an increasing progression toward more open and natural yards in outlying suburbs that merge with rural areas and natural habitats. The larger and more diverse yards at the edges of suburbs often help blur the distinction and diversity between human landscapes and natural landscapes.

Ornamental trees, shrubs, flowers, gardens, and lawns that characterize almost all suburban habitats provide a series of artificial habitats that can actually increase wildlife diversity. Again, the chief wildlife benefactors are species that can best ecologically exploit the unnatural blend of woodland, edge, and meadow that suburban landscapes offer. It is no accident that some of the most common components of suburban wildlife include thrushes such as robins, finches, and cardinals, titmice, blue jays, crows, and many other similar birds. All of these species are actually responding to the structural components of the suburban landscape, which provide suitable substitutes for their natural landscapes.

The blend of ornamental and garden vegetation offered by most suburban landscapes offers food for a diversity of what were once considered less tolerant wildlife. Deer, wild turkey, grouse, and a host of other animals, large and small, make periodic forays into suburbs in search of foods. Crepuscular and nocturnal wildlife is much more likely effectively to exploit food sources offered by suburban landscapes than diurnal wildlife, which is more at risk because of its high visibility during daylight hours.

Well-wooded suburban habitats that attract a variety of wildlife also attract an increasing number of predators. American kestrels (*Falco sparverius*), Cooper's hawks (*Accipiter cooperi*), barn owls (*Tyto alba*), screech owls (*Otus* spp.), and little owls (*Athene noctua*) provide but a small sampling of birds of prey that nest deep within urban and suburban environments, taking advantage of open-space habitats deep within cities and quickly exploiting unused areas within most suburbs. Terrestrial predators are almost equally common, but most are nocturnal or nearly so; consequently, their contacts with humans are quite limited. Many urban predators are, in fact, mistaken for neighborhood pets and left alone or avoided: Coyotes (*Canis latrans*) are often mistaken for dogs, especially when seen in twilight. The wily coyote is equally at home in the suburbs of Los Angeles, California, and the urban parks of New Haven, Connecticut, joining a host of small and medium-sized mammal predators such as foxes (*Vulpes* spp.) and scavengers such as opossums (*Didelphis marsupalis*), raccoons (*Procyon lotor*), and skunks (*Mephitis mephitis*). These urban predators have many behavioral attributes in common. All are omnivorous and able to feed on a wide variety of natural foods such as fruit, small birds and mammals, insects, and invertebrates such as beetles, grasshoppers, and earthworms.

Foraging and food habits of urban predators sometimes conflict with human concerns. Urban foxes hunt and kill cats, especially kittens, if given the opportunity, while the larger and stronger urban coyote will often not hesitate to kill and eat cats and dogs, to the pet owners' dismay.

Conservation and Management of Urban and Suburban Wildlife

Urban wildlife must be much more closely managed than wildlife of natural environments because urban and suburban habitats attract an enormous number of pest species as well as interesting and beneficial species. Introduced species such as starlings may also transmit histoplasmosis, a fungal disease that attacks human lungs. Other birds may also be harbingers, carriers, and vectors of various diseases, the most notable of which are the parrots and parakeets, which transmit parrot fever or psittocosis. Rats and mice (Rodentia) carry and spread disease and despoil both residential and public buildings and other structures.

The growing interest in urban wildlife has stimulated innumerable programs to promote beneficial wildlife. Both public and private organizations and agencies have embarked on a variety of programs aimed at remodeling existing habitats and even creating new habitats for urban wildlife.

Programs aimed at creating new or modifying existing urban habitats come in a variety of categories, such as linear parks, greenways, urban wildlife acres programs, backyard gardens, and treescaping streets and roadways, all of which create biodiversity, which in turn provides attractive habitats for colonization by additional animals and plants. Modification of existing habitats to increase animal biodiversity includes "critter crossings," roadside habitats, backyard gardens, and arbor plantings, all of which provide refuges, shelters, breeding sites, connecting corridors, and safe havens that promote the welfare of urban and suburban wildlife.

Many existing open-space habitats are also being modified. Many urban renewal commissions have placed new and more restrictive regulations on the use of pesticides and fertilizers on golf courses, which not only reduces the incidence and intensity of nonpoint pollution from the golf courses but also reduces the incidence of wildlife poisoning. These steps cannot help but increase the biotic potential of golf courses for supporting local biodiversity.

—Dwight G. Smith

See also: Birds; Dogs, wolves, and coyotes; Ecological niches; Ecosystems; Foxes; Habitats and biomes; Hawks; Mice and rats; Opossums; Owls; Raccoons and related mammals; Scavengers; Skunks; Sparrows and finches; Weasels and related mammals.

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VELOCIRAPTORS

Types of animal science: Classification, evolution
Fields of study: Anatomy, evolutionary science, paleontology, systematics (taxonomy)

Velociraptors are a group of human-sized theropods (carnivorous dinosaurs) that existed during the Cretaceous era in North America and Asia.

Principal Terms

CLADISTICS: a method of analyzing biological relationships in which advanced characters of organisms are used to indicate closeness of origin

CRETACEOUS: a period of time that lasted from about 146 to 65 million years ago, the end of which was marked by the extinction of the dinosaurs

ECTOTHERMY: a form of metabolism in which internal temperature is regulated by the ambient temperature

JURASSIC: a period of geological time that lasted from about 208 to 146 million years ago

PUBIS: one of the three bones that make up the pelvis (the others are the ischium and ilium)

SAURISCHIA: one of the two main dinosaur groups, characterized by a pelvis in which the pubis points forward

Velociraptors are represented by the genus *Velociraptor* ("speedy predator"), which is one of a group of human-sized theropods or carnivorous dinosaurs that existed during the Cretaceous in North America and Asia. Theropods include all dinosaurian carnivores and are allied to the sauropods, very large, long-necked herbivores, in a major group of dinosaurs called the Saurischia. These dinosaurs are all characterized by the forward projection of the pubis, which separates them from the other major group, the Ornithischia, in which the pubis is directed backward. Velociraptors are most closely related to a group of similar predators that includes the dromaeosaur *Deinonychus*, which is extremely well known from articulated skeletons found in Montana and Wyoming, described by Yale University's John Ostrom in the late 1960's and early 1970's. One result of cladistic analysis of the relationships of this group is that they have been shown to be the closest relatives of *Archaeopteryx*, the earliest known bird. *Archaeopteryx* is known only from the latest Jurassic, and the dromaeosaurs are entirely Cretaceous, so it has been suggested that either dromaeosaurs represent a group of secondarily flightless birds,

Velociraptor Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Reptilia
Order: Saurischia
Suborder: Dromaeosaurida (medium-sized carnivores with an enormous claw on the second toe of the hind foot)
Geographical location: North America and Asia
Habitat: Terrestrial habitats
Gestational period: Unknown
Life span: Unknown
Special anatomy: Medium-sized bipedal carnivores with a well-developed, sickle-shaped claw on the hind foot

Image Not Available

or alternatively that ancestral forms in the Jurassic await discovery.

Anatomy and Life Habits

The velociraptor *Deinonychus* ("terrible claw") is the best-known genus of this group and is thus often used as a typical example. It has an elongated, lightly built skull with numerous backward-curving, serrated teeth, and a relatively large brain. There are large openings in the side of the skull for the eyes and for jaw muscles, which suggest a sharp-eyed predator with a fearsome bite. The neck was quite slender and flexible in contrast to the back and tail, which were fairly stiff due to the presence of ligaments and (in the tail) bony rods that provided support to the vertebral column. The arms were unusually long, and the three-fingered hands bore long, sharp claws. The hind leg is particularly interesting, as the relatively short femur (upper leg bone) indicates a fast-running animal while the second toe is modified to form a large, sickle-shaped claw that must have been held above the ground during locomotion.

These anatomical features suggest that *Deinonychus* (and other velociraptors) was a nimble predator that was able to grasp its prey and dispatch it with lethal kicks from its sickle-claw. The femur has a special process on it for the attachment of a muscle that would have allowed a very powerful backward and downward kick, enabling effective use of the claw. Additionally, the tail is flexible near the body but stiffened by bony rods more distally, which would have made it ideal as a balancing organ. The only actual evidence of velociraptor predation comes from a specimen of *Velociraptor* from Mongolia, in which the individual is interlocked with the skeleton of a small *Protoceratops* (a herbivore), suggesting that they died in mutual combat. The most common herbivores found with *Deinonychus* remains are ornithopods, large, bipedal animals that would have been too large for attack by a solitary individual. This has been used as the basis for the hypothesis that velociraptors might have attacked in packs, which in turn suggests a level of organization not usually present in reptiles. The active and agile lifestyle of velociraptors, together with the possibility of group behavior in hunting, have been advanced as evidence that they had an endothermic metabolism, similar to that of modern mammals, in which internal temperature was controlled by food intake. As dinosaurs are reptiles, they had been thought to have an ectothermic metabolism similar to that of modern reptiles. Velociraptors have become well-known dinosaurs due to their role in the film *Jurassic Park* (1993), where they are depicted as intelligent and warm-blooded, in contrast to the long-held perception of dinosaurs as ponderous and slow-witted animals.

—David K. Elliott

See also: *Allosaurus*; *Apatosaurus*; *Archaeopteryx*; Dinosaurs; Evolution: Animal life; Extinction; Fossils; Hadrosaurs; Ichthyosaurs; Paleoecology; Paleontology; Prehistoric animals; Pterosaurs; Sauropods; Stegosaurs; *Triceratops*; *Tyrannosaurus*.

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VERTEBRATES

Types of animal science: Anatomy, classification, reproduction
Fields of study: Anatomy, marine biology, ornithology, zoology

Vertebrates, chordate animals with backbones, include fish, amphibians, reptiles, birds, and mammals. Although numerically smaller than invertebrates in total population, vertebrates are the largest animals on earth, due to the increased weight-carrying capacity allowed by the spine and endoskeletal system.

Principal Terms

ARTICULATE: interconnect by joints
BONE: dense, semirigid, calcified connective tissue, the main component of skeletons of adult vertebrates
CARTILAGE: elastic, fibrous connective tissue, the main component of fetal vertebrate skeletons, it turns into bone
COLLAGEN: a fibrous substance plentiful in bone, cartilage, and other connective tissue
CONNECTIVE TISSUE: fibrous tissue that connects or supports organs
NOTOCHORD: a flexible, rodlike structure in lower chordates and vertebrate embryos, it supports like the backbone of a vertebrate

The Vertebrata are a subphylum of the phylum Chordata. The six vertebrate classes are lampreys, true fish, frogs and toads, reptiles, birds, and mammals. A vertebrate animal has a spinal column (backbone) made of bone or cartilage, and a brain case (skull). Vertebrates also have two pairs of limbs (though some have lost limbs through evolution), and a bilaterally paired muscular system. The backbone that gives the subphylum its name is a group of small bones or cartilage pieces with articulating surfaces (vertebrae). Ribs and bones that support the limbs are attached to the backbone. The ribs protect the heart, lungs, and other internal organs, and can expand and contract. The earliest vertebrate fossils occur in rock from the Paleozoic era.

The vertebrae serve to encase and protect the spinal cord, a major part of the vertebrate nervous system. The central nervous system also has an enlarged, highly differentiated upper portion, the brain. The bony skull of a vertebrate also serves to encase and protect that brain, as well as providing a base for the vulnerable sensory organs of eyes, ears, nose, and mouth, which are thus efficiently located close to the brain.

The more primitive members of the phylum Chordata have notochords, solid or segmented columns that cover the nervous system. Vertebrates resemble chordates in having notochords in their embryonic state. The vertebrae develop around the notochord. The trunk of a vertebrate is a hollow cavity in which the heart, lungs, and digestive tract are suspended. The central nervous system branches out from the spinal column to reach all internal organs, muscles, and skin. The support offered to the brain and nervous system by the vertebrae has allowed vertebrates to evolve increasingly large brains, which in turn has allowed vertebrates to become increasingly intelligent and responsive to their environment.

Bone and Bones

Bone, the material that form the vertebrae, first evolved 500,000 years ago. Bone is the hard supportive framework of all vertebrates. The framework, a skeleton, has hundreds of separate parts; for instance, there are 206 bones in a human skeleton. Bones protect delicate organs, such as the brain and lungs. Muscles, attached to bones, enable walking, flying, swimming, and all other means of motion. Bones provide body calcium needs and contain sites for making blood cells.

Much bone in adult vertebrates arises from cartilage, an elastic, fibrous connective tissue, and the main component of fetal vertebrate skeletons. Such bone is cartilage bone. Cartilage is an extracellular matrix made by chondrocyte cells. It is firm and elastic, due to its collagen fibrils. The fibrils provide mechanical stability and high tensile strength, while allowing nutrients to enter chondrocytes. Blood vessels around cartilage supply nutrients and remove wastes.

Cartilage-containing skeletons of newborn vertebrates become bone by a process of calcification, chondrocyte destruction, and replacement by bone cells. In young vertebrates, cartilage is the site of growth and calcification that lengthens bone to attain adult size.

The Common Characteristics of Vertebrates

- Complex, paired eyes
- Muscular mouth and pharynx
- Epidermis and dermis, often modified into protective coverings such as scales, feathers, or hair
- Blood containing red (hemoglobin-carrying) and white blood corpuscles
- Large body cavity for holding internal organs
- Digestive system consisting of digestive glands, liver, and pancreas
- Two- to four-chambered ventral heart
- Paired, ducted kidneys
- Male and female genders (with appropriate reproductive organs)

Vertebrae

In higher vertebrates, each vertebra consists of a lower part, called the centrum, and an upper, Y-shaped part, called the neural arch. The arch has a downward and backward projection, which can be felt as the bumps along a vertebrate's back, and two sideways projections, where muscles and ligaments can attach. The space between the arms of the Y on the neural arch and the centrum create an opening called the vertebral foramen, through which the spinal cord passes. Intervertebral disks, made of cartilage, separate the centrums and serve as shock absorbers.

The vertebral column has five regions: the cervical region (neck), thoracic (chest), lumbar (lower back), sacral (pelvic girdle), and caudal (tail). The top two cervical vertebrae, called the atlas and axis vertebrae, make a joint to attach with the skull. The number of vertebrae varies by species.

Vertebrate Evolution

Vertebrates, all designed on the same general plan, flourish on land, in the air, and in both fresh and salt water. Vertebrates first evolved in the Silurian period, around 438 to 408 million years ago. In the intervening millennia, according to need, evolution produced valuable morphological changes to optimize vertebrate biofunctions. For example, whales, once land dwellers, evolved into ocean dwellers with lungs and sonar to help them navigate and find food. Birds developed wings to ride the air, and mammals proliferated in forms that fit varied habitats worldwide. Fish were the first vertebrates to appear, around 480 million years ago. Amphibians and reptiles appeared around 360 million years ago, while birds and mammals begin to appear around 205 million years ago.

Morphological change led to a balance of nature, where herbivores ate plants, preventing their overgrowth, and carnivores ate herbivores, preventing their superabundance. Then the ultimate vertebrates, humans, developed civilization. Humans domesticated animals for food, clothing, transportation, and pets. In so doing, many species have been eradicated, endangered, or put at risk. For example, blue whales were endangered because their blubber was useful. Wolves and tigers have been eradicated or endangered by the quest for hunting trophies and to keep them from eating livestock. Mustelids were treated similarly because their pelts made attractive fur garments. Fortunately, human tolerance for this treatment of animals is decreasing, lest many species be seen only in zoos or faded photographs.

—*Sanford S. Singer*

See also: Amphibians; Animal kingdom; Birds; Bone and cartilage; Brain; Circulatory systems of vertebrates; Endocrine systems of vertebrates; Endoskeletons; Fish; Fur and hair; Hormones in mammals; Invertebrates; Mammals; Muscles in vertebrates; Nervous systems of vertebrates; Reproduction; Reproductive systems of female mammals; Reproductive systems of male mammals; Reptiles; Water balance in vertebrates; Zoology.

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VETERINARY MEDICINE

Types of animal science: Anatomy, behavior, fields of study, physiology, reproduction, scientific methods

Fields of study: Anatomy, biochemistry, cell biology, embryology, genetics, histology, marine biology, neurobiology, ornithology, pathology, physiology, reproduction science, zoology

Veterinary medicine enables professionals to treat and prevent diseases and injuries in animals to better their quality of life and as a public health measure to protect humans from transmissible diseases through contact with infected animals and contaminated animal by-products.

Principal Terms

BRUCELLOSIS: cattle disease caused by brucellae bacteria

CHOLERA: gastrointestinal diseases

DISTEMPER: viral disease affecting respiration

LEPTOSPIROSIS: bacterial infection of spirochetes spread by urine

RABIES: viral disease of the nervous system

TUBERCULOSIS: communicable disease caused by the tubercle bacillus

ZOONOSES: diseases transmissible from animals to humans

The treatment and prevention of animal diseases is crucial to maintain animal vigor and to secure public health. The term "veterinary" is derived from the Latin word *veterinarius*, which refers to beasts of burden and was used to describe people who were animal healers. Before veterinary science became professionalized in the late nineteenth century, animal owners tended to their livestock's health needs. Gradually, universities worldwide included courses which focused on specific animal ailments and wounds, and professional organizations such as the American and Canadian Veterinary Medical Associations were established. Because horses were essential for transportation, and cattle, sheep, and goats provided necessary meat, skins, wool, and milk, early veterinary practitioners focused on tending to the health concerns of those domesticated animals.

Veterinary medicine gained public acceptance because of campaigns to eradicate and control zoonoses that threatened humans. Legislation affirmed veterinarians' status as public health professionals responsible for inspecting and vaccinating animals. Licensing procedures established educational and professional standards for qualified veterinary practitioners. Globally, cultural beliefs regarding animals and health care determined the degree to which veterinary medicine was incorporated in societies.

Veterinarians pursue many roles, such as practicing at private hospitals or zoos, teaching, researching, consulting with pharmaceutical industries, and working for national, state, and local governments as food inspectors, military veterinarians, and other such positions. Veterinary medicine is crucial for disease control in domestic animals through the examination of animals for parasites and contagious diseases and the quarantine of imported animals until they pass health inspections.

Prevention

Veterinarians strive to protect both animals and humans from animal-transmissible diseases such as rabies. Bacterial, viral, fungal, and parasitical diseases can weaken animals already genetically predisposed to certain conditions. The livestock industry relies on veterinarians to inoculate swine, poultry, cattle, goats, sheep, and other animals raised and sold as meat, milk, and hide and fur producers. Ill animals can detrimentally affect agriculturists' profits and the overall farm economy due to the necessity of destroying valuable animals exposed to hazardous diseases, especially in confinement units where animals live closely together.

During the twentieth century, veterinarians achieved some control of hog cholera, brucellosis, and tuberculosis. With serums, medicated dips, and quarantines, they continue efforts to eradicate these diseases and prevent further outbreaks and transmission to additional herds. Through mandatory regulated meat and dairy inspections, veterinarians prevent contaminated foodstuffs from reaching human consumers, although some people in several countries have encountered tainted meat from bovines suffering from mad cow disease.

By the mid twentieth century, the popularity of keeping small animals and some large livestock, such as horses and ponies, as pets led many veterinarians to begin specializing in practices especially for those animals. Owners relied on veterinarians' preventative measures to ensure the healthy well-being of their pets. Dogs and cats were the most frequently seen patients, but veterinarians also attempted to prevent diseases in more exotic pets, including birds, rodents, fish, reptiles, and amphibians.

Routine Examinations

Veterinarians initiate preventive measures by taking a medical history of each animal, preferably first examining them when they are several weeks old. The condition of the animal is assessed and basic diagnostic tests for parasites and infectious diseases such as distemper are administered and evaluated. If animals test positive, appropriate treatment is begun. For both cats and dogs, a heartworm test is crucial. When a mosquito that has bitten an infected animal bites another dog or cat, these spaghetti-like parasites are injected as

Image Not Available

Emergency Veterinary Medicine

Veterinarians dress wounds, inject snake antitoxin and antibiotics, splint broken limbs, and euthanize animals as needed after accidents. Educating clients about possible dangers, veterinarians provide safety information for preemergency preparations for pets and livestock. Veterinarians distribute guides advising how animal owners should respond when faced with natural disasters such as fires, floods, earthquakes, hurricanes, blizzards, and tornados. Other emergencies that can victimize animals include hazardous materials spills, evacuations, gas leaks, and airplane, train, and car crashes.

Anticipating critical care needs, veterinarians instruct clients how to prepare animal evacuation and first aid kits with copies of veterinary records, proof of ownership, pharmaceuticals, and instructions appropriate for their pets. They also provide owners emergency supplies such as animal identification tags with veterinary contact information and waivers for veterinary care in case owners are separated from their animals.

After an emergency, veterinarians open their animal hospitals to treat victims or travel to accident and disaster sites where both domestic and wild animals need assistance. When areas have been evacuated during a storm or emergency, veterinarians help locate, rescue, restrain, shelter, and identify animals left behind and administer first aid and medication to panicked or shocked animals unable to be moved.

After disasters, Veterinary Medical Assistance Teams (VMAT) assist the Red Cross, humane societies, and local animal control officials. To protect public health, they examine carcasses and food and water sources for possible contamination. They also vaccinate animals with tetanus and rabies boosters to prevent postemergency epidemics. Veterinarians assist in the reunion of owners and missing pets.

larvae into the skin, then migrate to the bloodstream. Adult heartworms can grow as long as fourteen inches inside host animals' hearts, impeding their circulation and potentially causing death. Mosquito control and regular doses of heartworm medicine help prevent the spread of heartworms. Cats are also tested for feline leukemia virus, a fatal, contagious disease. Horses are given a Coggins test to detect equine infectious anemia.

A series of vaccinations prevent diseases from occurring in young animals and are given as immunity boosters in mature animals. Some diseases can be combated with combination injections which combine vaccines for distemper, hepatitis, leptospirosis, parvovirus, and parainfluenza. Rabies vaccinations are required by law in many countries to prevent the disease spreading between animals and from animals to people.

Veterinarians recommend parasite control through flea and tick repellents, many of which can be applied topically to the skin or swallowed in a pill, as well as nutritional diets to prevent many diseases from occurring. Some veterinarians offer other preventive measures in the forms of tattoos and implanted microchips to prove ownership in case animals are stolen or lost.

Treatment

Veterinarians treat animals infested with parasites with deworming medicines. Tapeworms are prevalent in dogs and cats because they often ingest fleas or raw fish and meat which carry worm eggs. Some animals are born with roundworms. These parasites can cause serious health problems for both humans and animals, and infestations must be carefully treated to rid animals of the parasite without killing the host. Veterinarians also treat animals who have been exposed to poisons and toxins from plants, insects, and reptiles or that have suffered extremes of heat or cold. They set fractured limbs and suture skin tears.

Animal reproduction is another aspect of veterinary treatment. Veterinarians advise pet and livestock breeders before conception, then monitor the mother animals during their pregnancies and often assist in the births. Evaluating the newborn animals, some veterinarians perform cosmetic surgery such as docking tails and cropping ears to meet societal expectations for appearance. Others observe animals' development in order to fix anatomical defects. Veterinarians also routinely spay and neuter animals to prevent unwanted litters from being born, and also to assure good reproductive health by eliminating prostate and uterine cancers.

Research and Specialties

Many veterinarians choose to research a specific veterinary medicine topic. These professionals often earn advanced degrees and certification in veterinary science or related fields such as biochemistry. Usually affiliated with veterinary colleges or universities, research veterinarians provide expertise for the specialized diagnostic testing or treatment that some animals require. Pharmaceutical research concerning the control of parasitic heartworms and the parvovirus were two of the most outstanding twentieth century developments in veterinary medicine. The parvovirus, an acute, contagious intestinal disease, was first identified in 1978 in the United States and is the most common infectious canine disorder.

Many veterinary experiments explore the role of genetics in health and also examine alternative methods for reproduction, such as artificial insemination and embryo transplantation. Veterinarians also devise methods to use technology such as ultrasound to diagnose animals' ailments.

Most veterinary medicine specialties address physiological aspects such as dentistry, dermatology, radiology, cardiology, orthopedics, nutrition, toxicology, anesthesiology, pharmacology, and ophthalmology. Other specialties concern animals' intellectual and emotional capabilities; veterinarians specializing in behavior seek new ways to measure how animals react to stimuli and how to utilize this information to train animals. Some veterinarians also address legal and ethical issues related to veterinary medicine. Others seek alternative veterinary medical techniques through holistic healing, massage, and acupuncture.

Military Veterinary Medicine

Veterinary medicine has played a crucial role during wars throughout history because armies rely on animals for transportation, food, and communication. Before warfare was mechanized during World War II, cattle and poultry were driven behind troops to assure fresh meat supplies, and veterinarians often inspected these animals prior to slaughter to protect troops from transmissible diseases and local populations from epidemics.

Horses were vital as cavalry mounts to carry troops. Both horses and mules pulled artillery and supply wagons. Veterinarians treated these animals' wounds and injuries in the field and at evacuation hospitals, where they determined whether the animals should be quarantined, rehabilitated, or destroyed.

In modern wars, veterinarians inspect and evaluate military animals such as pigeons and dogs. They vaccinate war dogs at training camps before canines are sent to warfronts and provide care throughout their service.

Many veterinarians have enlisted as soldiers during wars and were assigned animal-related duties. These veterinarians often lacked adequate and suitable supplies in the field and innovated and adapted surgical procedures to save animals' lives from wounds, parasites, and diseases. For example, war dogs serving in the World War II Pacific theater received blood collected from local donor dogs who were immune to indigenous parasites. Veteran veterinarians returned home and applied useful wartime methods to their peacetime practices.

Veterinary corps were established to maintain a sufficient quantity of enlisted veterinarians to meet military demands. During peacetime, military veterinarians monitor the health of working and ceremonial military animals and conduct laboratory research essential to combat biological warfare.

Because advances in veterinary medicine have resulted in animals aging beyond previously expected life spans, geriatric practices have gained demand. Veterinarians are exploring new ways to treat conditions associated with old age, such as arthritis, cancers, organ failures, and reduced senses. Some veterinarians participate in ventures such as Operation Arctic Care to vaccinate and examine animals in remote regions who would otherwise receive no veterinary attention.

—Elizabeth D. Schafer

See also: Aging; Biology; Birth; Breeding programs; Diseases; Domestication; Embryology; Ethology; Fertilization; Life spans; Nutrient requirements; Physiology; Pregnancy and prenatal development; Zoos.

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VISION

Types of animal science: Anatomy, behavior
Fields of study: Anatomy, biochemistry, cell biology, evolutionary science, neurobiology, physiology

Vision is the ability of animals to analyze light information in their environment. Given the many unique visual worlds in the animal kingdom, there are many different types of eyes and light gathering mechanisms in them.

Principal Terms

ACCOMMODATION: changing the shape of the lens in order to keep objects at different distances focused on the retina

FOVEA: area, often a pit in the retina, of maximal acuity, where each photoreceptor has its own nerve cell, as opposed to many receptors converging on one nerve cell

OPSIN: a membrane-bound protein or pigment, which absorbs light

PHOTON: a unit used to describe light intensity

PHOTORECEPTOR: cell containing membranes which house light-sensitive pigments

RETINA: the light-sensitive film at the back of the eye

Despite the fact that it is often taken for granted, vision is one of the more interesting and complex sense systems. Different animals have, over the course of their evolution, independently fine-tuned their visual systems to adapt to their unique environments and needs. The possession of a good visual system can be the factor dictating a species' survival. Vision is essential for many animal behaviors, such as foraging for food, prey avoidance, and mate choice. Upon considering the many different species in the world, it is evident that there must be many different types of vision; for example, a fish in its unique underwater environment would have a vastly different visual world than an insect in the rainforest.

When animals forage for food, vision is used along with many other senses, especially the senses of smell and hearing, to make a good food choice. Many animals scan a visual field before deciding to forage; thus, the visual system must be acute, enabling the animal to understand what is in its field of view, often in a very short time. The brain must be able to determine such things as shape, form, and color of objects. Many animals utilize color vision when foraging. Cues as to the suitability of a food choice are often indicated by color, for example, the difference between a poisonous berry and an innocuous one. Eye placement (the exact positioning of eyes on the head) is crucial; appropriate positioning of the eyes from each other, as in humans, makes binocular vision possible. Binocular vision gives the viewer a sense of depth in the field of view, critical for many animals when catching prey. Species with laterally spaced eyes have a smaller amount of binocular vision, and some of their visual field has to be viewed monocularly.

Vision is essential in many animals' communication with each other. Body markings and displays in many species are often used as mating signals. Birds provide a striking example of visual communication in animals, where often specific body markings are used to attract mates. Some birds attract mates by elaborate nest construction; the bird with the most elegant nest attracts a mate and ensures reproduction and the passing of its genes to the next generation.

The Physiology of Vision

In simple terms, the visual system takes a signal in the form of light and translates it into a chemical change and later a nervous impulse in the brain; this nervous impulse is what the animal perceives as sight. The two main characteristics of eyes, no matter how complex or simple, are light-sensitive receptors (photoreceptors), and a mechanism to control light. In simple eyes, the light-sensitive receptors make up a layer known as the retina. The nature of a photoreceptor is dictated by opsin, the photosensitive proteinaceous pigment present within the membranes in the photoreceptor. The photoreceptors are variable in size, shape, and content. There are two types in vertebrates: rods and cones. Rods are especially sensitive to light and as such make up the majority of the retina of nocturnal species, who require as sensitive a system as possible. The photopigment in rods is called rhodopsin. Cones are less sensitive to light, but there are different types which are sensitive to light of different wavelengths (or colors), and can give animals color vision. There are many different types of cones, and hence many types of color vision; possession of these cone types and their specific positioning within the retina is an evolutionary adaptation particular to animals who benefit from color vision.

There are two main types of eye design in the animal kingdom: simple eyes and com-

The eagle's keen vision, necessary for its raptor lifestyle, has led to the term "eagle-eyed" for exceptional sight. (Adobe)

Polarized Light Vision

Polarized light plays an important role in the visual world of many animals, including many species of fish and insects. These animals are able to use their visual systems to decode one particular aspect of polarized light, namely the angle of polarization. Light which is polarized has an electric vector which has a specific angle, or orientation. Natural light is unpolarized, but becomes polarized by scattering in air, water, or by reflection off surfaces. Scattering of the ultraviolet (UV) light in sunlight is quite predictable and produces obvious patterns in the sky, invisible to humans without a polarizing filter. These patterns are analyzed by some insects and are used as a kind of map for navigation, for example, to get back to the nesting area after a foraging trip. Similarly, the polarization pattern aids in orientation of the animal. Analysis of the skylight polarization patterns is possible because of the unique positioning of the microvillar photoreceptors within the eye. Pairs of microvillar photoreceptor populations are positioned perpendicular to each other. The light-sensitive molecules within the photoreceptor lie parallel to the axes of the microvilli. Each member of the pair of photoreceptors is maximally sensitive to a different angle of polarized light, and the combined response to a given angle of both members allows the animal to compute the exact angle of polarization. Enhancement of contrast is an advantage of polarized light vision used by fish, although the mechanism of detection of the light is obscure.

pound eyes. Simple eyes have a single layer of photoreceptors, which, in the least complicated case, form a cup of photosensitive material. The human eye, with its complex light-focusing apparatus, is still a simple eye. Compound eyes, which are present in most insects, have many separate optical units, called ommatidia. Each ommatidium has a rhabdom, containing a group of up to nine tubular rhabdomeres, with ciliary or microvillar (finger-shaped) photoreceptors. The orientation of groups of photosensitive cilia is structured, often with pairs of rhabdomeres organized at right angles to each other. This is especially key in analysis of polarized light.

Many visual systems have mechanisms to control light. Restriction of the amount of light entering the eye is useful; the opening through which light enters is referred to as an aperture, as in a camera. Many animals have a contractible iris which constricts and dilates to control light entry through the pupil. For example, in dim light conditions the iris can dilate and let in as much light as possible. Some eyes have lenses which enable light to be focused on the retina, allowing for better resolution of objects in the visual field. Many are able to change the shape of the lens in order to bring an image to focus on the retina, a process called accommodation. Other animals use a cornea to bend light onto the retina, although the cornea is rigid and cannot change shape. On the other hand, there are many species with much simpler eyes, which do not possess any kind of light control apparatus.

Upon reception of light by a photoreceptor, a biochemical cascade of events occurs within the photoreceptor itself, which amplifies the original signal received. The result of this cascade is a nervous signal which proceeds through many neural layers to the brain. Throughout most of the retina in the simple eyes of vertebrates, several photoreceptors connect to one neuron (convergence), but there is often an area of the retina where one photoreceptor connects to one neuron. This area is called the fovea and is the part of the retina which has best acuity. The area within the retina which comprises the fovea is variable. Fish possess what is known as a "visual streak" fovea, which gives excellent vision along a horizontal slice of the visual field. This is an ideal adaptation for fish given their particular habitat.

Information is passed through the nervous system in layers of neurons. The retina is, in fact, an extension of the brain, and contains many nerve cells. The exact arrangement and mechanism of action of neural cell types, and the precise pathway to and within the brain, differ greatly from species to species. Phototransduction in vertebrates is different from that of invertebrates, from the arrangement of the retina to the biochemical cascade and the types of neurons involved.

Ultraviolet (UV) Light Vision

Sunlight is the natural source of ultraviolet light, whose wavelength runs from less than 280 to 400 nanometers. For the sake of vision, however, one need only be concerned with UV light between 320 and 400 nanometers, since any light below these wavelengths becomes absorbed by air before it reaches earth. Many members of the animal kingdom are able to see in the ultraviolet region of the spectrum, due to their possession of a particular class of opsin molecule which is maximally sensitive to UV light. Humans also possess a UV-sensitive opsin, but are unable to actually see UV because the lens, which is yellow, absorbs UV light. There are certain behavioral advantages for the species who do possess UV vision. For example, fish use UV vision extensively in signaling and communication with members of the same species; many fish and birds have UV markings on their bodies which make it easier for other individuals to see them and which may also be involved in mate choice. There are also very strong UV markings on flower petals, which act as guides for pollinators such as bees.

Color Vision

Reflected natural light has a unique property that may be exploited by the visual system of an animal, namely its wavelength, or color. Color vision can be vital for a species in regard to mate choice and foraging. Photoreceptors can be sensitive to different wavelengths of light, or colors; in vertebrates the color-sensitive receptors are called cones because of their shape. The maximum sensitivity of a photoreceptor is dictated by the nature of the photo-sensitive protein (opsin) within the receptor. Opsins can be classified according to the approximate wavelength of light that stimulates them maximally. Opsins have been studied that are sensitive to light from the ultraviolet region of the visible spectrum all the way to the far red region.

To have the possibility of color vision, an animal must possess at least two photoreceptors with differing sensitivities. The brain must then be able to compare the outputs of both these receptors and discriminate color. Often more than two types of photopigment type are present, as in the fish retina, which results in very complex color vision, including sensitivity to ultraviolet light. Color vision has been shown to exist in many animals within the animal kingdom. Positioning and distribution of the different types of photoreceptor within the retina are also key to the ability to discriminate color. In vertebrates, this aspect of retinal structure is called the cone mosaic, and its nature is often closely related to some behavioral aspect of the animal in question. Color vision also requires a central processing system that can decode the various light signals and turn them into a brain output which is useful to the animal.

—*Lucy A. Newman*

See also: Anatomy; Brain; Ears; Eyes; Hearing; Nervous systems of vertebrates; Noses; Physiology; Sense organs; Vocalizations.

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VOCALIZATIONS

Types of animal science: Anatomy, behavior, physiology
Fields of study: Anatomy, physiology

Vocalization is any sound produced through the action of an animal's respiratory system and used in communication. In the animal kingdom, vocal sounds are limited to frogs, crocodilians, geckos, birds, and mammals. Animal calls are used to locate mates, define territory, or indicate the location of food. Mammals also vocalize to express emotion, while primates utilize more complex cries to indicate danger, show aggression, and exhibit love. The complex auditory communication system of humans is a distinguishing mark of the species.

Principal Terms

LARYNX: the vocal mechanism of mammals, consisting of a structure of cartilage at the upper end of the trachea containing the vocal folds

PHARYNX: lower part of vocal tract, connecting the mouth and nasal cavities to the larynx

SYRINX: the vocal mechanism of birds, consisting of one or more membranous structures at the lower end of the trachea, where the windpipe divides into two bronchial tubes leading to the lungs; the membranes vibrate due to pressure differences when air streams across their surfaces

TRACHEA: a cartilaginous tube that transports air from the lungs to the pharynx

VOCAL FOLDS: small, laminated sheets of muscle which meet at the front of the larynx; they are open for breathing, and are brought together to vibrate for voiced sounds

A vocal mechanism typically consists of lungs to provide an air stream, a trachea to conduct the air to a larynx or syrinx, a pharynx, and the associated oral and nasal cavities. Vocalization, any sound produced by the respiratory system, implies that air flowing from the lungs has been converted into an oscillating air stream. The sound can be melodious or noisy; when the vocal folds vibrate the sound is termed phonation.

Animal vocalizations evolved with hearing because of the many evolutionary advantages of sound communication. Sound can be varied in pitch, duration, tonality, and repetition rate, making it possible to communicate considerable amounts of detailed information quickly. Animals may vocalize while keeping their limbs free or while hiding. Because sound waves pass readily through vegetation and around obstacles, vocalization is used among insects, frogs, and birds to indicate sexual receptivity.

Vocalizations are also an important component in the behavioral displays of reptiles, birds, and mammals. Although animals typically employ body language and nonvocal noises in their displays, vocalization provides an impressive elaboration impossible to achieve otherwise. The fearsome sight of a gorilla beating its chest and stomping the ground is enhanced considerably by its bloodcurdling roar.

There are two different types of sound-generating mechanism used for animal vocalizations. The first requires a vibrating structure, such as the voiced sounds of human speech produced by vibrating vocal folds. The second is aerodynamically excited, such as for unvoiced sounds or whistled tones. The vibrating element of voiced sounds is a flow valve, which vibrates when pressure is applied from the lungs. Two different systems occur in the animal kingdom. The first is the larynx, common among mammals; when pressure is applied from the lungs, the vocal folds swing outward, stretching muscular ligaments which tend to restore them. These alternating forces induce vibration in the form of air pulses, which propagate through the trachea to be emitted by the mouth or nose. The second is the avian syrinx, which is blown open by excess pressure on either side of the mechanism and restored by forces supplied by pressurized air sacs surrounding the syrinx. In both cases, pitch can be varied by the muscles associated with the valve mechanism. Airflow through the valve is nonlinear, generating a complete set of harmonics in the radiated sound.

Whistled sounds are created when an air jet impinges on a sharp edge or an aperture, creating a sinuous instability in the air stream. The sound is considerably louder when the air stream is acoustically coupled to a resonating oral or nasal cavity, the size and shape of which determines the resulting pitch.

In any acoustic communication system, signals must compete with noise in the environment. The environment has a preponderance of natural low-frequency noise, but high frequencies are produced more easily by small animals. Most vertebrates, however, do not communicate with high frequency sounds, because they are more readily attenuated and thus do not travel far. The optimum frequencies for auditory communication thus depend on the desired communication range. High frequencies are best for small animals communicating over short distances, while low frequencies better serve large animals communicating over longer distances.

Reptiles and Frogs

Although the vocal apparatus of alligators is rather primitive, they can produce noise-excited roaring and hissing vocalizations when provoked by low-frequency sounds, such as a horn or a cannon. Crocodilians live as lone individuals and establish individual territories defined by their loud vibrant roars. To roar, crocodiles tense their body

Wolves vocalize at dawn and dusk to establish and maintain their territories. (Corbis) muscles and raise their heads and tails high above the water. The emitted sound vibrates the animal's flanks so violently that water is sprayed into the air. Crocodiles are also capable of deep grunting sounds, used during courtship. Geckos are small nocturnal lizards with soft skin. Their voice varies, by species, from faint chirps to loud squawks.

Frog vocalizations encode several pieces of information; the species, the sex, and whether or not it has mated. Male mating calls attract females and indicate the number of other males nearby, critical information for females who wish to deposit their eggs in the most receptive habitat. The vocalizations are produced by primitive vocal cords, consisting of a pair of slits at the throat opening in the floor of the mouth. When the frog forces air from the lungs, the cords vibrate to produce sound. Many species also have a vocal sac, an inflatable chamber located in the throat region of males, which swells to a large size when calls are produced. Air vibrates the vocal cords while passing back and forth between the lungs and the sac, while the vocal pouch acts as a resonating chamber which amplifies the sound. The frog's mouth remains closed while vocalizing, so it can call even while under water.

Birds

In birds, the voice is well developed, having such distinctive sound patterns that many species are named onomatopoeically, such as the whippoorwill. Although birds use different calls for different purposes, each species has a primary song, often repeated incessantly, used for species recognition. Male birds also use vocalizations to mark their territory and to attract mates. Some species can even identify their mates by sound. During the breeding season, the male emperor penguin leaves for several days to forage for food; when he returns he is able to locate his mate, out of a pack of hundreds of birds, from the calls emitted.

The green-backed sparrow utters a hoarse scream when attack or escape is likely to occur, and medium hoarse notes when the bird's indecision between the two courses of action make it unlikely that either will occur. To a family of migrating geese, the sounds of other geese on the ground conveys the information that there is probably food and a safe shelter.

Cuckoos are a highly vocal species; they use a variety of contact calls, alarm notes, and melodious songs used to define territory or attract mates. The male's song is characterized by a repetition of loud, short notes on a descending scale. The common cuckoo found throughout Europe, Asia, and Africa emits the well-known two-note call imitated in cuckoo clocks.

Owls produce a variety of vocalizations with a pitch, timbre, and rhythm unique to each species. Most vocalize at dusk and dawn before beginning to hunt. Their songs vary from the deep hoots of large species to the chirps and warbles of small owls. When its nest is threatened, the nestling burrowing owls emit a buzzing noise, resembling the warning sound of the rattlesnakes that frequently inhabit rodent burrows. North American screech owls begin mating when a special song, commenced by the male, is answered by a distant female. After fifteen minutes of antiphonal singing while gradually approaching, the couple meets, sings a duet with a different song pattern, and mates. Other calls of the screech owl include sounds to prompt the young to reveal their location, a food-soliciting call by the young, and barking calls used to eject the matured young from the parents' territory.

The "voicebox" used by birds to produce birdsong is the syrinx, located where the windpipe divides into the two bronchial tubes leading to the lungs. The syrinx varies considerably among different birds. In the ordinary chicken it is quite simple, consisting of four uncomplicated membranes, which produce the characteristic clucking sounds when activated. An asymmetric chamber at the base of the ducks' trachea adds a noise component to its vocalization, which humans hear as "quacking." The trachea of trumpeter swans enters the sternum, flexes twice into bony pockets, then coils back to the lungs, somewhat analogous to bass orchestral wind instruments. This long resonator implements the production of its clarion, trumpetlike call.

The human brain can perceive speech in sounds having only the remotest resemblance to speech if the rhythm and intonation matches that of a simple sentence. Mynah birds use this phenomenon to deceive us into believing they can speak. They have a syrinx valve on each bronchial tube which can be independently controlled to produce two simultaneous wavering tones, which we perceive as speech when they mimic the rhythm of a sentence.

Mammals

Among mammals, vocalization is used first for survival. Infants vocalize to express hunger or pain, or to be located when lost. Other cries, such as the lion's roar or the trumpeting of an elephant, mandate caution. Animal vocalizations of this type, often accompanied by an offensive posture, are used to startle or intimidate an opponent. There is a direct correlation between vocal anatomy and behavior among mammals. Social animals that readily vocalize have larynges which open less widely when they breathe, thus reducing breathing efficiency. The vocal folds must close to start phonation (wailing of cats, howling of wolves). For breathing, they must open wide so as to not obstruct air flow to the lungs. Horses and animals whose survival depends on running long distances while breathing aerobically have simple vocal folds that can open wide to offer an unobstructed air passage, but which consequently cannot be effective phonators. The giraffe's vocal folds are so poorly developed that the animal was long thought to be mute. In actuality, giraffes can phonate to a limited extent; they groan when injured and call their young when they stray. The more highly developed vocal folds of primates enhance phonation, but at the expense of a more constricted airway.

Vocalization is an important aspect of mammal communication. When the wild dogs of India (dholes) hunt, the leader coordinates the pack's motions with a series of sharp yelps. The black-tailed prairie dog combines a visual and vocal display consisting of jumping into the air with its nose straight up while emitting an abrupt two-part vocalization. This display indicates that some behavior is about to be interrupted or prevented by fleeing, which usually occurs immediately thereafter. The display is only employed when an alternative to flight also exists. Hyenas have no organized social behavior but often cooperate while

Evolution of Human Language

Both the anatomy and the brain mechanism involved in human speech resulted from the evolutionary development of organs originally used for other purposes. The mouth, throat, and larynx were designed for swallowing food and breathing, but evolutionary modification rendered them capable of producing a variety of easily understood sounds. Unfortunately, a flexible speech-producing organ was achieved by so rearranging the throat anatomy that humans are particularly susceptible to choking on food that lodges in the larynx. Even our closest living relatives, the great apes, do not possess a vocal system capable of producing human speech.

In conjunction with a flexible organ of speech, the brain must evolve to allow the fine motor control necessary to control the speech mechanism precisely and to decipher the semantic content of vocal utterances. This process began about two million years ago, when the brains of tool-using hominids began to grow rapidly in proportion to the body. This was probably when human language began, and it is highly plausible that human thought and ingenuity evolved concurrently with articulate speech. As the new hominid societies evolved, groups of males hunted with tools in order to provide meat for females and children. Language was necessary to keep these societies together, and accurate communication was essential for the hunt. The development of language encouraged the brain to grow even faster; by 150,000 years ago the brain and basic anatomy of hominids had attained their modern structures.

hunting. Their cries suggest human laughter—a low-pitched, hysterical chuckling that rises to higher tones. The female deer emits a sharp, staccato bark to warn its young when it senses danger, and lions coordinate a hunt by grunting while stalking prey.

Elephants use their trunks for communication by trumpeting, humming, roaring, piping, purring, and rumbling. At least three dozen distinct elephant vocalizations have been documented, including an assortment of trumpeting sounds ranging from outright blasts to a low groan that males use to indicate that a jousting session is finished. Elephant screams range from expressions of social agitation to the pulsating bellow emitted by a female pursued by an unwanted suitor. Babies scream when they want milk; the scream gets progressively louder until their hunger is satisfied.

Elephants also communicate with infrasonic frequencies (below the range of human hearing), which humans detect as an air pulsation accompanied by low-frequency rumblings. Rumbles constitute the majority of elephant vocalizations and explain the uncanny ability of widely separated groups to coordinate their activities. There are rumbles of reassurance, rumbles to say "Let's go," rumbles to maintain contact, rumbles to cry "I'm lost," courtship and mating rumbles, and a humming rumble produced by mothers for newborn calves. Rumbles also coordinate activities within a given group when preparing to fight a dominance battle with another group, and mothers use a special rumble to reassemble the younger members of her family. About fifteen of the known rumbles have an infrasonic component, which enables elephants to maintain contact over long distances. Because low frequencies dissipate less rapidly in air, they can travel up to five miles. Elephants also emit infrasound to alert others to listen carefully for faint, higher-frequency sounds containing more detailed information.

Highly territorial mammals, such as lions, coyotes, and wolves, vocalize extensively at dawn and dusk to establish and maintain territory. Some species vocalize to attract mates and to intimidate rivals. Male moose give hoarse, bellowing cries during mating season to locate cows; the cows respond with a softer, somewhat longer lowing sound. The male elk, in an effort to collect as large a harem as possible, challenges competitors by emitting a buglelike sound. This vibrant call begins in the low register, ascends to high pitch, then abruptly drops in a scream. Bull seals, arriving at breeding grounds before the females, attempt to obtain as many cows as possible for their harems by frightening away competitors with loud roaring.

Bats and dolphins utilize high-frequency ultrasonic vocalization, or echolocation, as a type of animal sonar to find prey and to navigate in the dark. High frequencies are desirable to locate small targets, as high frequency waves are more directional, and a wave cannot "see" an object smaller than its wavelength.

Primates

Primates communicate by various vocal sounds as well as by facial expressions. Apes and monkeys use growls, grunts, twitterings, chirpings, whispers, barks, screams, and cries to warn of danger, indicate alarm or distress, and keep the members of a clan together. Velvet monkeys are known to have three different alarm calls: One warns of eagles, one of snakes, one of leopards. Howling monkeys emit loud, disconcerting, barking roars. The sound is produced by air passing through a resonating chamber in the throat. Rival groups fighting over territory engage in a duel of roaring until one group retreats. While roaring, all other activity, such as feeding, playing, or exploring comes to a halt. A female howler may also wail in distress when one of her young falls from a tree, while the youngster emits diminutive cries to indicate its position.

Primates lower the natural resonant frequencies of their vocal tracts when faced by danger in order to project the sonic aura of a larger animal. Apes and monkeys achieve this by protruding and partly closing their lips to generate low-pitched, aggressive sounds.

Among the great apes, gibbons are the most vociferous. Their raucous cries, especially boisterous at sunrise and sunset, can carry more than a mile. Apes only vocalize to express an emotional state. The ability to produce vocal sounds not linked to instinct or emotion is the primary difference between human speech and ape calls. The changing sound patterns of human speech represent abstract concepts, while apes produce simple melodies tied to their mood. The seat of human language is the cerebral cortex, while ape vocalizations are controlled by the subcortical neural structures involved in emotion. Emotionally based human vocalizations, such as sobbing, crying, laughing, giggling, or shouting in pain, are also controlled subcortically.

—*George R. Plitnik*

See also: Brain; Communication; Defense mechanisms; Ears; Emotions; Eyes; Groups; Hearing; Mammalian social systems; Mating; Noses; Sense organs; Smell; Vision.

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VULTURES

Types of animal science: Anatomy, classification, ecology, reproduction
Fields of study: Anatomy, reproductive biology, zoology

Vultures are large, carrion-eating birds, useful ecologically because decomposing carrion might otherwise endanger the health of humans and animals. Vultures live in Europe, Asia, the Americas, and Africa.

Principal Terms

CARRION: corpses of dead animals
NEW WORLD VULTURES: storklike vultures of the Americas
OLD WORLD VULTURES: hawklike vultures of Europe, Asia, and Africa
THERMAL UPDRAFT: rising air currents, encountered where the sun warms the air

Vultures comprise two groups of carrion-eating birds. They are useful because they eat carrion, which otherwise might decay and endanger the health of other animals. The twenty-one vulture species inhabit temperate to tropical regions of the Americas, Europe, Asia, and Africa.

All vultures exhibit similar eating habits, behavior, and appearance, including bare heads and necks. Many also have somber-colored feathers. Vultures of Europe, Asia, and Africa (Old World vultures) arise from eaglelike birds. Vultures of the Americas (New World vultures), similar in appearance to Old World vultures, are anatomically related more closely to storks.

Some Characteristics of Vultures

Vultures have bare heads and necks and hooked bills. Carrion is their main food, and on some occasions they attack newborn or wounded animals. Most hunt by long-distance soaring to scavenge with their keen sight. New World vultures differ from Old World vultures in their lack of the ability to vocalize. Six species compose New World vultures. Three live in North America: turkey vultures of the southern United States and northern Mexico; black vultures of the southwestern United States and Central America; endangered California condors; king vultures; Andean condors; and yellow-headed turkey vultures of South America.

There are fourteen Old World vulture species. Among the most interesting are the cinereous (with a color resembling ashes) vultures of southern Europe, northwest Africa, and Asia; the similar griffon vultures; white (Egyptian) vultures found from the Mediterranean to India; and the bearded vultures (lammergeiers) of Europe, Asia, and Africa.

Vultures lack feathers on their heads and necks, which keeps them free of gore from carrion. Among New World vultures, several have interesting appearances. Black vultures have black heads and plumage, with white feathers under the wings. King vultures, in contrast, have feathered neck ruffs and yellow, red, white, and blue heads.

California condors, the largest North American land birds, average four feet in length, with wingspans up to eleven feet. They have black neck ruffs, bald, orange to yellow heads, and black plumage except for white feathers under wings. Andean condors are similar. South American yellow-headed turkey vultures resemble North American turkey buzzards.

Notable among Old World vultures are cinereous vultures, about four feet long with bare, pinkish heads and black feathers. They inhabit Europe, northwest Africa, and Central Asia. Griffon vultures are similar in size and appearance.

Egyptian vultures, two feet long, have yellow heads and white feathers except for black wings. They inhabit Mediterranean areas and are found as far east as India.

Bearded vultures (lammergeiers) are especially interesting. They live on Asian, African, and European mountains. They have tan plumage on the chest and stomach and dark brown wing and tail plumage. Lammergeiers have red eyes in white heads. Conspicuous black feathers surrounding the eyes end in beardlike tufts and led to the name "bearded." These vultures average four feet long and weigh up to twenty-four pounds. Their huge wings allow soaring for hours on thermal updrafts. Lammergeiers are unusual in building large, conical nests on or in rock ledges or caves. A mated, monogamous pair uses the nests many times.

Life Cycles of Vultures

Most vultures nest on bare ground underneath mountain overhangs, or in caves. They build no nests, and females lay eggs on bare rock. After hatching, both parents feed the chicks partly digested carrion regurgitated into their mouths. For example, Andean (great) condors live in mountain caves, and females lay one or two greenish-white to bluish-white eggs on the cave floor. Both parents incubate the eggs until they hatch. The scarcity of the California condor is partly due to the fact that it lays only one egg at two- to three-year intervals. Young condors fly in six months, but parents feed them for another eighteen months. Andean condors first mate at seven years old, and at two-year intervals after that. They are monogamous and may live for forty-five to fifty years. Lammergeiers, as noted, are unusual in building several nests used over and over. The female lays her eggs, incubates them, and feeds chicks with the help of the male.

Image Not Available

Vulture Facts

Classification:
Kingdom: Animalia
Phylum: Chordata
Subphylum: Vertebrata
Class: Aves
Order: Falconiformes
Family: Accipitridae (Old World vultures), with subfamily Aegypiinae (ten genera, twenty species); Cathartidae (New World vultures, five genera, five species)

Geographical location: Temperate to tropical regions of the Americas, Europe, Asia, and Africa

Habitat: Mountains, deserts, and other regions where carrion is available

Gestational period: Up to four months

Life span: Fifteen to fifty years, depending on species

Special anatomy: No feathers on head or neck; weak and blunt claws; New World vultures lack larynxes and thus lack voices

Marabous: Storks or Vultures?

Marabou storks (marabous) combine stork and vulture anatomy and occur throughout Africa. Adults are five feet tall. They have long, storklike legs and sharp, straight bills. Their heads and necks are vulturelike. Most marabou food is deer, antelope, and zebra carrion.

Marabou plumage is gray on the back and wings, with white bellies and ruffs encircling red necks. Most inhabit African wetlands, rivers, and lakes. Pairs build nests in trees or on rocky terrain. Usually, three eggs are laid and incubated by both parents. Chicks hatch during dry season when carrion is plentiful. They stay with their parents for six months. Marabous live for over twenty years.

Vultures consume carrion, preventing decay and danger to health. This activity is one of their main ecological functions. Some vultures (such as condors) eat live food, giving them another ecological function, killing injured or weak members of other species. This helps the species that are eaten to select for individuals which enhance long-term survival.

—*Sanford S. Singer*

See also: Beaks and bills; Birds; Feathers; Flight; Molting and shedding; Nesting; Respiration in birds; Scavengers; Wildlife management; Wings.

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WARM-BLOODED ANIMALS

Types of animal science: Anatomy, behavior, physiology
Fields of study: Anatomy, environmental science, physiology, zoology

Warm-blooded animals—mammals and birds—maintain a consistent body temperature by adjustments in behavior, insulation, and metabolism when exposed to differing environmental temperatures; however, their body temperature can vary through a wide range depending on the time of day, season of the year, and the nutritional state of the animal.

Principal Terms

CORE TEMPERATURE: the internal body temperature around the heart, brain, and spinal cord; warm-blooded animals maintain a consistent core temperature; however, the skin or peripheral temperature varies with their surroundings

ECTOTHERMIC: heat from without; cold-blooded, animals that depend on environmental heat sources, usually solar radiation, to maintain body temperature

ENDOTHERMIC: heat from within; the preferred term for warm-blooded animals because it describes how they maintain their body temperature

HIBERNATION: a sustained period of torpor (lack of activity) where an animal reduces its metabolic rate

HOMEOTHERM: an animal with a constant, steady body temperature

METABOLIC RATE: the rate (expressed in calories per minute) at which an animal produces and consumes energy; can be indirectly measured by the amount of oxygen consumed per minute

METABOLISM: the conversion of carbohydrates, proteins, or fats into chemical energy that can be used to accomplish work and generate heat

POIKILOTHERM: an animal with a changing body temperature

Warm-blooded animals (birds and mammals) were so named because they are warm to the touch. However, a cold-blooded animal lying in the sun would also feel warm, so additional terms have been created. Homeotherm (same temperature) and poikilotherm (changing temperature) have been used for warm- and cold-blooded animals, but hibernating warm-blooded animals reduce their body temperature to a few degrees above their surroundings, and some cold-blooded deep-sea fish live in a constant temperature environment, thus maintaining a constant body temperature.

More accurate terms have been developed that focus on the heat source maintaining body temperature. Warm-blooded animals use the heat generated from their body's metabolism to maintain body temperature, whereas cold-blooded animals depend more on outside sources of heat, such as solar radiation, to maintain body temperature. Thus, warm-blooded animals are called endotherms (heat from within) and cold-blooded animals are called ectotherms (heat from outside). Warm-blooded animals also use solar radiation to help warm themselves on a cold day, and cold-blooded animals have some internal metabolic heat to maintain their body temperature, but endotherm and ectotherm best describe the primary difference between warm- and cold-blooded animals.

The Metabolic Furnace and Body Temperature

Warm-blooded animals (endotherms) are characterized by using metabolism to keep their body temperature relatively constant and independent of the environmental temperature. The overall metabolic process is about 25 percent efficient, which means 25 percent of the food energy accomplishes work and the other 75 percent is lost as heat. The internal organs such as the heart, kidneys, brain, and lungs generate the majority of the heat, which is then distributed throughout the body by the circulatory system.

Because warm-blooded animals produce heat, they must also lose heat to maintain a steady body temperature. The rate of heat loss from the body is dependent on the difference between the skin temperature and the surroundings. The colder the surroundings, the faster heat is lost. To maintain a steady body temperature, warm-blooded animals can adjust their behavior, insulation, and metabolic rate.

Small rodents and insectivores seek shelter in burrows to reduce heat loss, while larger animals, such as elk and deer, graze on warm, sunny slopes on cold winter days to gain solar radiant heat. Penguins huddle together to reduce heat loss in cold Antarctic winds, otherwise the metabolic heat required to keep warm would deplete their body fat stores before the winter's end.

The arctic fox reduces its heat loss by growing a thick, insulating fur coat. In contrast, diving mammals such as the Weddell seal use a thick layer of fat (blubber) under the skin to insulate and reduce heat loss to cold ocean water.

If behavioral adjustments and increased insulation cannot prevent excess heat loss, then warm-blooded animals increase their metabolic rate to generate additional heat to maintain body temperature. Shivering produces an increase in muscle metabolism, and the heat produced adds additional warmth. These metabolic adjustments are costly and indicate that heat loss is greater than metabolic heat production. In this situation, an animal will have difficulty in maintaining a steady body temperature in its surroundings.

Warm-blooded animals that live in cold environments, such as bears, have thick fur coats to help retain their natural body heat. (PhotoDisc)

Cooling the Body

During periods of cold weather and reduced food supply, small warm-blooded animals will decrease their body temperature to a few degrees above their surrounding temperature to reduce heat loss and conserve bodily energy stores. This can be a hibernation lasting throughout the winter months or a period of torpor lasting for the night. This lower body temperature, however, is not a decrease in body temperature as observed in cold-blooded animals, but a new, highly regulated body temperature attained by lowering the animal's metabolic rate. It is a very important strategy for energy conservation and survival.

To maintain a steady body temperature, warm-blooded animals depend on a balance between heat produced by metabolism and heat lost to their surroundings. When the ambient temperature exceeds body temperature, an animal will gain heat instead of losing heat to the surroundings. This situation can then elevate body temperature. Body temperature, however, is held constant by heat loss through evaporation of water from the animal. Water, in changing phases from liquid to vapor, requires energy (heat), and this represents the only mechanism available to an animal if the surrounding temperature is greater than body temperature.

Two mechanisms for cooling the body by increasing water loss are panting and sweating. Zebras, gazelles, and bison are examples of closed-mouth panters. These animals rapidly move air through the nostrils, which cools the tissues lining their upper airways (nasal cavities). Dogs are the best example of open-mouth panters; they move air rapidly over the moist tongue to remove heat. In contrast to panting, sweat glands secret a hypotonic salt water over the skin surface. The sweat evaporates and cools the body surface. Both panting and sweating can reduce an animal's bodily water reserves, resulting in dehydration. Thus, increasing water intake during periods of hot weather is especially important.

Camels are known for their tolerance of hot environments. Although they are closed-mouth panters, they also allow their body temperature to rise during the day by 3 to 4 degrees Celsius. This helps the camel tolerate a hot environment in two ways. By increasing its body temperature, the camel will gain less heat from the environment because there is less of a difference between the surroundings and the camel's temperature. Second, the camel can reduce the amount of panting and water loss needed to keep a steady body temperature. A camel stores body heat during the hot day and loses this heat during the cool desert night. The camel's humps are not stores of water, but fat. This makes the camel's skin thinner, which allows for better heat loss at night.

—*Robert C. Tyler*

See also: Cold-blooded animals; Fur and hair; Hibernation; Mammals; Thermoregulation.

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WASPS AND HORNETS

Types of animal science: Anatomy, classification, reproduction
Fields of study: Anatomy, entomology, zoology

Wasps, stinging insects of the order Hymenoptera, are hornets, which are social species, or mason, digger, carpenter, and mud-dauber wasps, which are solitary species. They help humans by killing insect pests.

Principal Terms

DRONE: a male wasp
HORNET: a social wasp
MANDIBLE: a wasp jaw
SOCIAL WASP: a wasp living in a large colony

Wasps are stinging insects of the order Hymenoptera. Many live in large colonies which have a queen, males, and sterile female workers. Such social wasps are hornets. Wasps are called solitary if they do not live in communities, but build small brood nests to hold their young.

Social wasps (hornets) make paper nests. One example is white-faced hornets, found all over North America. These wasps, 1.25 inches long and black with white markings, build nests, up to half-bushel size, in tree limbs. Yellow jacket species live in colonies of many thousands, close to or under the ground. Giant European hornets, in the United States since the 1850's, are brown with yellow streaks and nest in hollow trees. In some wasp species, no workers are born and females lay eggs in the nests of other wasps. Wasp size varies from parasitic wasps, that can develop in insect eggs, to species attaining body lengths of over two inches.

Physical Characteristics of Wasps and Hornets
Wasp bodies, which are covered by coarse hairs, have a head, thorax (midbody), and abdomen (hind body) segments. Thoraxes hold four wings and six legs. The bodies are steel blue, black, yellow, or red, with abdominal rings. Reproductive, digestive, and excretory systems are in abdomen and thorax. Females have stingers at abdomen ends. Parasitic wasps use stingers to insert eggs into hosts. Female nonparasite wasps (which are most wasps) use stingers to paralyze their prey and inject venom. The stings are painful, because the venom contains histamine and a factor that

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dissolves red blood cells. Wasp stings, especially by hornets, can kill allergic humans.

Wasp heads contain sharp, strong mandibles (jaws), designed to chew hard things, tear up food, dig burrows, and pulp wood and earth. Wasp mouths can also lap liquids. Above the mandibles, their heads contain paired, keen, compound eyes and paired sensory antennae. Queen wasps in social species are reproductive females who use sperm obtained in mating flights to fertilize eggs that become females. Unfertilized eggs become drones (males). Production of queens-to-be or female workers depends on diet.

Wasp Nests and Life Cycles

Nests of social wasps range from combs without protecting covers, to round nests up to ten inches in diameter, having paper tiered combs and waterproof outside covers. Social wasps nest wherever possible. Small combs occur under porch roof and rafters or in trees. There are two yellow jacket types, the long-faced and short-faced species. Long-faced yellow jackets nest in trees, bushes, and roofs, while the short-faced type nests in the ground.

A wasp colony lasts one year. Wasps store no food, and in fall the whole colony dies except for the future queens. They hibernate in crannies over the winter and become queens of new colonies in spring. A colony starts after a queen makes a few cells, lays an egg in each, and feeds larvae with chewed-up insects. Next, larvae spin cocoons and pupate for several weeks, emerging as workers. After this, a queen does nothing except lay eggs. The eggs yield worker wasps until late summer, when the queen lays eggs that will become males and queens. Workers tend the young and enlarge the nests. A hornet nest may have thousands of males, females, workers, and young.

Solitary wasps live alone except for breeding. Afterward, females build flat, one-comb nests. Instead of being papermaker wasps, they are mason, carpenter and digger wasps. Among mason wasps are potters and stoneworkers. Potters wasps make mortar of mud and saliva and place brood nests in trees. Mud dauber wasps mix mud with saliva and build nests under porch roofs. Stone worker wasps mix pebbles with mud and nest on rocks. Carpenter wasps tunnel into trees and digger wasps tunnel into the ground.

All adult wasps eat caterpillars, spiders, beetles, flies, other insects, and nectar. Solitary wasp species feed their larvae with specific live insects. Mothers set up nurseries, paralyze prey by piercing nerve centers with their stings, and take the live food to nests. Then they lay an egg on each body. Larvae feed on the insects until they begin

Wasp and Hornet Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Uniramia
Class: Insecta
Order: Hymenoptera (wasps, ants, and bees)
Suborders: Apocrita, Symphyta (wood wasps)
Superfamilies: Vespoidea, Sphecoidea, Bethyloidea, Scolioidea, Chalcidoidea
Families: Include Vespidae (hornets), Sphecidae, Chrysididae (cuckoo wasps), Pompilidae (spider wasps), Tiphiidae, Scoliidae, Mutillidae
Genus and species: Include *Vespula*, such as *V. vulgaris* (common wasp, or yellow jacket); *V. maculata* (bald-faced or white-faced hornet), *V. crabro* (European hornet); *Polistes*, such as *P. fuscatus* (golden paper wasp); *Eumenes iturbide pedalis* and *E. fraternus* (potter or mason wasp); *Sceliphron caementarium* (black-and-yellow mud-dauber wasp); *Pepsis limbata* (tarantula hawk); *Sphecius speciosus* (cicada killer)

Geographical location: Europe, Asia, and the Americas

Habitat: Trees in forests, woods, and plains; on or under rocks; in the ground; around human habitations

Gestational period: About one month for hatching and pupation

Life span: Varies; queens live up to ten months, while drones or workers live for a few weeks

Special anatomy: Six legs, three on each side of thorax; two pairs of wings spinning cocoons to pupate, emerging after pupation as adult wasps.

Yellow Jackets

North American short-faced yellow jacket wasps (hornets) are 0.75 inches long, with yellow and black head, thorax, and abdomen markings that give them their name. They nest below grass level near decaying wood. Their nests are paper, made from saliva and wood.

Each nest has a queen, who lays all eggs. Fertilized eggs become females and unfertilized eggs become males. Reproductive females are produced when the colony is ending its one-year life span. Sterile females tend the nest and larvae. Reproductive females eventually become queens, and males mate with queens-to-be.

The yellow jacket diet is insects, fruit, and nectar. Only worker yellow-jackets hunt food, which they eat by tearing it with their mandibles. Queens live for ten months, while drones or workers only live for a few weeks.

Helpful Wasps

Most wasps help humans and the environment. They damage some fruit, but they destroy myriad caterpillars, beetles, flies and other harmful insects. Thus, they do far more good than harm. Several species pollinate farm crops. Furthermore, the parasitic varieties lay their eggs in the bodies and eggs of pests such as aphids, thereby reducing their numbers.

—Sanford S. Singer

See also: Bees; Insect societies; Insects; Termites.

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WATER BALANCE IN VERTEBRATES

Type of animal science: Physiology
Fields of study: Cell biology, physiology

Water balance in vertebrates must be maintained within narrow limits so that electrolytes and enzymes are in the correct concentrations for proper functioning. Since sources of water are limited and the losses occur from systems with very different functions, the integration of retention and excretion is complex but essential.

Principal Terms

APOCRINE GLAND: a type of sweat gland that becomes active at puberty and responds to emotional stress; the glands are found at the armpits, groin, and nipples

ECCRINE GLAND: a type of sweat gland that helps maintain body temperature; the glands are located on the palms and soles, forehead, neck, and back

EXTRACELLULAR FLUID: the fluid outside cell membranes, including fluid in spaces between cells (interstitial), in blood vessels (plasma), in lymph vessels (lymph), and in the central nervous system (cerebrospinal)

HOMEOSTASIS: the dynamic balance between body functions, needs, and environmental factors which results in internal constancy

HYPEROSMOTIC: a solution with a higher osmotic pressure and more osmotically active particles than the solution with which it is being compared

HYPOOSMOTIC: a solution with a lower osmotic pressure and fewer osmotically active particles than another solution with which it is being compared

ISOSMOTIC: a solution with the same osmotic pressure and the same number of osmotically active particles as the solution with which it is being compared

Water, which makes up about 60 percent of the body weight of vertebrates, may be the most neglected nutrient. Drinking and eating are the obvious ways of obtaining water, but metabolism, the processes of synthesis and breakdown within the body's cells, also provides water for organisms. In fact, diet and metabolism provide 40 percent of the water necessary for human life.

Drinking water is limited by the environment. Areas such as deserts, which have little rainfall, have little potable groundwater available; even plants have to develop some means of conserving the little water their roots can find or the dew that settles on exposed surfaces during the cool desert night. With no surface water and few plants as sources of water, some desert mammals, such as the kangaroo rat, get most of their water from metabolism. They often do not drink even when a supply of water is nearby.

Water balance varies both daily and seasonally as environmental factors such as temperature, humidity, and wind vary and as activity levels change. The body must maintain nearly constant volume and composition of the extracellular fluid despite fluctuations caused by drinking, eating, metabolism, activity, and environment.

Water Loss from Kidneys and Lungs

There are four sites of water loss: kidneys, lungs, skin, and intestines. Control of water balance depends on the efficiency of water retention compared with the necessity of water loss in the normal functioning of both terrestrial and marine vertebrates. For freshwater vertebrates, for example, excretion of excess water without losing salts is vital.

The kidney can produce urine that can be highly concentrated or very dilute. For humans, urine can be four times more concentrated than body fluids and contain 1,200 milliosmoles of solute. Other animals, particularly some desert species, can produce urine five times more concentrated than that. The more concentrated the urine, the more water is retained during the excretion of waste materials.

Generally, increasing length of the loop of Henle in the nephron is associated with increased concentrating ability of the kidney in mammals. Although some of their nephrons contain loops of Henle, birds cannot match the mammals' concentrating ability. The maximum urine-to-plasma concentration ratio in birds is only a little more than five. The reason for this is that mammals excrete osmotically active urea, whereas birds excrete precipitates of uric acid and uric acid salts that do not contribute to osmotic pressure. The osmotic pressure of birds' urine primarily comes from sodium chloride. Birds also allow their plasma to become twice as concentrated as that of mammals during dehydration.

When water must be conserved, urine is concentrated to a greater degree than when water is plentiful. As water becomes scarce, the concentrations of solutes in the body fluids increase. Osmoreceptors in the hypothalamus sense the increase and stimulate the release of antidiuretic hormone (ADH). Antidiuretic hormone is a small peptide that varies somewhat in composition among vertebrate classes. It affects kidney cells, increasing the permeability of the distal tubule of the nephron and the collecting duct to water. More water is reabsorbed and, therefore, retained by the body. In some species, ADH also affects the numbers of nephrons filtering.

The earliest water-balance problem that the vertebrates faced in their evolutionary history was an excess of fresh water and a scarcity of sodium. The hormone aldosterone evolved in the fishes to cope with this. Aldosterone is secreted by the adrenal gland and increases the reabsorption of sodium by the kidney. Some potassium is lost from the body in exchange for sodium, but since plants are rich in potassium, its loss could be made up in the diet.

Water is also lost or gained when respiring; all gas-exchange surfaces must be moist. Aquatic organisms take in water through their gills in fresh water and lose water through the gills in marine environments. Terrestrial organisms have lungs, and the moist exchange surface is inside the body. Even if the atmosphere is dry, air entering the lungs is moistened to nearly 100 percent relative humidity during its passage through the airways. Expired air loses water to those same airway walls as it leaves the body. Some moisture, however, remains in the air and is lost to the body. The cloud of vapor seen as animals exhale in cold weather is this lost moisture condensing in the cold air.

Breathing rate and volume influence the amount of water lost from the lungs. As breathing rate increases, air moves out of the body more quickly, and there is less time for moisture to condense on the cool airway walls before it is exhaled. The movement of greater volumes of air also increases loss of water vapor from the respiratory tract, because less comes in contact with the airway walls. Since heavy exertion often involves breathing through the mouth rather than through the moisture-conserving nasal cavity, further water is lost. As much as 25 percent of the moisture present in expired air may be lost in a dry environment.

Water Loss from Skin and Intestines

The skin is another site through which water is lost. The sweating which occurs in warm weather is an obvious example. Even during the winter, when the air is cool, "insensible perspiration" occurs as water diffuses through the skin. Insensible perspiration occurs at all times. The perspiration that can be sensed comes from eccrine glands. They secrete a watery fluid that cools the skin by using body heat to evaporate the liquid. The amount of salts and nitrogenous wastes in perspiration is not large; however, when one is working in a hot environment, the loss may be significant.

Primarily, though, it is water that is lost and must be replaced.

The apocrine sweat glands are located in the armpits and groin. They become active during emotional stimulation. These are the glands associated with the musky odor that some animals exude. These glands are not important in regulating body temperature, and their evaporation of water is not a major component of water balance mechanisms. The losses of water from the respiratory tract and the skin are obligatory, usually amounting to about 850 milliliters a day.

The intestinal tract is a source of water gain, as it ingests both liquids and food (with its associated water). Some water, however, is also lost because the copious intestinal secretions contain water. In fact, one day's intestinal secretions may amount to twice the body's plasma volume (from which it is derived). Not all water is reabsorbed in the passage through the stomach, small intestine, and large intestine: About one hundred milliliters are lost in the feces each day.

In a normal human diet, ingested fluid tends to exceed the minimum required by about one liter. Whatever excess is not used in evaporative cooling and lost from expired air or in feces is excreted by the kidney. The minimum water uptake required for balance is defined as that required to provide minimum urine volume without weight loss. The stomach and the small intestine reabsorb most of the ingested and secreted water. Only 35 percent reaches the large intestine. The large intestine is specialized to absorb water and produce semisolid feces for excretion. The maximum rate of water absorption by the intestines lies well above what is normally required.

The body fluid compartments provide an excellent example of the steady-state system characteristic of living things. Intracellular fluid must maintain a composition that promotes chemical reactions and diffusion despite the changes that those reactions bring. Extracellular compartments must retain their individual characteristics even though they communicate with one another. Hormones and nerves coordinate the interactions of the digestive, respiratory, integumentary, and urinary systems, which contribute to the constant conditions of volume and composition of the body fluid compartments.

Studying Water Balance

The study of water balance is often difficult because so many body systems and physical factors are involved. Gross methods include measuring moisture in respired air, feces, and urine, as well as in ingested foods. In other studies, the weight of water in bodies or organs may be obtained by drying: The amount of water is the difference between the wet and dry weights. These methods are crude and give rough estimates of the fluid volume or fluid balance in the body or an individual compartment or organ.

To obtain more precise information, dilution techniques are used. One method is the injection or infusion of an indicator or test substance. This substance must be distributed only in the fluid compartment being measured. It must be safe for the organism, while not being metabolized or synthesized in the body. If the substance can be excreted, it must be measurable in the excreta. Radioactive tracers are also used to determine dilution of an injected or infused sample. The isotope chosen must not influence the mechanisms governing the size and composition of the compartment being measured. Moreover, the body must not be able to distinguish between the radioactive molecule and the unlabeled isotope.

The concentration of the test substance in a sample of the blood, or lymph, or cerebrospinal fluid gives an indication of the dilution caused by the volume of the fluid within the compartment. There is no perfect test substance; each is associated with problems affecting the accuracy of the measurement. Inulin is used to determine the volume of interstitial fluid, but inulin diffuses slowly through dense connective tissue. Radioactive sodium enters most compartments, but it binds to the crystalline structure of bone. The dye Evans blue, which binds to plasma proteins, and radioiodinated serum albumin are used to measure plasma volume, but these substances move out of capillaries.

All the fluid compartments communicate, but some, such as bone and cartilage, communicate more slowly than others, such as lymph and plasma. The resistance between compartments is often supposed to be at the interface between compartments. There is evidence, however, that the rate-limiting factors may not only be the permeability of the cell membrane alone but also the physical state of some of the water within the compartment. For example, in red blood cells, some water is bound to protein and is not accessible to solutes. A portion of the water in mitochondria is not free to participate in osmotic processes. For these reasons, dilution techniques may underestimate the amount of water in the compartment being measured. Although dilution techniques use sophisticated technology, the measurements are often extrapolations and not exact. These techniques do provide a general picture of the distribution of body fluids, but since water balance is a continuing, dynamic process, the values are not stable.

Regulating Water Loss

Loss of water through the skin and respiratory tract is obligatory. All respiratory surfaces must be moist so that gases can pass through them. Amphibians are limited in their geographical distribution primarily because their skin is a respiratory surface and, therefore, water loss from it cannot be curtailed. The water losses vary with environmental factors such as temperature, humidity, and wind. Because of this, amphibians must remain near a source of water which their skin can imbibe.

Loss of body water through "insensible perspiration" is not controllable; it is obligatory. The sweating that helps regulate body temperature is facultative, and it varies with weather and exercise. If sweating is prevented when the ambient temperature is high, the body temperature can rise explosively. This will cause death as surely as the dehydration which was prevented by not sweating would have.

Mammals and birds can minimize water loss by modifying the depth and rate of breathing. On exertion, the rate and depth increases, and correspondingly, the loss of water through the airways and across the skin surface increases. Unless the organism intends to quit breathing and allows its body temperature to rise, some water must be lost in this way.

Losses through the digestive tract are often involuntary. Diarrhea and vomiting accompany many illnesses, and since these uncontrolled losses are from the digestive system, which secretes a volume twice that of the plasma each day, their unreclaimed losses are massive. Dehydration and electrolyte imbalance follow quickly if these losses are not made up. This is particularly crucial for infants, for whom the daily diet makes up 25 percent of the total body water. With dehydration, the volume of the circulatory system decreases and circulatory failure results. In addition, since the extracellular fluid compartments are continuous with the intracellular compartments, the fluid inside the cells becomes hyperosmotic, and metabolic reactions cannot take place.

The retention of water depends upon several conditions. The most important is the sources of water available. If fresh water is not available, a human will die after eleven to twenty days, depending upon the rapidity of onset of dehydration. By that time, the person will have lost 15 to 20 percent of initial body weight. The excretion of wastes, the act of breathing, and insensible perspiration (even in moderate temperatures with shade available) are accompanied by obligatory water losses that cannot be reduced.

For other organisms, water is present in excess and becomes a problem. Freshwater fish take in water through their respiratory surface, the gills. They must release great quantities of urine without losing the salts necessary to maintain proper internal osmotic conditions. The hormone aldosterone promotes that salt absorption from the nephrons.

For marine creatures, on the other hand, the entry of salt is a problem. They must eliminate the excess salt without losing too much of their precious body water. Because kidney function always involves water loss as well as the loss of ions, and because fish and reptiles do not concentrate urine efficiently, many of these vertebrates have evolved salt glands. The salt glands use metabolic energy to excrete sodium chloride with very little water. Each environment presents its own water-balance problems to an organism. Yet even in the world's harshest, driest conditions—in the Antarctic—tiny mites and spiders, penguins, and predatory birds have found ways to live and obtain all the water they need in a land where water is solid most of the time.

—Judith O. Rebach

See also: Kidneys and other excretory structures; Osmoregulation; pH Maintenance; Thermoregulation.

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WEASELS AND RELATED MAMMALS

Types of animal science: Behavior, classification, reproduction
Fields of study: Anatomy, classification

Weasel family members live throughout the world, in many different habitats. They include badgers, martens, mink, otters, skunks, weasels, and wolverines. Most are carnivores, and all are hunted for their fur.

Principal Terms

CARRION: dead, partly decomposed animal bodies
ERMINE: valuable white fur made from weasel pelts taken in winter
GESTATION: time period for carrying developing mammalian offspring in the uterus
MUSK: bad-smelling liquids animals make to mark territory or for self-defense
OMNIVOROUS: able to eat both plants and animals
PERINEAL: located between scrotum and anus in males or the equivalent region in females

About seventy species belong to the weasel family (Mustelidae). These furry mammals weigh from three ounces to one hundred pounds. Included are weasels, mink, martens, wolverines, otters, skunks, and badgers. Mustelids live worldwide, except for Antarctica, Australia, and the Sahara Desert. Their habitats range from the Arctic to tropical rain forests. Some live on the ground, others live in trees, and still others inhabit rivers or oceans.

Most weasel family members have long, slender bodies and all have short legs. Each mustelid paw has five toes, with sharp claws for grasping prey and burrowing. The smallest mustelids, least weasels, weigh three ounces. River otters, the largest mustelids, are four to six feet long (with tails) and weigh up to seventy pounds. Sea otters can weigh ninety to one hundred pounds. Beautiful, luxurious mustelid fur is sought for use in fur garments.

All mustelids have perineal glands which make unpleasant-smelling musks, causing their characteristic odors. Musks mark territory or are used for self-defense. The odor of mustelid musk is most offensive in skunks, which use it for self-defense.

Male and female mustelids often live alone, except when mating. Mating seasons vary with species and habitat. Pregnancy for mustelids ranges from one to nine months. Litters contain one to ten young, depending on species and food availability. Life spans of mustelids that reach old age are one to twenty-five years.

Weasels

Weasels, like most mustelids, are carnivores. They eat other animals, carrion, and insects. All weasels have keen eyesight, keen smell, and are excellent hunters. They are bloodthirsty, often killing for fun and leaving prey carcasses uneaten. Humans hunt weasels in response to their bloodthirsty natures and for their beautiful, soft fur. This is especially true of weasels that live in cold climates and grow white winter coats that collectively provide ermine.

Weasels are known for their unpleasant odor, from musk made in perineal glands. The long-tailed weasel is the best-known North American species. It has a white belly, a brown back, and a black tail tip. Males and females are 1.5 and 1 foot long, respectively. The least weasel, also North American, is the smallest known carnivore, only six to eight inches long.

Martens and Fishers

Martens are carnivorous mustelids, genus *Martes*. They occur in northern forests of the eastern and western hemispheres. Martens are long and graceful, with short legs and sharp-clawed toes. They live in hollow trees and take over woodpecker or squirrel holes. They eat rabbits, squirrels, birds, mice, eggs, and carrion. They mate in July and August. Nine months later, one to five young are born.

The most common North American marten is the pine marten (American sable). Pine martens are most plentiful in the northern Rockies, Canada, and Alaska. They also occur as far south as the Adirondacks, and west to Colorado. A pine marten is twenty-four to thirty inches long, including a six-inch tail. Its brown fur is thick and soft, with orange or white throat and chest patches. Pine martens are hunted for their valuable fur. Their enemies are lynx, owls, and humans. Similar animals, the baum and stone martens of Europe and Asia, have yellow and white throats, respectively.

Another important marten is the fisher, a pine marten subspecies and the largest of martens. Fishers are 4.5 feet long, including 16-inch tails, and weigh up to fifteen pounds. Their luxuriant fur is medium to dark brown, with gold or silver head and shoulder tops and creamy chest patches. Fisher fur is also quite valuable. The fisher habitat range is like that of pine martens, but not as far north. Fishers are the only animals that kill and eat porcupines without being hurt. Otherwise, their diets are like those of other martens.

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Otters

Otters are mustelids that live mostly in water, either in rivers or oceans. River otters are found worldwide, except for Australia, New Zealand, and Antarctica. River otters of Europe, Asia, and North America have thick, four-foot-long, flexible bodies and tails about two feet long. Otter heads are broad and flat, with round ears and blunt snouts. Their nostrils are closed when diving. Beautiful otter fur is dark brown and desired for fur garments. As in other mustelids, otter legs are short. Otter feet are both webbed and powerfully clawed.

River otters live in waterside dens with underwater entrances. Their gestation period of two months produces two to three offspring, which stay with their mother for a year. These otters are rapid swimmers and expert divers. They eat fish, crayfish, snails, shellfish, frogs, insects, birds, and small water animals. River otters are friendly and playful.

Sea otters inhabit the Pacific coasts of Asia and North America. They live mostly in the water. Sea otters are 2.25

to 4 feet long and live on a diet of sea urchins, crabs, snails, and shellfish. They have one or two offspring per litter. Red-brown to black sea otter pelts may cost over two thousand dollars each. Sea otters have been so hunted that they are very cautious. They are protected species in U.S. waters.

Skunks

Skunks are found throughout the United States, in Mexico, and in southern Canada. Cat-sized, these stocky mustelids have long, pointy noses, arched backs, and short legs. Skunk fur is long, thick, shiny, and black, with white stripes down the back. Stripe patterns differ among species. Skunks have white forehead patches and long bushy tails, black on top and white underneath. Striped (common) skunks have long black fur and white stripes running from head to tail. They breed in late winter or early spring and have three to five offspring, after a 2.5-month gestation. Offspring suckle for two months and then their mother teaches them to hunt.

Skunk self-defense uses paired perineal glands on either side of its anus, near the tail. These glands are found in all other mustelids. In skunks they are relatively large and contain terrible-smelling liquid musk. Frightened skunks squirt musk distances up to twelve feet. The horrible odor keeps enemies away. Animals that are sprayed smell bad for days. Skunks inhabit hollow trees or burrows and eat rodents, birds, lizards, eggs, insects, honey, and bees.

Badgers

Badgers are two-foot-long mustelids with short, strong legs, squat, broad bodies, and forelegs having claws that are efficient burrowing tools. They are nocturnal, heavily furred, and very strong. Badgers live in deep burrows on and in prairies, woods, or hills. Like other mustelids, they have perineal glands which make fetid musk. Their pelts are valued garment furs. American badgers are found in western North America, east to Ohio and north to southern Canada. Their shaggy fur mixes gray, black, and brown hair. They eat field mice, squirrels, and gophers, digging animal prey out of underground homes.

European badgers are like American badgers in size and color, but have teeth designed for omnivorous diets. They live in forests in deep burrows, and their litter size is four or five young. These badgers eat fruits, nuts, eggs, birds, rodents, frogs, snails, worms, and insects, and love honey and wasp or bee larvae. Shaggy hair protects them from being stung. All badgers are quarrelsome. Caged together, they fight continually. They are also very brave and fight savagely, if cornered.

Wolverines

Wolverines are mustelids of the genus *Gulo*. They are among the most powerful animals of their size. Wolverines live in northern woods of North America, Europe, and Asia. They have long, ta-

Mustelid Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Carnivora
Family: Mustelidae
Subfamilies: Mustelinae (weasels and allies, ten genera, thirty-three species), Mephitinae (skunks, three genera, thirteen species), Lutrinae (otters, six genera, twelve species), Melinae (badgers, six genera, eight species), Mellivarinae (honey badger)

Geographical location: Worldwide, except Antarctica, Australia, and the Sahara

Habitat: From the Arctic to tropical rain forests; most live on the ground, some live in trees, and still others inhabit rivers or oceans

Gestational period: From one to nine months

Life span: From one to up to twenty-five years

Special anatomy: Paws with sharp digging and grasping claws, luxurious fur, webbed feet in otters

Mink

Mink, mustelid carnivores (genus *Mustela*), inhabit North America, from the Gulf of Mexico to the Arctic, and Northern Europe and Asia. They den near rivers and lakes, combining weasel land habitats and otter water habitats, and make foul-smelling musk. Mink, like otters, hunt in water for crayfish, frogs, and minnows. On the land, like weasels, they hunt rodents and snakes. Mink musk has a nauseating smell. Mink are nocturnal animals that live in burrows and are solitary except when mating (February to March). Mink gestation, 1.5 months, usually yields around six offspring.

Mink have short legs and slender, 2.5-foot bodies (including bushy, 6.0-inch tails). Males weigh two pounds, and females are half that weight. Bobcats, foxes, owls, and humans kill mink. Humans do this for their beautiful, soft, durable fur, highly valued for garments. The fur has two layers, an oily, water-repellant outer layer, and a thick, soft, warm inner layer. Wild mink are brown or blackish brown. Fur farms raise mink for genetically selected black, blue, silver gray, or white fur.

pering heads, heavy 2.5-foot-long bodies, bushy 8-inch tails, short legs, and large feet with sharp claws. Wolverine teeth are long and sharp. Their powerful jaws can crush the bones of prey. Wolverines look like small bears, and their dark, white-marked pelts make fine fur garments. This has made them rare, after ruthless hunting. Males and females can weigh fifty-five and thirty pounds, respectively.

Wolverines are solitary, except for mating in spring and summer. Nine months later, females give birth to around four offspring. Offspring nurse for ten weeks and stay with their mothers for a year. Wolverines do not stalk or chase. They pounce from trees or rocks and kill animals much larger than themselves, such as reindeer. Wolverines also eat smaller animals, birds, and carrion. Wolverine predators are bears, pumas, and humans. When attackers get near wolverines, they spray smelly musk. If this warning does not work, the wolverines fight attackers fiercely.

Mustelid Preservation

Several animal protection groups, such as the World Wildlife Fund and Friends of Animals, have long feared that many animal species will soon be extinct and that making and wearing fur garments is cruel. Thanks to their actions, the U.S. Congress passed an Endangered Species Conservation Act (1973) and its convention (1977). Therein, the United States and eighty other nations designed ways to control and monitor the import and export of fur of imperiled species. Endangered species were defined as in danger of extinction, while threatened species are likely to be endangered soon. Among the covered animals are otters and badgers. Other mustelids may be added soon. Under the act and convention, participant countries must stop fur movement in intercountry or interstate commerce unless they have proof that species involved are not threatened or endangered.

—*Sanford S. Singer*

See also: Endangered species; Fur and hair; Otters; Skunks; Urban and suburban wildlife.

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WHALE SHARKS

Type of animal science: Classification
Fields of study: Anatomy, behavior, ethology, marine biology, physiology, zoology

The whale shark, Rhincodon typus, *is the largest fish species in the world. Like all sharks and rays, its skeleton is composed of cartilage instead of bone. Unlike most sharks, however, the whale shark is a filter feeder, subsisting on plankton that it strains from the water column. Whale sharks are not commonly encountered, and much remains to be learned concerning their biology.*

Principal Terms

CARTILAGE: a tough and flexible tissue that constitutes the skeleton of all sharks and rays

CAUDAL FIN: the tail fin of fishes, which supplies the forward thrust in locomotion

CLASPER: a modification of the pelvic fins in male sharks and rays which acts as the male sexual organ in internal fertilization of the female

ELASMOBRANCHS: the suborder of the sharks and rays

GILL RAKERS: sievelike strainers found upon the gill arches of whale sharks, used to filter food from water taken in though the mouth

HETEROCERCAL: a type of caudal fin in which the spinal column extends into the upper lobe, producing an asymmetrical and distinctly sharklike tail

The whale shark, *Rhincodon typus*, is the largest extant species of fish in the world and may attain lengths in excess of twelve meters (forty feet). Despite its very large size, the whale shark is a generally placid and inoffensive creature that feeds upon plankton, swimming crustaceans, and small species of schooling fish in the water. The whale shark is a filter feeder, and it cruises through the water column with its mouth open. Any food in the water is caught by the large and extensive gill rakers, which are large, sievelike structures located upon the gill arches. The water then passes to the exterior of the animal through the gill arches, and the trapped food is swallowed. The whale shark occasionally exhibits more specialized feeding behavior, hanging almost vertically in the water and opening its mouth. The powerful suction caused by the opening of the mouth draws in water and any food in the vicinity.

Whale sharks are believed to be highly migratory, and are encountered either singly or in groups of up to several hundred individuals. Although comparatively little is known about the lives of these animals, they have been observed to congregate at various locations, such as Ningaloo Reef in Western Australia, at predictable seasonal times. These aggregations are believed to be associated with particularly favorable feeding conditions, such as the spawning cycles of corals. When they are not congregating at these sites, whale sharks are known to make long voyages. Satellite tracking of radio tags attached to whale sharks for periods as long as thirteen months have demonstrated that these fish may range far and wide, crossing the oceans.

Reproductive and Life Cycles

Although a few young whale sharks have been maintained in captivity for short intervals, much remains to be learned about their biology, including their reproductive cycles. As in all sharks and rays, fertilization is internal. The males possess pelvic fins that are modified to form claspers,

Whale Shark Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Superclass: Gnathostomata
Class: Chondrichthyes
Subclass: Elasmobranchii (sharks, skates, and rays)
Order: Orectolobiformes (carpet sharks)
Family: Rhincodontidae
Genus and species: Rhincodon typus
Geographical location: Worldwide, generally in warm temperate and tropical seas except for the Mediterranean, where it is conspicuously absent
Habitat: Coastal and oceanic
Gestational period: Unknown
Life span: Unknown
Special anatomy: The largest shark species, reaching total lengths of at least twelve meters (forty feet); broadly blunt and flattened snout with a very large mouth located almost at the very tip of the animal and containing many minute teeth; a small whisker, or barbel, located on the nostrils above either side of the mouth; eyes located just behind the mouth, comparatively very small; prominent longitudinal ridges extending down the length of the body trunk; large heterocercal tail that is asymmetric (as in all sharks), with the upper lobe larger than the lower lobe and a prominent lateral keel located where the tail joins the body trunk; body coloration characterized by a checkerboard pattern of light stripes and spots against a dark grayish or brownish background on the upper surfaces and pale white below

which are long, cylindrical structures. These are inserted into the female reproductive tract to release sperm, which fertilize the eggs of the female.

Whale sharks were once believed to be an oviparous (egg-laying) species, but more recent evidence has demonstrated that they are ovoviviparous. In this style of reproduction, the fertilized eggs are maintained within the female's uterus both prior to and after hatching. At about the time that the yolk of the embryonic egg has been completely absorbed, the embryos are released into the water to fend for themselves. A single pregnant female was found to have three hundred embryos contained within the uterus, ranging in size from forty-two to sixty-four centimeters (sixteen to twenty-six inches) in length. The length of the gestation period is unknown.

The life span of whale sharks is not known, and because of its immense size it is believed to have few natural enemies upon achieving adulthood. A recent report, however, has described a fatal attack on a whale shark by killer whales (orcas) in the Gulf of California, so these latter must be considered as whale shark predators. Humans may pose a threat to these gentle giants as well; small harpoon fisheries that fish for whale sharks exist in some Pacific cultures, including the Philippines.

—John G. New

See also: Fins and flippers; Fish; Marine animals; Migration; Sharks and rays; Reproduction; White sharks.

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The whale shark is the largest fish species in the world, yet it feeds on tiny plankton, crustaceans, and small fish. (Digital Stock)

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WHALES, BALEEN

Type of animal science: Classification
Fields of study: Anatomy, marine biology, physiology, zoology

These huge marine mammals, in the order Cetacea, live in earth's oceans. All of them use baleen to capture a diet of small sea creatures, and they are the endangered prey of whalers.

Principal Terms

BALEEN: whalebone mouth plates that capture and strain small food animals eaten by baleen whales

ECHOLOCATION: batlike determination from sound echoes of positions of unseen objects; it is used by baleen whales

KRILL: tiny, shrimplike crustaceans eaten by baleen whales

UNGULATE: a hoofed mammal, such as a horse; includes animals deemed ancestors of whales

Baleen whales belong to the order Cetacea, the only mammals which spend their entire lives in the water of the earth's oceans. There are seventy-six cetacean species, and the baleen whales make up ten of them. Among baleen whales are blue (sulfur-bottomed) whales, the largest animals that have ever lived. They grow to lengths of over one hundred feet and can weigh 400,000 pounds (200 tons). This makes them more than fifty times the size and weight of a bull elephant and much larger than any dinosaur.

Like all whales, baleen whales are thought to be descendants of a land animal, believed to have been an early ungulate (hoofed mammal). The huge size of the baleen whale is possible because it lives in the water. This supports its mass and frees it from the limitations of land animals, which can only grow to the sizes and weights their legs will support or their wings can carry into the skies.

Why the ancestors of baleen whales entered the oceans is not understood. It is guessed that the return to the oceans was due to the need for a new food supply or to escape from predators. Most paleontologists believe that it happened sixty million years ago, twenty million years before the first whale fossils occur. No fossil that links baleen whales to their landbound ancestors has yet been found, although the search goes on.

Physical Characteristics of Baleen Whales

The most characteristic physical feature of baleen whales is that, rather than teeth, they have hundreds of baleen plates hung vertically from their upper jaws. The plates, with bristles on their inner edges, capture the krill the whales eat. A feeding baleen whale swims with its huge mouth open and engulfs several tons of seawater containing krill. Then the whale shuts its mouth, it presses its tongue against the back of the baleen bristles, and forces the water out of its mouth. This traps the krill on the baleen plates.

In all whales, evolution yielded streamlined, fishlike mammals. Furthermore, their front legs became paddle-shaped flippers whose bones resemble jointed limbs and digits. In contrast, the external hind limbs disappeared, although in many cases their vestiges are found internalized. The horizontal tail flukes that propel whales are not anatomically related to hind limbs. They are boneless and shaped by fibrous and elastic tissues. Nor are flippers related to fish tail fins, which differ in composition and are orientated vertically.

The whale body is surrounded by a thick blubber (fat) layer. This greatly enhances whale buoyancy, insulates, and is an excellent energy store-house. The insulating ability of blubber may explain why whales living in warm waters have much thinner blubber layers than those living in cold waters. In addition, a whale's soft rubbery skin lacks pores, sweat glands, and sebaceous glands. It is hairless, except for small patches on areas near the chin and atop the head. These hair patches support the theory that baleen whales evolved from animals having hair or fur.

Whales, like all mammals, have lungs and breathe air through one or two nostrils, depending on species, located in a blowhole. Just prior to dives whales close their nostrils tightly. If kept submerged indefinitely, whales would drown. Whale nostrils are located on top of the head for functional convenience in diving. They connect directly to the lungs. Contrary to popular belief, a whale's visible "spout" is not water. It is exhaled, warmed water vapor and spent air from the lungs, plus any water present in the depression around the blowhole.

Four physiological adaptations allow whales to dive deeply and for prolonged time periods. First, they have more blood than land mammals and a huge capacity to store oxygen in blood and muscle. Second, each whale breath replaces 85 percent of the air in its lungs, compared with 15 percent in land mammals. Third, whales can resist the carbon dioxide buildup that triggers involuntary breathing in land mammals. Consequently, most baleen whales can hold their breath for an hour or more under water. Finally, they are able to restrict blood flow to various organs during deep dives, limiting oxygen flow to inessential sites. This protects the whale heart and brain from oxygen deprivation in long dives.

Baleen Whale Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Class: Mammalia
Order: Cetacea (whales)
Suborder: Mysticeti (baleen whales)
Families: Eschrichlidae (gray whale), Balaenopteridae (rorquals, two genera, six species), Balaenidae (right whales, two genera, three species)
Geographical location: Every ocean on Earth
Habitat: Oceans
Gestational period: Varies between ten and sixteen months, depending on species
Life span: Most estimates suggest eighty to one hundred years for animals that survive into old age
Special anatomy: Baleen in the mouth; lungs like land mammals; blow hole; flippers evolved from front legs; horizontal tail; nasal cavity that produces echolocation and vocalization

Special Senses and Baleen Whale Intelligence

Baleen whales have small eyes, lack external ears, and have brains much larger than those of humans. These physical characteristics have led to the belief that the whales use sound and hearing in the way vision and smell are used by land mammals. Two kinds of sounds are made by baleen whales: echolocation and vocalizations. Both are thought to arise from air moving between nostrils and the nasal passages that lead to the lungs

Echolocation sounds are thought to function like biosonar, as in terrestrial bats. That is, whale echolocation is perceived as the means by which they explore the world around them. On the other hand, vocalizations, such as the "songs of humpback whales," are perceived as the language by which members of the same whale species communicate. It is thought that the whale identifies the size, distance, and other characteristics of an object by the directing sounds made in a whale's head toward it and receiving sound waves that bounce back off it. Evidence for the role of echolocation is taken from observations made on whales in captivity. In addition, some beached whales have had parasites in their inner ears that lead scientists to believe that the whales ran aground due to losing the ability to echolocate shorelines and stay away from them.

The great ability of water to carry and amplify sound waves is deemed to be the reason why cetaceans have been able to discard the external ear that land mammals developed to gather airborne sounds. Operation of this system of sensing would have obvious use in navigating and in the capture of prey in dark, often murky ocean water. There it would provide the means to scan by sound for the information almost all land mammals get by seeing.

The unusual sensory capabilities of whales have given rise to considerable speculation as to their intelligence. This is stimulated by the observation that cetaceans are the only animals except elephants (with ten-pound brains) to have brains larger those of humans (three pounds). For example, an adult sperm whale has a twenty-pound brain. However, the relationship of brain size to intelligence, in this size range, is not clear.

Supporting the contention of brain size paralleling intelligence, whales and dolphins show considerable capacity for learning when studied in captivity. Their great playfulness, intraspecies communalism, and the affectionate care of offspring make many people strong advocates of cetacean "language" and great intelligence. These concepts remain unproven.

The Life Cycle of Baleen Whales

Baleen whales reproduce in a fashion similar to that in other mammals. Adults enter a period of courtship. This includes side-by-side swimming, body nuzzling, and body rubbing. Copulation soon follows. The pregnant female carries her unborn young for ten to sixteen months, depending on whale species. Next, a large, very well-developed calf (or occasionally, two) is born underwater. Healthy whale calves can swim well at birth and immediately find the ocean surface, with no help from the mother.

Baleen whales navigate by echolocation, but it is believed that the vocalizations of humpbacked whales are also a kind of language. (Digital Stock)

The calves nurse from two teats situated in a pocket located on either side of the mother whale's genital opening. Whale milk is white and very rich in minerals, protein, and fat; as a result, the calves grow quite fast. Usually a whale calf that weighs one to two tons at birth doubles its weight in the first week. It is reported that nursing occurs very rapidly. A calf approaches the mother whale, touches the nipple of the mammary gland, and milk immediately and copiously squirts into the calf's mouth. Mother whales are reportedly quite affectionate to and protective of their offspring.

Young whales are weaned between one and two years after birth, the age at which most of them leave their mothers. A whale is an adult, capable of reproduction, by six to ten years of age. The life spans of whales vary with maximum species size. The smaller species can live for thirty to forty years. The largest species can live for as long as eighty years. As with all other wild animals, not all whales—in fact, relatively few of them—survive to the ripe old ages noted.

Some Baleen Whale Species

Blue whale (*Balaenoptera musculis*): up to 110 feet long; blue-gray with white spots on sides and belly; small dorsal fins and flippers eight feet long; baleen are short, coarse, and blue-black; lives in all oceans except the Arctic Ocean.

Bowhead whale (*Balaena mysticetus*): up to sixty-five feet long; black; arched, bowlike upper jaw; baleen are up to fourteen feet long; lives only in the Arctic Ocean.

California gray whale (*Eschicthius robustus*): up to forty-five feet long, gray-black; flippers short and blunt; short, cream-colored baleen; lives in the North Pacific on both Asian and American sides.

Finback whale (*Balaenoptera physalus*): the most plentiful whale; up to ninety feet long; very streamlined body; dark gray-brown on back, white on belly; black dorsal fin; short flippers and baleen which are gray with black stripes; lives in all oceans except the Arctic Ocean.

Humpback whale (*Megaptera novaengliae*): up to sixty-five feet long; black, marked with white splashes; many tubercles with hairlike bristles on jaws and atop head; flippers fifteen feet long; short, black baleen; lives in all oceans.

Right whale (*Balaena glacialis*): up to fifty-five feet long; black; seven-foot-long black baleen; lives in the North and South Atlantic Oceans.

Sei whale (*Balaenoptera borealis*): up to forty-five feet long; bluish-black back, gray sides, white belly; long, very fine baleen; lives in all tropical oceans.

Baleen Whales as an Endangered Species

Past, uncontrolled whaling reduced the numbers of almost all baleen whale species so much that they are perceived as being endangered. At first, quotas on whales were set by the International Whaling Commission (IWC) for the purpose of managing whales so as to allow the continuation of the whaling industry. By the early 1990's, most major whaling nations belonging to the IWC had stopped whaling. It is hoped that these actions, in the absence of clandestine whaling, will allow baleen whales to make a comeback by natural increase. Only the future will tell whether this will happen.

—*Sanford S. Singer*

See also: Convergent and divergent evolution; Dolphins, porpoises, and toothed whales; Endangered species; Fins and flippers; Ingestion; Lactation; Mammals; Marine animals; Migration; Respiratory system; Ungulates.

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WHITE SHARKS

Type of animal science: Classification
Fields of study: Anatomy, behavior, ethology, marine biology, physiology, zoology

The white shark, Carcharodon carcharias, *is the largest predatory fish and has become well known through its media-enhanced reputation as one of the most dangerous of sharks. This large and active shark is found worldwide, principally in temperate and subtropical coastal waters. Despite its fearsome reputation, much remains to be learned about the biology of these remarkable and formidable fish.*

Principal Terms

AMPHISTYLY: the mechanism by which the jaws of sharks are suspended from, but not directly fused to, the skull

CARTILAGE: a tough and flexible tissue that constitutes the skeleton of all sharks and rays

CAUDAL FIN: the tail fin of fishes, which supplies the forward thrust in locomotion

CLASPER: a modification of the pelvic fins in male sharks and rays which acts as the male sexual organ in internal fertilization of the female

ELASMOBRANCH: the classificatory subbranch of sharks and rays

HETEROCERCAL: a type of caudal fin in which the spinal column extends into the upper lobe, producing an asymmetrical and distinctly sharklike tail

OVIPHAGY: a mode of reproduction in which embryo sharks develop in the maternal uterus and feed on unfertilized eggs produced by the mother

The white shark (*Carcharodon carcharias*), also known as the great white shark, white pointer, or white death, is one of the best-known sharks principally due to interest surrounding the occasionally fatal interactions between humans and this species. Nevertheless, surprisingly little is known about their biology. White sharks are large, active fish that are only infrequently encountered by humans and which have not survived long in the few attempts that have been made to keep them in captivity. Attempts to study the biology of white sharks are therefore limited to brief observations of their biology and what can be inferred from the anatomy of captured dead sharks.

White Shark Anatomy and Physiology

Like all sharks, the white shark possesses a skeleton composed of cartilage, a tough elastic connective tissue found in all vertebrates. The cartilage in the skeleton of white sharks is strengthened by deposits of calcium carbonate, but there is no true bone as in most other fishes. Like most sharks, the white shark has five pairs of gill slits located just in front of the broad pectoral fin and a heterocercal tail, in which the spinal column extends into the upper lobe. The tail, or caudal fin, of the white shark, as in all members of the family Lamnidae, is almost symmetrical and possesses a pronounced lateral keel at the point where the tail is attached to the body trunk. Such a lateral keel may improve the efficiency of the tail in swimming and turning and is a common element of many large, fast-swimming fishes. The upper jaw of white sharks is suspended from the skull by ligaments rather than fused directly to the skull, as in most terrestrial vertebrates. This amphistylic suspension of the jaws allows them to be pushed forward and out, increasing the efficiency of the biting mechanism in a mouth that is located below and behind the broadly conical snout. White sharks, like all sharks, lack a gas-filled swim bladder to provide buoyancy in the water and rely on the lifting action of their fins and body shape to prevent them from sinking. The streamlined, spindle-shaped body, broad fins, and powerful, symmetrical tail of the white shark suit it well to a fast and powerful swimming style, and white sharks, like others in the family Lamnidae, are among the most active sharks.

White sharks possess special modifications of the circulatory system in the body wall and central nervous system that are known as rete mirabile. These modifications permit the shark to return the heat generated by metabolism to the body core, rather than losing it to the surrounding water as in most fish. The rete mirabile allows white sharks to maintain a core body temperature that is higher than the surrounding water; this may provide an advantage to the shark by raising its metabolic rate and permitting greater activity in the cooler waters which they typically inhabit.

White Shark Reproduction and Feeding Habits
Little is known about the reproductive biology of white sharks. Like all sharks and rays, fertilization is internal, and the males possess special modifications of the pelvic fins called claspers, which are inserted into the female oviduct. White sharks are believed to be viviparous (“born alive”), with juvenile sharks developing within the uterus of the mother until they are ready to be born. During early embryonic development the developing white sharks are nourished by the yolk sac of the egg. When this is consumed, the developing shark consumes unfertilized eggs produced by the mother, a reproductive strategy known as intrauterine oöphagy. There have been relatively few captures of pregnant females or free-swimming juveniles, and the duration of gestation and the size of the juveniles at birth are unknown. The best estimate of white shark size at birth is between 1.2 and 1.4 meters.

White sharks are known to reach a length of six meters (twenty-one feet) and may possibly grow larger. Their life span is unknown. As the white shark grows, the nature of its diet changes; juvenile white sharks appear to feed principally upon fish, whereas marine mammals play an important role in the diet of mature sharks. The high energy yield of the blubber in seals and sea lions may make them attractive prey for these very large predators. White sharks hunt seals and sea lions by swimming deep below them and searching for their silhouettes against the bright surface. Once prey is spotted, the shark attacks with a very swift lunge from below and inflicts an incapacitating or mortal wound with its bite.

White Shark Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Chordata
Subphylum: Vertebrata
Superclass: Gnathostomata
Class: Chondrichthyes
Subclass: Elasmobranchii (sharks, skates, and rays)
Order: Lamniformes
Family: Lamnidae (mackerel sharks, also porbeagle salmon and mako sharks)
Genus and species: Carcharodon carcharias
Geographical location: Worldwide, generally in temperate and subtropical seas, occasionally in tropical seas
Habitat: Continental shelf and occasionally inshore
Gestational period: Unknown
Life span: Unknown
Special anatomy: Large (up to six meters long) and moderately stout-bodied, with a blunt, conical snout and an almost symmetrical caudal fin; pronounced lateral ridge or keel where the tail is attached to the body; large teeth, broadly triangular and serrated; gray-blue or gray-brown (often bronze) on the upper body surfaces, with a white belly; a black spot often present at the axil (armpit) on the bottom surface of the pectoral fin

White sharks have been responsible for fatal attacks on humans, but humans are not a normal part of their diet. It is more likely that the shark mistakes a human for a marine mammal or may merely be curious. White sharks themselves are in considerably more danger from humans, and several nations and states have passed laws protecting these sharks from the effects of human depredations.

—*John G. New*

See also: Fins and flippers; Fish; Marine animals; Migration; Sharks and rays; Reproduction; Whale sharks.

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White sharks have jaws that are specially adapted to increase their biting power. (Digital Stock)

WILDLIFE MANAGEMENT

Type of animal science: Ecology
Fields of study: Ecology, environmental science, ethology, wildlife ecology

Wildlife management strives to allow the use of ecological communities for human benefit while preserving their ecological components unharmed. It also seeks to restore biological communities by managing habitats and controlling the taking of organisms for sport or economic gain.

Principal Terms

CARRYING CAPACITY: the number of individual animals that a habitat can support

COMMUNITY: all the living organisms existing in an area at a particular time

FURBEARERS: mammals that are harvested for their fur, such as muskrat, mink, and beaver

GAME: economically important animals, usually birds or mammals; it includes those taken for recreation or products and those that damage human property

HABITAT: a specific type of environment or physical place where an animal lives; it usually emphasizes the vegetation of an area

HOME RANGE: the physical area that an animal uses in its daily activities to get all its needs, such as food and water

SUCCESSION: change in a plant or animal community over time, with one kind of organism or plant being replaced by others in a more or less predictable pattern

SUSTAINED ANNUAL YIELD: the harvest of no more animals than are produced, so that the total population remains the same

WILDLIFE: traditionally, the term included only mammals and birds that were hunted or considered economically important; today, it includes all living organisms

Wildlife management, also known as game management, is often compared with farming or forestry, because one of its goals is to ensure annual "crops" of wild animals. Aldo Leopold, in 1933, defined "game management" as the art of making land produce sustained annual crops of wild game for recreational use. At that time, animals considered to be game included deer and animals such as coyotes that do damage to domestic animals or crops. Now, however, the term "wildlife" has replaced game, and virtually all living organisms, including invertebrates and plants, are included in management considerations.

Approaches to Wildlife Management

The process of wildlife management has moved through a sequence of six approaches: the restriction of harvest (by law); predator control; the establishment of refuges, reserves, and parks; the artificial stocking of native species and introduction of exotic ones; environmental controls, or management of habitat; and education of the general public. All six are used in modern wildlife management programs, but most emphasis is placed on habitat management and control of harvest.

Primitive man practiced a form of wildlife management simply by setting fires. These fires stimulated the growth of new grasses that lured grazing animals to the areas near tribal camps. It was then easier to kill the animals for food. Tribal taboos often regulated the use of animals, but the first written wildlife law is probably contained in the biblical Mosaic law (in Deuteronomy 22:6). The Egyptians hunted for sport, and the Romans

Preserves

Putting aside land for the benefit of its animals and plants was a novel concept in the early 1800's. Prior to this period, there was too much undeveloped wilderness, and no one gave much thought to saving it in its natural state. The attitude was to develop the wilderness so that it could be put to productive use. In addition, the wilderness was a menacing place where strange and unknown forces lurked. However, as urban and rural areas overtook the wilderness, attitudes began to change.

Yellowstone was the first national park, established in 1872. Establishment of national parks in Australia, Canada, New Zealand, and other countries soon followed. The term "national park" has had a variety of meanings. One version of the national park concept is the wildlife preserve (or reserve). These are parks having game conservation or management as their primary objective. The first national game preserves may be those established in South Africa during the 1890's. While many national game preserves are now found throughout Africa, regional, state, or local game preserves exist in many other countries.

In the United States, game preserves were established in the early 1900's for placing captive-bred bison back into their natural habitat after they had become extinct in the wild. The first of these preserves was the Wichita Forest Reserve in Oklahoma, established in 1905. State wildlife agencies have also set aside lands as game management areas. Some of these areas were initially for the use of hunters, but after the 1960's these areas began to serve nongame species and conservation as well. Others are still maintained for sport hunting and are managed in an effort to control game species populations. At the same time these areas are used for hunting some species, they also preserve habitat for all of the area's species. The hunting preserve has a long history going back to ancient societies, such as those in Mesopotamia, Egypt, and China, starting about 3000 B.C.E.

Although preserves are often set aside for specific wildlife species, they save habitat for all the species found there. Thus, wildlife preserves protect all forms of animals and plants, as do similar areas with different names (such as national park, national seashore, forest reserve, scenic river, wilderness area, and so on). Since these areas change over time, they must be managed. This management is based on ecological and wildlife management principles, but it is difficult to manage for the needs of all the species simultaneously. It is also important to link preserves with corridors so they are incorporated into a self-sustaining environmental system. Maintaining undeveloped areas as preserves is becoming increasingly important, not only for the health and well-being of the animals and plants, but for humans as well.

—Vernon N. Kisling, Jr.

and Greeks had game laws. The first comprehensive wildlife management program was in the Mongol Empire: Marco Polo reported in the thirteenth century that the Great Khan protected animals from hunters between March and October and provided food for animals during the winter.

During feudal times in Europe, wildlife belonged to the royal family; today it legally belongs to the landowner. In most other countries of the world, wildlife belongs to the state, province, or federal government. In the United States, wildlife belongs to the state, as originally granted legally by the Magna Carta, in 1215, to the people of England—the right was transferred to the state when independence was won by the colonies from England.

Only in the last century has the philosophy of wildlife management been not only to preserve but also to increase wildlife abundance. All fifty states of the United States have departments responsible for wildlife conservation. An appointed board of directors or commission oversees the actions of the departments. Groups for wildlife law enforcement, research, management, and information and education make recommendations to the board of directors regarding wildlife management actions. The federal government of the United States also has many agencies that manage

Image Not Available

wildlife on public lands. The U.S. Fish and Wildlife Service is involved with animals that cross state lines, including migratory birds such as waterfowl, marine mammals, and any plants and animals listed as rare or endangered by the National Environmental Protection Act. Other agencies, such as the U.S. Forest Service, Bureau of Land Management, Soil Conservation Service, and the U.S. National Park Service, do extensive wildlife work. Many private organizations, such as the National Wildlife Federation, the Audubon Society, and the Sierra Club actively promote wildlife conservation.

Wildlife management decisions involve the entire range of biological, sociological, political, and economic considerations of human society. Today, the wildlife resource in the United States is managed primarily either for consumptive use (such as sport hunting) or for nonconsumptive use (such as bird watching). Virtually all wildlife management problems are related to the large human population of the earth. Some specific problems are habitat losses (for example, the destruction of tropical rain forests), pollution, diseases introduced by domestic animals into wildlife populations, and the illegal killing of animals for their parts, such as the poaching of elephants for their ivory.

The Process of Management

A wildlife manager must first determine the physical and biological conditions of the organism or organisms being managed. Issues include what the best habitat for the animal is and how many animals this habitat can support. The stage of ecological succession determines the presence or absence of particular animals in an area. All animals need food, water, and protection from weather and predators. Special needs, such as a hollow tree in which to raise young, for example, must be fulfilled within the animal's home range. Wildlife managers attempt to remove or provide items that are most limiting to a population of animals. In many respects, solving wildlife management problems is an art; it is similar to medicine in that it often must deal with symptoms (birds dying, for example) and imprecise information.

The stage of ecological succession may be maintained by plowing lands, spraying unwanted plants with a chemical to kill them, or using fire, under controlled conditions, to burn an area to improve the habitat for a certain wildlife group. Refuges and preserves may be set aside to assure that some of the needed habitat is available; nest boxes and water supplies may even be provided.

Periodic surveys of the number of animals in a population provide guidelines for their protection. If animals are more abundant than the lowest carrying capacity, a controlled harvest may be allowed. Sustained annual yield assures that no more than the population surplus is taken. Wildlife laws protect the animals, provide for public safety, often set ethical guides for sporting harvest, and attempt to provide all hunters with an equitable chance of obtaining certain animals (for example, by setting bag limits). If proper wildlife management procedures are followed, no animal need become rare or endangered by sport hunting. Market hunting, the taking of animals for the sale of their products, such as meat or hides, has been stopped in the United States since the 1920's and is also illegal in most other areas of the world. There are almost no societies left that are true subsistence hunters—that is, living exclusively on the materials produced by the wildlife resource.

The Need for Wildlife Management

The proper management of wildlife resources, based on sound ecological principles, is essential to the well-being of humans. All domestic plants and animals came from wild stock, and this genetic reservoir must be maintained. Maintaining the web of life that includes these organisms is necessary for man's survival. Wildlife resources are used by at least 60 percent of the citizens of the United States each year, and about 6 percent are sport hunters. Wildlife provides considerable commercial value from products, such as meat; it also offers aesthetic values of immeasurable worth. Seeking and observing wildlife provides needed relief from the everyday tensions of human life. Moreover, by observing wildlife reactions to environmental quality, investigators can monitor the status of the biological system within which man lives. Wildlife populations serve as a crucial index of environmental quality.

Wildlife management is a dynamic force that, to be effective, must reflect an understanding of and respect for the natural world. It cannot be practiced in a vacuum but must encompass the realm of complex human interactions that often have conflicting goals and values. Aldo Leopold once defined conservation as man living in harmony with the land; successful wildlife management will help assure that this occurs.

—David L. Chesemore

See also: Biodiversity; Biogeography; Cloning of extinct or endangered species; Competition; Demographics; Ecological niches; Ecology; Ecosystems; Endangered species; Extinction; Fauna: Africa; Fauna: Antarctica; Fauna: Arctic; Fauna: Asia; Fauna: Australia; Fauna: Caribbean; Fauna: Central America; Fauna: Europe; Fauna: Galápagos Islands; Fauna: Madagascar; Fauna: North America; Fauna: Pacific Islands; Fauna: South America; Habitats and biomes; Mark, release, and recapture methods; Population analysis; Population fluctuations; Population genetics; Predation; Zoology; Zoos.

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WINGS

Types of animal science: Anatomy, evolution
Fields of study: Anatomy, biophysics, developmental biology, evolutionary science, ornithology, paleontology, systematics (taxonomy), zoology

Insects, reptiles, dinosaurs, birds, and mammals have developed different types of wings to take them into the air. The anatomy of each of these wings is quite different. Although pterosaurs, dinosaurs, birds, and bats used their forelimbs to support their wings, their forelimbs evolved very differently.

Principal Terms

CAMBER: the degree to which wings are convex on their top and concave on their underside

LIFT: the upward force that is developed by moving wings, which opposes the pull of gravity

SLOTTING: the separation of primary feathers at the tip of the wings

THRUST: the forward force that is developed by engines, rotors, or moving wings, which pushes planes, helicopters, or flying animals and which opposes drag

It is believed that insect wings evolved from bilateral, dorsal flaps called gill plates on thoracic and abdominal segments. These gill plates are seen on some fossilized early insects. During the evolution of gill plates into winglike appendages, the appendages grew larger and became restricted to the second and third thoracic segments. Some early insects used these winglike appendages to sail on the surface of ponds or glide in gentle updrafts and air currents.

Fly Wings

In the fruit fly *Drosophila*, each wing develops from a packet of epithelial cells called the imaginal disk. The imaginal disk grows into a wide, baglike structure that flattens out to become a transparent wing only a few cells thick. Hemolymph-filled veins along the anterior wing margin and within the wing support the fragile wing and supply the wing cells with nutrients and water.

Drosophila powers its single pair of wings quite differently than the more primitive dragonflies and grasshoppers that have two pairs of wings. Flies have internal dorsoventral (vertical) muscles on each side of the body that pull the top of the thorax down when they contract. This moves each of the wings up because the wing bases are inserted into the top of the thorax. Contracting longitudinal muscles (running along the length of the thorax) force the top of the thorax back to its original position. This causes each of the wings to move down. Wing movement in most advanced flying insects is associated with the extremely rapid deformation of the thorax. Houseflies can flap their wings up to two hundred times per second, whereas gnats can flap up to one thousand times per second.

The wings of true flies not only flap up and down but they also alter their angle of attack while moving forward during the down stroke and moving backward during the upstroke. These complex movements provide both lift and thrust and require a number of highly evolved muscle groups.

Lift

For many insects, simple wing flapping cannot generate sufficient lift for flight or for hovering. This is especially true of tiny insects or for insects that have small wing size to body-weight ratios, such as bumblebees. Some flying insects are less than one millimeter long and have extremely small wings that have difficulty moving through air. The viscosity of the air prevents the development of sufficiently small leading-edge vortices. So how do insects produce sufficient lift for flight and hovering?

Beginning with wings above the body, the downstroke moves the wings down and forward through the air at a high attack angle that produces lift. Leading and lagging edge vortices that lower the air pressure above the wing cause lift. As the wing moves down and forward, it continues to rotate slightly, creating larger vortices above the wing that increase the lift. The leading edge vortex begins near the base of the wing and develops quickly toward the tip. Air entering the vortex moves from the base of the wing to the tip. The upstroke provides insects with additional lift. In the upstroke, the wing rotates so that the leading edge is still ahead of the trailing edge. The wing moves up and backward through the air. During the upstroke, lift is created by air reentering the wake created by the down stroke. This moving air pushes against the wing and provides lift. Lift is the sum of "delayed stall" during the downstroke and "wake capture" on the upstroke. In most insects, wing curvature also plays a small role in the development of lift. Most insect wings do not remain flat or rigid during flight or hovering.

Unlike airplanes, which use wings only for lift and have propellers or jet engines for thrust, insects use their wings to generate both lift and thrust. Although lift is generated during both the downstroke and upstroke, thrust is generated only on the upstroke. In fact, during the downstroke there is a force on the insect that slows it or causes it to hover.

Flying Fish

Some fish have greatly elongated their pectoral fins into winglike appendages that can be extended and used for gliding through the air. In water, the pectoral fins are kept folded against the body. Powerful tails propel these fish up to ten miles an hour in the water. After swimming out of the water, they extend their pectoral fins and glide for forty to two hundred yards, a flight that lasts two to fifteen seconds. They sometime reach air speeds of thirty miles per hour if they encounter a tail wind. Some flying fish of the southern Atlantic Ocean have large, oval wings supported by an array of long, bonelike rods that radiate from the base of the pectoral fin. Their pectoral fins are nearly half the length of the fish. Some flying fish have not only elongated their pectoral fins but also their pelvic fins into wings. The pelvic fins are about a quarter of the length of the fish. It is claimed that some flying fish of the Amazon basin actually fly short distances by buzzing their pectoral fins.

Pterosaur Wings

The first pterosaurs appeared in the fossil record about 215 million years ago. They were a very successful group of reptiles, surviving until the mass extinction that marks the Cretaceous-Tertiary boundary 65 million years ago. These flying animals evolved from a population of tetrapod, carnivorous reptiles. Their wings consisted of leathery skin supported by forelimbs, body trunk, and hind legs. The leathery skin of the wings was reinforced by stiff fibers that ran from the front of the wing to its trailing margin.

The forelimbs of these flying reptiles consisted of an upper arm bone (humerus), two forearm bones (radius and ulna), wrist bones (carpals), palm bones (metacarpals), bones of three claw-tipped fingers (phalanges), and the bones of a fourth, very long, clawless finger (phalanges). The first, second, and third finger bones are the thumb, the index finger, and the middle finger. The greatly elongated palm and fourth finger bones along the distal front edge of the wing was longer than the upper and lower arm combined and supported about three-quarters of the wing.

The wings of all pterosaurs were long and sickle-shaped, yet they could fold up like a fan along the sides of the body. Pterosaurs and their wings varied in size. The smallest pterosaurs were about the size of a starling, with a wing span of

The downstroke of wings from above the body provides the lift that allows birds to fly. (PhotoDisc)

about one foot, whereas the largest animal, belonging to the genus *Quetzalcoatlus*, was about twenty-six feet in length from bill to trailing feet, with a wing span of nearly forty feet. The elongated palm and fourth finger bones were over fifteen feet. *Quetzalcoatlus* was the largest flying animal ever, weighing up to two hundred pounds. The long, thin, swept-back, sickle-shaped wings suggest that the pterosaurs were rapid flyers and consummate gliders.

Bird Wings

Approximately 155 million years ago, birds began to evolve from a population of feathered, bipedal, meat-eating dinosaurs. Their wings consisted of feathers supported by the forelimbs. The forelimbs of these early, birdlike animals consisted of an upper arm bone (humerus), two forearm bones (radius and ulna), wrist bones (carpals), palm bones (metacarpals), and bones of the three claw-tipped fingers (phalanges).

In modern birds, the wing bones of the palm and fingers have changed significantly. The palm and first finger bones have been fused and greatly shortened so that a single, small thumb bone protrudes near the wrist. The feather or feathers originating in the skin at the end of the thumb is known as the alula. The palm bones associated with the second and third fingers have partially fused at their ends to become a bone that roughly resembles a fused miniature radius and ulna. The second finger that supports the feathers forming the tip of the wing has become shorter. The third finger has been reduced to a single, tiny bone. The long feathers protruding from the skin covering the palm and second finger are called primaries, whereas the long feathers attached to forearm are known as secondaries. Feathers attached to the upper arm are called tertiary feathers.

Wing flapping is powered by muscles that stretch from the base of the humerus to the large, keel-like sternum. Muscles attached to the top of the humerus base and to the sternum pull the wings up, whereas muscles attached to the bottom of the humerus base and the sternum pull the wings down.

Wing Shapes for Special Tasks

A bird's lifestyle and habitat have selected for wings that may be divided into a number of major categories. Birds that live in forested or densely wooded habitats or birds that prey on flying insects and other fast-moving animals have short, broad wings, sometimes described as elliptical wings. Elliptical wings allow birds to carry out rapid, intricate maneuvers. These wings have a high degree of camber and extensive slotting. Highly cambered wings provide greater lift than more flattened wings. The separation of primary feathers at the wing tip provides most of the needed thrust by acting as miniwings. In general, the primary feathers that constitute the wing tip generate most of the thrust and even some lift.

Gliding Reptiles

The oldest known flying reptile, *Coelurosauravus*, is from the Upper Permian. It had membranous wings supported by twenty-four to twenty-eight long, bonelike rods originating in the skin along the side of the animal. The rods were hollow, with thin walls, and probably developed from ossification of dermal (skin) tissue. Skin connected the rods.

The most anterior seven rods began as a bundle along the side of the animal. The first bundle of rods was followed by four more bundles containing five, four, three, and two rods respectively. The most posterior six or seven rods were not bundled. The rods were not extensions of the ribs, since these lizards have only thirteen thoracic vertebrae. The rods and wings folded against the body when not in use; however, the rods became radially arranged when the wing was extended. The front edge of the wing formed a fifty to sixty degree angle with the body and was not attached to the forelimbs. The trailing edge of the wing was supported by the distal ends of the posterior rods and was not attached to the hindlimbs. There were no large muscles that could power flapping motion of the wings. Thus, these reptiles were incapable of powered flight, only gliding.

The wings of the extant "flying" gecko, *Ptychozoon*, appear to be constructed in much the same way as those of the extinct *Coelurosauravus*, except that there are fewer rods supporting the wings. A gliding lizard in the genus *Draco* that lives in tropical forests of Southeast Asia has winglike folds of skin that are supported by five to seven rods that extend from the body.

The first finger (thumb) has one or more feathers, parallel to the anterior wing margin, which can be raised above the front of the wing to eliminate air turbulence above the wing. While turbulence significantly decreases lift, the raising of the alula decreases turbulence and increases lift.

Sparrows, finches, cuckoos, barn owls, warblers, grouse, and similar birds have elliptical wings that develop a high degree of camber and slotting. Because of these wing characteristics, birds with elliptical wings are capable of intricate maneuvers. Pigeons have broad wings for maneuverability but also elongated, pointed tips to increase their speed. To muffle the noise generated when barn owls swoop down on prey, their flight feathers have developed fringed edges and their coverts have become soft and downy.

Large birds of prey, such as vultures, buzzards, eagles, condors, swans, and storks, have high-lift wings. Their wings are wide and highly cambered with extensive slotting at the tips. The slightest updraft of air provides lift for these heavy birds. The inner flight feathers provide most of the lift within a thermal, whereas the long primary feathers that resemble fingers are used for maneuvering and creating thrust as well as additional lift. The larger the bird, the fewer wing-beats per second. Large vultures flap their wings about once each second.

Many marine birds that live along the shore and fly long distances to find food, as well as many migrating birds, have nearly flat, narrow, long, pointed wings. These wings are associated with rapid flying and, in some cases, with hovering. Peregrine falcons, gulls, geese, ducks, swifts, and swallows are examples of fast-flying birds. Long, narrow, swept-back wings are found in some birds that develop high speeds, such as swifts, swallows, and falcons. The common swift flies up to five hundred miles each day, gathering insects for its chicks. The Arctic tern is known for its long migration from the North American Arctic via Europe and Africa to Antarctica, approximately eleven thousand miles. The peregrine falcon is an extremely rapid flyer, sometimes reaching speeds of 175 miles per hour when it dives in pursuit of other birds.

Kingfishers, hummingbirds, and kestrels are both fast and capable of hovering. Hummingbirds beat their wings forty to eighty times each second, depending on their size. In addition, they can hover and fly backward for short distances. To achieve these feats, the wing bones evolved quite differently than in other birds. Hummingbird wing bones are mostly hand bones, as the forearm

Features of Bird Wings

Wing Type	*Wing Length to Width Ratio*	*Camber*	*Lifestyle and Habitat*	*Slotting*	*Birds*
Elliptical wings for maneuvering	Low (1.0-2.5) short, wide wings	High	Prey on flying insects and other rapidly moving animals and/or live in densely wooded habitats	Moderate to extensive	Wallcreepers, warblers, rollers, sparrows, cuckoos, thrushes, owls, blackbirds, woodpeckers, flycatchers, finches, sparrows, grouse, pheasant, kingfishers, doves, pigeons
High-lift wings for soaring	Moderate (2.5-2.8) very large, long wide wings	High	Heavy birds of prey or carrion eaters	Extensive	Storks, hawks, secretary birds, buzzards, swans, vultures, condors, eagles, pelicans
Wings for speed, gliding, or hovering	High (2.8-4.8) long, narrow, pointed wings, often swept-back	Low	Very fast moving birds that obtain their food on-the-move and/or migrate long distances	Very little to none	Sandpipers, kestrels, cormorants, loons, cranes, geese, gulls, herons, skimmers, hummingbirds, swallows, curlews, swifts, pintails, peregrine falcons, arctic terns, ducks
Wings for long-distance gliding	Very high (4.8-7.0)	Low, nearly flat	Mostly marine birds that fly long distances to feed or migrate long distances	None	Frigate birds, albatrosses
Wings for swimming	High (3.5-5.5)	Flat	Flightless swimmers that use wings as flippers	None	Penguins
Wings for display or warmth			Flightless birds that use wings to keep warm and/or to display their beauty		Rheas, ostriches, emus, kiwis

and upper arm became extremely short. The wrist joint and elbow became rigid, so that the wing only rotates at the shoulder. Their wings are thin, flat, pointed and can become highly slotted. When these birds hover or fly backward, they obtain lift on both the up- and downstrokes of the wing, somewhat like insects. Larger birds usually only generate lift on the downstrokes.

Accomplished gliders, such as the albatrosses and frigate birds, have nearly flat, extremely long, narrow wings. These wings efficiently create lift from updrafts and surface air movements over water and land. These marine birds, which fly long distances when feeding or during migrations, have very long, slender, pointed wings. Each of these birds catches updrafts and is able to glide long distances without using much energy flapping their wings.

Bat Wings

Bats evolved from tetrapod, insectivorous mammals some time after the Cretaceous-Tertiary mass extinction 65 million years ago. Their wings consist of elastic, leathery skin supported by forelimbs, body trunk, and hind legs. The upper arm and forearm support the proximal half of the extended wing, while the elongated hand and digit bones support the distal half of the wing like the struts of an umbrella. Greatly elongated palm bones and digits two, three, four, and five provide the outer wing struts. The thumb, midway along the anterior margin of the wing, is a mere stump. Depending upon the bat, sometimes the thumb has a claw the bat uses to hold onto its perch.

Bats are extremely agile fliers because they can alter the camber and shape of their wings. The skin between the body and the fifth finger and the tail membrane generate most of the lift. The skin between the second and fifth fingers produces forward thrust. Highly maneuverable bats have relatively short, broad wings, whereas migrating bats have exceptionally long, narrow, pointed wings. These long wings increase lift and allow for extended gliding, but bats with long wings are not as agile as those with broader wings. Tail membranes are continuations of the wings and are used for sudden turns and changes of direction. The tail membrane is controlled by the back legs. The tail membrane is also used during landings to brake and help flip the bat upside-down so it can attach to its roost. The bat uses both its wings and its tail membrane to stall as it lands.

Some species of bats are strong enough to take off from the ground, but most initiate their flight from an elevated roost. Although bats do not have a keeled sternum like birds, some are able to take off from the ground and most are very agile fliers.

—Jaime Stanley Colomé

See also: *Archaeopteryx*; Bats; Birds; Feathers; Flight; Insects; Locomotion; Pterosaurs; Respiration in birds.

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WOODPECKERS

Types of animal science: Anatomy, behavior, classification, ecology
Fields of study: Anatomy, ornithology, wildlife ecology

Woodpeckers are scansorial (tree-creeping) piciform birds which are found in areas with trees all over the world, except in Madagascar, Australia, New Zealand, and Oceania. They are members of the family Picidae and consist of 215 species, of which 25 are found in North America.

Principal Terms

ALTRICIAL: type of development in which hatchlings are born naked, blind, nearly immobile, and helpless

BRISTLES: specialized feathers that protect the nostrils

DISPLAY: visual signal used by a bird to trigger behavior in courtship or attacks

DRUMMING: type of nonvocal communication produced by banging bill on a hollow tree trunk or other noise-producing object

RECTRICES: tail feathers

REMNANTS: nesting material not deliberately placed in nest by birds

ZYGODACTYL: type of foot with two toes directed forward and two toes directed backward

Woodpeckers are found worldwide in areas with trees and a temperate climate. They range in size from 3.5 inches to 2 feet. The largest North America species is the pileated woodpecker, which is 16.5 inches long with a wingspan of 29 inches. Most species have a dominant plumage pattern of black or brown and white, with additional splashes of red or yellow. Woodpeckers are scansorial, much like the ancient bird *Archaeopteryx*. To facilitate tree climbing, they have sharply curved claws and strong zygodactyl feet. Most birds have four toes, with one toe (hallux) directed backward and the others forward (anisodactyl foot). This type of foot is ideal for perching, but in woodpeckers the fourth toe is directed backward along with the hallux to produce a foot with two toes forward and two toes rearward, more suited to tree climbing and clinging. A few woodpecker species have lost one of the rear toes and are referred to as three-toed woodpeckers. Rectrices act as props for the woodpecker when climbing, resulting in a hitching motion as the bird moves. These stiff tail feathers are critical for climbing activities, and during molting, the center two feathers are preserved until the rest of the tail feathers are replaced, whereas in other birds the center feathers are the first to be lost.

Stout, chisel-like bills are used to peel bark and excavate wood in search of insects or larvae to eat. Bills are also employed to carve out roosting and nesting cavities in trees and for drumming. Both the skull and bill are designed to absorb the shock of repeated pounding on wood. The sturdy feet and claws together with the rectrices form a triangular brace for the hard pounding by the bill. Woodpecker tongues are very long and wrap around the skull to anchor at the base of the bill. Extension of the tongue to retrieve food is accomplished by a complex system featuring long hyoid (tongue-base) bones. Some woodpecker tongues have barbs to help extract insects and larvae from chiseled holes, while sapsucker tongues are shorter, with fine, hairlike processes to aid in capturing sap and associated insects. Nostrils of woodpeckers are protected from the "sawdust" that excavating bills create by bristles or by being reduced to narrow slits.

Wings are tapered, with a low aspect ratio (ratio of length to width). This wing configuration is designed for rapid takeoff and swift evasive flight maneuvers to capture prey, such as flying insects, or to escape predators. The eyes are positioned on the side of the head, giving the bird a wide field of vision to help spot predators. This ocular arrangement produces a predominantly monocular vision in which the environment is seen by only one eye. Binocular vision, providing depth perception important for flying and landing, is present in a relatively narrow field of vision straight ahead.

Woodpecker Behavior

Some species of woodpeckers live up to fifteen years in the wild. Woodpeckers are monogamous (one male mates with one female). Some of the earliest sounds emanating from the woods in the spring are the drumming of woodpeckers. Woodpeckers vocalize with calls rather than songs. Drumming functions instead of song to proclaim territorial boundaries and attract mates. Both males and females drum. Dry branches, hollow tree trunks or logs, or any other object capable of producing a loud noise may be selected. Most woodpeckers drum in a burst with a rate characteristic of the species. For example, hairy woodpeckers drum at a rate of twenty-six drums per second, but the smaller downy woodpecker drums at a rate of fifteen drums per second. Sapsuckers drum more rhythmically, with a varying rate slowing at the end. Territoriality and courtship are also announced by displays. Bowing, bobbing, and side-to-side head motions, along with partial spreading of wings and tail, are performed during these displays. Some of the most lively and spectacular displays are given by flickers in the spring.

Woodpeckers use their stiff tail feathers for support while they peck. (Adobe)

Nearly all woodpeckers nest in unlined tree cavities, which they excavate. Typically, both male and female birds excavate a new site each year, and old sites are abandoned, to be used by other species of cavity-nesting birds that lack the carving talents of woodpeckers. Cavity nesting protects the eggs and young birds from predators and bad weather. Holes often face the sun to help with warming. Eggs are laid on wood chips and "sawdust" that are deposited at the bottom of the nesting cavity as a consequence of excavation. These remnants are not supplemented by other nesting materials. An average of four (a range of three to nine) eggs are laid. The eggs are white since the protection afforded by the nest cavity obviates the need for camouflage coloration. Incubation takes about two weeks and is shared by both male and female birds during the day, but is done solely by the male at night. Incubation begins prior to the last egg being laid, resulting in asynchronous hatching. Hatchlings are born immobile, downless, and with eyes closed, and are fed by the parents (altricial development). Feeding is by regurgitation and is performed by both parents until the birds are completely developed, in about four weeks. First-born birds have an advantage and are more likely to survive.

Woodpeckers eat insects lodged in the trunks or limbs of trees, and some species also feed on the ground or catch insects in the air. Nuts, fruit, seeds, and tree sap are also consumed, depending upon the particular species. Ants are the insect preferred by many woodpeckers. It should be noted that the effects of woodpeckers on trees are rarely harmful and are usually beneficial as a result of pest control. Nest holes are drilled in diseased or dead trees.

Bird watchers can easily identify woodpeckers at a distant by their characteristic posture and flight. They are usually seen clinging to branches or tree trunks using their rigid tail feathers as props. Woodpeckers fly in a pattern of moderate rises and falls. This bounding flight pattern is produced when a short burst of wing beats (rising) alternates with a closed-wing glide (falling). Woodpeckers are not long-distance flyers, and most species are permanent residents or migrate modest distances, which may vary with the abundance of food. Most species are solitary or paired, but the acorn woodpecker lives in communal groups of up to sixteen birds. This clown-faced bird has a complex social structure and is known for its acorn hoarding. Birds harvest acorns in the fall and ram them into holes drilled in one or two "granary" trees, usually at the center of their territory. As many as fifty thousand acorns are each carefully matched to a hole which will result in a tight fit. As the acorns shrink in size with age they are relocated into slightly smaller holes to produce another snug fit. The secure fit makes it difficult for robbers to steal acorns from the tree without alerting the vigilant acorn woodpecker family.

Woodpecker Facts

Classification:
Kingdom: Animalia
Phylum: Chordata
Class: Aves
Order: Piciformes
Family: Picidae (woodpeckers and allies)
Subfamily: Picinae (true woodpeckers, thirty-three genera, seventy-two species)
Geographical location: Every continent except Australia and Antarctica
Habitat: Wooded areas with temperate climates
Gestational period: One to seven days
Life span: Up to fifteen years
Special anatomy: Feathers, including stiff retrices and bristles; two wings, low-aspect ratio; zygodactyl feet; stout bill; long tongue

Environmental Ecology

The largest (with a length of twenty-one inches) and most spectacular North American woodpecker was the ivory-billed woodpecker, now thought to be extinct. When European settlers first came to the United States, this species was found throughout the southeast, as far north as North Carolina and up the Mississippi Valley to southern Illinois and Ohio. These birds were killed for their bills, which were prized for head ornaments by tribal leaders and warriors among Canadian Indians. Hunters could get two or three buckskins in trade for one bill. An even greater impact resulted from logging. These huge birds required large trees for nest cavities which are up to nine inches across and fourteen inches deep. In the twentieth century, ivory-bills had been exterminated from all but a few isolated areas in Louisiana, Florida, and South Carolina. Their last stronghold was in the Singer Tract of large cyprus trees in Louisiana. Unfortunately, the Singer Tract was heavily logged with the help of German prisoners of war in 1941, destroying much of the habitat for the few remaining birds. The last authenticated sighting of an ivory-billed woodpecker was in April, 1944, in northwest Louisiana. Since that time there have continued to be unconfirmed sightings, and a glimmer of hope remains that some of these magnificent birds may yet live in the fifty thousand remaining acres of the Singer Tract, or in other forests in the southeastern United States or Cuba.

—H. Bradford Hawley

See also: Beaks and bills; Birds; Feathers; Flight; Molting and shedding; Nesting; Respiration in birds; Wildlife management; Wings.

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WORMS, SEGMENTED

Type of animal science: Classification
Fields of study: Anatomy, invertebrate biology, physiology

Segmented worms are a class (Annelida) whose body parts are arranged in a longitudinal series of rings, or segments. Many are hermaphroditic.

Principal Terms

HERMAPHRODITIC: a condition where both male and female reproductive organs are located in the same animal

NEPHRIDIA: excretory tubules specialized for excretion and osmoregulation, with an external opening and with or without an internal opening

PARAPODIA: paired lateral projections on each side of most segments, variously modified for locomotion, respiration, or feeding

SEPTA: a thin, muscular tissue used to separate segments into a series of ringlike cavities

SETAE: a needlelike, chitinous structure of the integument, used for locomotion

The Annelida are segmented worms in which the body wall, coelom (body cavity), epidermis, circular muscle, longitudinal muscle, and peritoneum are arranged into a longitudinal series of rings or segments. True segmented animals exhibit metamerism, a repetition of a structure or organ from segment to segment. Each segment has the same fundamental structures as all the others. With the exception of the digestive system, the major organ systems of the annelids are metameric in structure. Young annelids generally have few segments, but as they grow, new segments are formed by the division of the terminal segment. Annelids represent the most highly organized animals capable of complete regeneration.

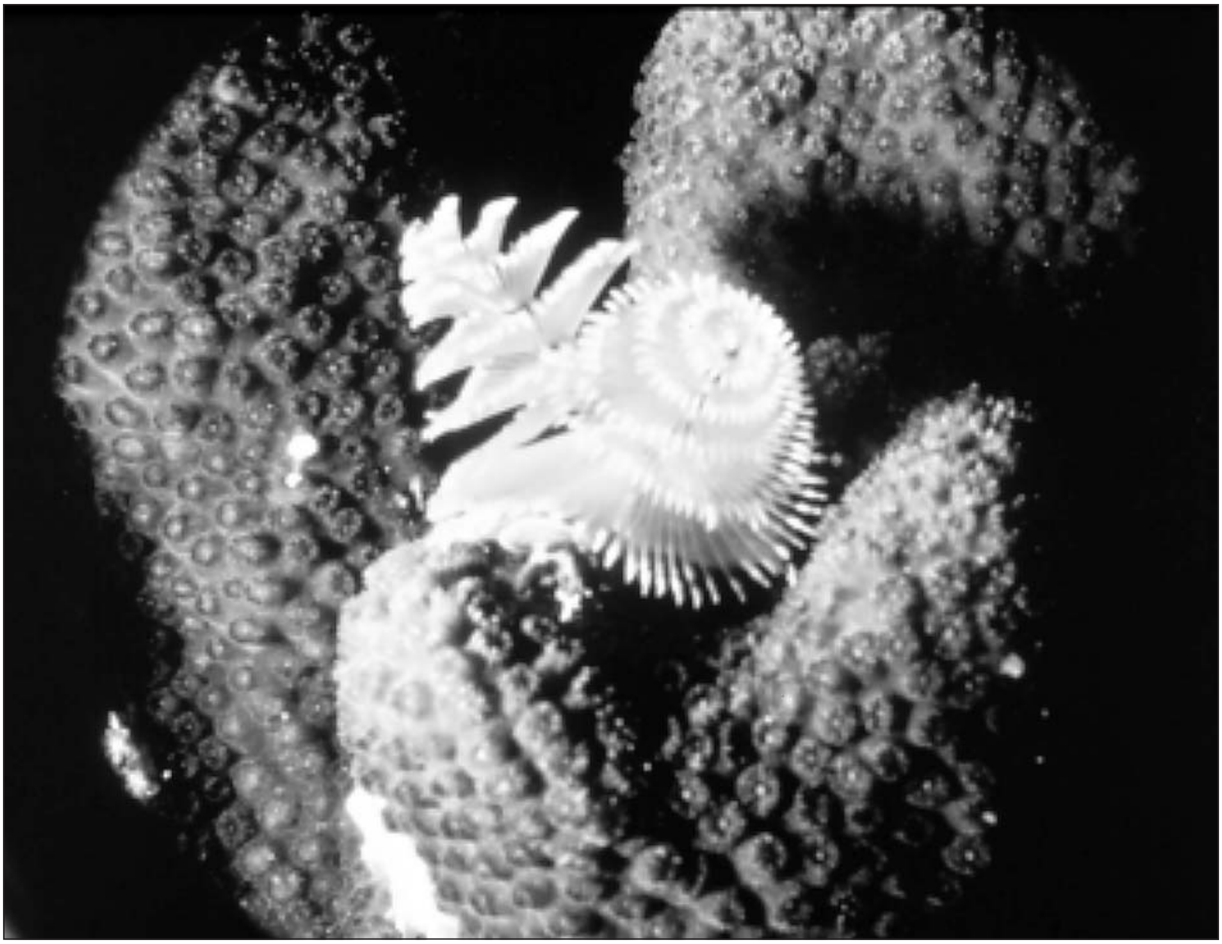
General Characteristics of the Annelids

The mouth lies between the first and second segments and forms one segment called the prostomium. In leeches, the mouth contains suckers for attaching to the body of a host. The brain originates in the prostomium and develops a pair of circumpharyngeal nerve rings that reach around the pharynx to form the ventral nerve cord, which appears as a chain of ganglia, one pair in each segment. In the Polychaetes, a pair of swimming or crawling parapodia are located on most of the segments. Both the Polychaetes and Oligochaetes contain external setae to assist in locomotion.

The annelid body is covered with a thin cuticle. Each segment has a ring of circular and longitudinal muscles that contract to either elongate or shorten the segment. A spacious coelom, divided by septa, lies between the body wall and an internal digestive tract. The coelom is filled with fluid and serves as a hydrostatic skeleton in all annelids except the leeches. The coelom also contains the circulatory and excretory systems. A system of large vessels (hearts) pump blood through a ventral vessel into capillary beds that invade all of the tissues. The blood is returned to the hearts via the dorsal vessel. Each segment, except the first and last, contains a pair of nephridia, which collect wastes and deliver them to the outside.

Reproduction in the Annelids

In many species of polychaete worms, fertilization is external and takes place in the open sea water. The palolo worm provides a good example of polychaete reproduction. Through most of the year, the worms exist as sexually immature ani-



Each section of a segmented worm, such as this marine fireworm, contains the same fundamental structures as all the other sections. (OAR/National Undersea Research Program)

mals called atokes, but during the breeding season, the posterior segments develop gonads, and the coelom becomes filled with gametes. On the night of breeding, individuals back out of their holes, and the posterior portion, called an epitoke, breaks free. The epitokes swim to the surface for a few minutes and burst, shedding eggs or sperm and leaving a rapidly disintegrating body. Reproduction in the palolo worms is tied to an annual cycle designating the month, a lunar rhythm designating the day, and a diurnal cycle designating the hour of reproduction. Over 90 percent of the population breeds within a single two-hour period of the entire year.

Oligochaete worms are hermaphroditic, with a pair of testes in the tenth and eleventh segments and a pair of ovaries in the thirteenth segment. During copulation, two worms exchange sperm. Once the eggs are fertilized, the clitellum, a swollen glandular region of the epidermis, secretes a membrane that slips forward along the body so that the eggs are laid directly into it as it passes. Finally, the cocoon slips off the head, and the eggs develop into tiny worms, which later emerge from the cocoon. The reproductive system of leeches is very similar to that of the Oligochaetes.

—D. R. Gossett

See also: Fertilization; Flatworms; Hermaphrodites; Hydrostatic skeletons; Regeneration; Roundworms.

Segmented Worm Facts

Classification:
Kingdom: Animalia
Subkingdom: Bilateria
Phylum: Annelida
Classes: Polychaeta (with parapodia and numerous setae), Archiannelida (small marine annelides with simple body), Oligochaeta (parapodia absent and few setae), Hirudinea (leeches, parapodia and setae absent)
Orders: Polychaeta—Errantia (palolo worms), Sedentaria (lugworms); Oligochaeta—Lumbricus (earthworms); Hirudinea—Rhynchobdellida (no jaws, pharynx eversible, colorless blood), Gnathobdellida (three jaws, red blood)

Geographical location: Found all over the world

Habitat: Polychaeta—mostly marine, found near the shore or on the bottom of shallow areas, with a few species in living in brackish water or freshwater; Archiannelida—marine; Oligochaeta—freshwater and terrestrial forms found burrowing in soil or leaf mold; Hirudinea—freshwater and terrestrial environments often found attached to the body of a host

Gestational period: Varies among species, but most species lay eggs within a few days after fertilization; eggs usually hatch within a few days to a few weeks after being deposited

Life span: Varies among species; can be as short as a year in some polychaetes and up to several years in some earthworms

Special anatomy: Elongated, metameric (segmented) bilateral invertebrates with appendages (parapodia) and chitinous setae in many species but lacking in Hirudinea; possess a true coelom (body cavity lined with epithelial tissue) divided by septa with a closed circulatory system, complete digestive system and an excretory system (nephridia) in each segment; leeches have specially adapted mouth parts for attaching to the body of the host

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ZOOLOGY

Type of animal science: Fields of study
Fields of study: Zoology

Zoology is the branch of biology devoted to the study of the animal kingdom. The study of zoology encompasses the analysis of and classification of animals.

Principal Terms

COMPARATIVE ANATOMY: the branch of natural science dealing with the structural organization of living things

ECOLOGY: the study of the interactions between animals and their environment

EMBRYOLOGY: the study of the development of individual animals

EVOLUTIONARY ZOOLOGY: the study of the mechanisms of evolutionary change and the evolutionary history of animal groups

MORPHOLOGY: the study of structure; includes gross morphology, which examines entire structures or systems, such as muscles or bones; histology, which examines body tissues; and cytology, which focuses on cells and their components

PHYLOGENETICS: the study of the developmental history of groups of animals

PHYSIOLOGY: the study of the functions, activities, and processes of living organisms

SYSTEMATICS: the delineation and description of animal species and their arrangement into a classification

TAXONOMY: the classification of organisms in an ordered system that indicates natural relationships

ZOOGEOGRAPHY: the study of the distribution of animals over the earth

Attempts at classification are known from documents in the collection of the Greek physician, Hippocrates, as early as 400 B.C.E. However, the Greek philosopher Aristotle (384-322 B.C.E.) was the first to devise a system of classifying animals that recognized commonalities among diverse organisms. Aristotle arranged groups of animals according to mode of reproduction and habitat. After observing the development of selected animal groups, he noted that general structures appear before specialized ones, and he also distinguished between sexual and asexual reproduction. Aristotle was also interested in form and structure, and concluded that different animals can have similar embryological origins and different structures can have similar functions.

In Roman times, Pliny the Elder (23-79 C.E.) compiled four volumes on zoology widely read during the Middle Ages. Some scholars have deemed those volumes little more than a collection of folklore, myth, and superstition. One of the more influential figures in the history of physiology, the Greek physician Galen (c. 130-c. 201 C.E.), dissected farm animals, monkeys, and other mammals and described many features accurately, although scholars have noted that some of these features were then wrongly applied to the human body. His misconceptions, especially with regard to the movement of blood, remained virtually unchanged for hundreds of years. In the seventeenth century, the English physician William Harvey established the true mechanism of blood circulation.

The Foundations of Zoology

Until the Middle Ages, zoology was little more than a collection of folklore and superstition. However, during the twelfth century, zoology began to emerge as a science. The thirteenth century German scholar and naturalist St. Albertus Magnus refuted many of the superstitions associated with biology and reintroduced the work of Aristotle. The anatomical studies of Leonardo da Vinci in the fifteenth century have been noted as being far ahead of their time. His dissections and comparisons of the structure of humans and other animals led him to several important conclusions. For example, Leonardo noted that the arrangement of joints and bones in the leg are similar in both horses and humans, thus embracing the concept of homology, or the similarity of corresponding parts in different kinds of animals, suggesting a common grouping. A Flemish physician of the sixteenth century, Andreas Vesalius, is considered the father of anatomy for establishing the principles of comparative anatomy.

Throughout most of the seventeenth and eighteenth centuries, classification dominated zoology. The Swedish botanist Carolus Linnaeus developed a system of nomenclature still in use today, referred to as the binomial system of genus and species. Linnaeus also established taxonomy as a discipline. His work was built on that of the English naturalist John Ray and relied upon the form of teeth and toes to differentiate mammals and upon beak shape to classify birds. Another leading figure in systematic development of this era was the French biologist Comte Georges-Louis Leclerc de Buffon. The study of comparative anatomy was further developed by men such as Georges Cuvier, who devised a systematic organization of animals based on specimens sent to him from all over the world.

A cell is the smallest structural unit of an organism capable of independent functioning. Although the word "cell" was introduced in the seventeenth century by the English scientist Robert Hooke, it was not until 1839 that two Germans, Matthias Schleiden and Theodor Schwann, proved that the cell is the common structural unit of living things. The concept of the cell provided impetus for progress in embryology and animal physiology, including the concept of homeostasis, referring to the stability of the body's internal environment.

The formation of scientific expeditions in the eighteenth and nineteenth centuries gave scientists the opportunity to study plant and animal life throughout the world. The most famous scientific expedition was the voyage of the HMS *Beagle* in the early 1830's. During this voyage, Charles Darwin observed the plant and animal life of South America and Australia and developed his theory of evolution by natural selection. Although Darwin recognized the importance of heredity in understanding the evolutionary process, he was unaware of the work of a contemporary, the Austrian monk Gregor Mendel, who first formulated the concept of particulate hereditary factors, later called genes. Mendel's work was not widely disseminated until 1900.

Electronic Zoology Resources

Conservation International: www.conservation.org. This Web site provides information about biodiversity conservation in the world's endangered ecosystems, including a map of global biodiversity hotspots, profiles of hotspots, and many other resources.

International Commission on Zoological Nomenclature (ICZN): www.iczn.org. This Web site describes the official body responsible for providing and regulating the system for ensuring that every animal has a unique and universally accepted scientific name.

International Species Information System (ISIS): www.worldzoo.org. This Web site offers information about this organization that helps zoological institutes manage their living collections by providing software for records keeping and collection management, and then pools this information.

Wildlife Conservation Society: www.wcs.org. This Web site offers information about the organization's conservation activities.

Modern Zoology

During the twentieth century, zoology has become more diversified and less confined to such traditional issues as classification and anatomy. Zoology, broadening its span to include such areas of study as genetics, ecology, and biochemistry, has become an interdisciplinary field applying a wide variety of techniques to obtain knowledge about animal kingdom. The current study of zoology has two main focuses, taxonomic groups, and the structures and processes common to these groups. Studies of taxonomy concentrate on the different divisions of animal life. Invertebrate zoology deals with multicellular animals without backbones; its subdivisions include entomology (the study of insects) and malacology (the study of mollusks). Vertebrate zoology, the study of animals with backbones, is divided into ichthyology (the study of fish), herpetology (amphibians and reptiles), ornithology (birds), and mammalogy (mammals). Taxonomic groups also subdivide paleontology, the study of fossils. In each of these fields, researchers investigate the classification, distribution, life cycle, and evolutionary history of the particular animal or group of animals under study. Most zoologists are also specialists in one or more of the related disciplines of morphology, physiology, embryology, and ecology.

Animal behavioral studies have developed along two lines. The first of these, animal psychology, is primarily concerned with physiological psychology and has traditionally concentrated on laboratory techniques such as conditioning. The second, ethology, had its origins in observations of animals under natural conditions, concentrating on courtship, flocking, and other social contacts. One of the important recent developments in the field is the focus on sociobiology, which is concerned with the behavior, ecology, and evolution of social animals such as bees, ants, schooling fish, flocking birds, and humans.

—*Mary E. Carey*

See also: Anatomy; Animal kingdom; Biology; Demographics; Ecology; Embryology; Ethology; Evolution: Animal life; Evolution: Historical perspective; Genetics; Marine biology; Paleoecology; Paleontology; Physiology; Systematics; Veterinary medicine; Wildlife management.

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ZOOPLANKTON

Type of animal science: Classification
Fields of study: Ecology, invertebrate biology, marine biology

Zooplankton are a free-floating collection of aquatic organisms that are carried by water currents. In contrast to phytoplankton, zooplankton are heterotrophic. Zooplankton is a term that includes organisms from many animal and protist phyla.

Principal Terms

AUTOTROPH: an organism that has the ability to make its own food from inorganic substances
BENTHIC: organisms that live at or near the bottom of the ocean
HETEROTROPH: an organism that requires the ingestion of food for survival
NEKTON: an aquatic organism that has the ability to swim
PHYTOPLANKTON: small, aquatic free-floating plants

Zooplankton is found in almost all major fresh and marine water bodies. Many species, however, are restricted to specific territories depending on conditions of light, temperature, salinity, chemical composition, and turbulence. Their range also varies geographically and vertically within the water column.

Zooplankton Types

The diversity of zooplankton makes classification difficult. Holoplanktonic zooplankton are free-floating their entire lives and are mostly invertebrates. Flagellated, ciliated, and amoeboid protozoa as well as several species from the animal phyla Cnidaria, Ctenophora, Chaetognatha, Mollusca, Annelida, Urochordata, Echinodermata, and Arthropoda make up the majority of collected organisms. Meroplanktonic zooplankton are the free-floating forms of organisms having swimming nekton or attached benthic stages as part of their life cycle. They consist mostly of egg and larval stages of marine benthic invertebrates that include worms, snails, clams, barnacles, crabs, starfish, and sea urchins, as well as many marine fish, such as tuna. Body forms, life cycles, diet, and location vary among species

Zooplankton are often divided according to size. The most common divisions and sizes for zooplankton are nanoplankton (2 to 20 micrometers), microplankton (20 to 200 micrometers), mesoplankton (0.2 to 20 millimeters), macroplankton (2 to 20 centimeters), and megaplankton (20 to 200 centimeters). Although generally small, even jellyfish several meters in size are considered zooplankton because they are unable to swim effectively against the current.

Copepods are one of the most studied forms and are classified as holoplanktonic zooplankton. Copepods have a segmented body with three distinct sections. Several pairs of legs and large antennae are used to create feeding currents that capture phytoplankton, especially diatoms, and other small zooplankton. Copepods are classified as mesoplankton and are nearly five millimeters in size. They are the most important herbivore in the ocean. Advanced collection techniques, however, have uncovered the presence of smaller zooplankton classifications that may be an important ecological first link.

Ecological Importance

Zooplankton diet varies greatly among species. There are carnivorous and herbivorous zooplank-

Zooplankton Facts

Classification:
Kingdom: Protista or Animalia
Phyla: Cnidaria, Ctenophora, Annelida, Nemertea, Arthropoda, Chaetognatha, Mollusca, Phoronida, Bryozoa, Echinodermata, Hemichordata, Chordata, Urochordata
Geographical location: Large bodies of freshwater and salt water
Habitat: Mainly in surface waters
Gestational period: Variable
Life span: Variable
Special anatomy: Highly variable between different phyla; generally small with a flattened body and many projections; zooplankton may also store oils used for buoyancy

ton, as well as those that feed on nonliving organic material. Herbivorous forms feed on phytoplankton through a process called grazing. This process prevents damaging blooms of phytoplankton from increasing in numbers. The link between phytoplankton and zooplankton is also important in passing the energy fixed by autotrophs to higher trophic levels of the food chain. Herbivorous zooplankton are eaten by carnivorous zooplankton, other invertebrates, or fish. The food chain may terminate in the top carnivores that include large fish, birds, and mammals, including humans.

Adaptations

Because of their small size, zooplankton are very sensitive to water conditions. Maintaining position in the water column is an important adaptation for many zooplankton species because they lack the ability to swim strongly enough to counteract the water current. Their density is often slightly greater than that of sea water. In addition, high salinity and low temperatures increase the viscosity of surrounding water, making it harder for zooplankton to move. A larger surface area and flattened body form covered by many projections or spines counteracts these obstacles and prevents the zooplankton from sinking. Several zooplankton also increase their buoyancy by storing low-density materials, such as certain oils. Small body movements, including the action of flagellae and cilia, also counteract the sinking motion.

Vertical Migration

The depth at which zooplankton exist is variable. While some float at the surface of the water, others may inhabit depths greater than four thousand meters. The concentration, or biomass, of zooplankton decreases with increasing depth. Many zooplankton exhibit a daily rhythmic vertical movement called diel vertical migration. They may migrate downward from the water surface during the day and upward at night. These movements may avoid predation and may conserve energy by slowing metabolism in colder deeper waters. Seasonal migrations from deeper waters in the winter months to surface waters in the spring are common. This migration may decrease metabolism and conserve energy throughout the winter when there is a lack of food.

—Paul J. Frisch

See also: Arthropods; Echinoderms; Marine animals; Marine biology; Mollusks; Protozoa.

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ZOOS

Type of animal science: Ecology
Fields of study: Conservation biology, environmental science, ethology, population biology, wildlife ecology, zoology

Keeping wild animals has evolved, over the past five thousand years, from animal collections maintained by ancient societies to modern zoological gardens and aquariums with significant programs in wildlife appreciation, education, science, and conservation.

Principal Terms

AQUARIUM: self-contained and self-supporting aquatic environmental exhibits, maintained either independently or in association with a zoo

EX SITU: conservation and research out of the animal's natural environment (at a zoo)

FROZEN ZOO: frozen tissue bank maintained at a zoo that contains wild animal tissue and reproductive samples for use in future breeding programs

IN SITU: conservation and research in the animal's natural habitat

MENAGERIE: a French word for zoos first used in the early 1700's to describe the keeping (and later exhibition) of animals

VIVARIA: a Latin word for a structure housing living animals, first used by the Romans to describe the places holding elephants and other animals for their shows

ZOO: an English abbreviation of the term "zoological garden"; first used in the early 1800's to describe the early British zoos, it tended to replace the word menagerie in the 1900's

Ancient rulers maintained wild animal collections beginning about 3000 B.C.E. in Mesopotamia (in the area that is now Iraq), Egypt, China, and possibly the Indus Valley (now Pakistan). From around 3000 B.C.E. in Mesopotamia, Sumerian, Babylonian, and Assyrian kings formed collections of native and exotic wildlife in royal parks. These parks were a combination protomenagerie, hunting reserve, and garden park. The parks were used for falconry, hunting wild beasts, entertaining guests, and personal pleasure. Animals kept in these parks often included elephants, wild bulls, lions, apes, ostrich, deer, gazelle, and ibex. Kings and wealthy individuals also had fishponds, flight cages for birds, and pets. Keepers and veterinarians were employed to care for these animals.

From around 2700 B.C.E., Egyptian pharaohs and wealthy Egyptians had animal collections as well. Native species were caught locally, and exotic species were obtained through commerce and tribute. These animals included lions, leopards, hyena, gazelle, ibex, baboons, giraffe, bears, and elephants. There were also fishponds and bird flight cages. Exotic animals came from the so-called Divine Land (Palestine, Syria, and Mesopotamia), Nubia (on Egypt's southern border), and Punt (the Ethiopia area).

In China, each ruling dynasty created animal reserves, beginning with the Shang dynasty, the first to unify the region, from about 1520 B.C.E. These royal parks were large, walled-in natural areas, where wild animals roamed freely and were maintained by park administrators, keepers, and veterinarians. Animals in these parks included fish, turtles, alligators, birds, camels, horses, yaks, deer, elephants, rhinoceroses, and possibly giant pandas.

Ancient and Medieval Animal Collections

The Greco-Roman societies, from 1100 B.C.E. to 476 C.E., were the next to evolve urban centers, overtaking the Mesopotamian and Egyptian civilizations and their animal collections, while the Chinese society and collections continued in isolation from the Western world. Greek curiosity, travel, and trade were favorable for the development of animal collections; however, their ruling city-states did not have the wealth or influence to develop large collections. There were pets, temple collections with animals used in processionals, showmen and animal trainers with animals used in itinerant animals acts, and small collections featuring native animals, including the large ones, such as bears and lions, that could still be found in the area. The Roman Republic (509-27 B.C.E.) provided its rulers and wealthy citizens with the opportunity to maintain small collections of native species. The first exotic animals seen in the Republic were Indian elephants taken in battle (280 B.C.E.). Hunts and processionals, which began during the Republic period, evolved into increasingly elaborate spectacles during the Empire period (27 B.C.E.-476 C.E.). Much has been made of these shows because of the large number of animals that were displayed and killed, but it is their appearances in these spectacles that reveal the introduction of exotic species to Rome. Unfortunately, little is known about the collections in which these animals were kept. Large collections kept in vivaria by emperors, municipalities, and military units supplied animals for the spectacles. Public entertainment also included itinerant performing animal acts. Private collections of native and exotic animals were kept in villa gardens, fresh and salt water ponds, bird enclosures, cages, parks, and hunting reserves.

Persian and Arabic societies between about 546 B.C.E. and 1492 C.E. also had gardens containing wild animals. During this period, Persian and Arabic collections extended throughout the Middle East, India, Asia, northern Africa, and Spain. Meanwhile, medieval Europe (476-1453 C.E.) saw the fall of the Roman infrastructure and the rise of monarchies, monasteries, and municipalities. These centers of administrative, religious, and social life were also centers for medieval animal collections. Kings and wealthy barons kept elephants, lions, bears, camels, monkeys, and birds, especially falcons. Monasteries maintained modest collections for economic and aesthetic reasons. Towns had animals in moats (when no longer needed for defensive purposes), pits, and cages; they often kept animals used in their coat of arms, such as deer, lions, bears, and eagles.

Collections even existed in the Americas, although it is not known when they began. Both the Aztecs of Central America and the Incas of South America had extensive animal collections. Montezuma's estates, in what is now Mexico, included a large bird building, which included freshwater and saltwater ponds, as well as a staff of three hundred keepers. A separate collection combined birds of prey, reptiles, and mammals, along with its own staff of three hundred keepers. The Incas also had animal collections, along with domesticated herds of guanacos and vicuñas.

Early Modern Menageries

Europe emerged into its Renaissance period as the sixteenth century dawned. The accompanying age of exploration brought to light many new species from distant lands. The proliferation of sixteenth century European animal collections was greatly influenced by these discoveries, increasing the collections in both size and number. Renaissance collections first developed in Italy, where the importation of animals from Asia and Africa was already well established, and then spread throughout Europe as the continental nation-states developed their own trade routes. Living animal collections, an essential part of royal courts, became commonplace among wealthy collectors. However, obtaining, shipping, and caring for wild, living animals was expensive and difficult, especially since little was known about the needs of the newly discovered species. Nevertheless, these new animals were status symbols and were of immense interest, and so the collections grew.

During the seventeenth and eighteenth centuries these collections, known as menageries, developed throughout Europe and the European colonies. The earliest colonial menageries began as acclimatization farms and animal holding areas at colonial botanical stations located at the more important colonial posts. A tremendous increase in these stations occurred during the nineteenth century, as the exchange of plants and animals became commonplace.

As the nineteenth century advanced, menageries could be found everywhere, due to the intense interest in the many new species and the exotic places from which they came. Knowledge about these animals increased and their transport was greatly improved. As a result, menageries evolved into zoological gardens during the early 1800's, and aquariums developed in the mid 1800's.

Early Zoos and Aquariums

The establishment of the Zoological Society of London's zoological garden at Regent's Park in 1828 was a significant event in the history of animal collecting and may be considered a transition in the evolution of zoos. This collection was intended from its inception to surpass any then in existence, with an emphasis on education and research. Private European menageries evolved into public zoological gardens, going from collections for the few (royalty and wealthy collectors) to zoological gardens for all citizens. In the United States, exotic animals were first introduced in 1716, when a lion arrived at Boston. Other species were gradually introduced over the remainder of the eighteenth century, and menageries containing many species appeared toward the end of this century. Traveling and circus menageries became popular in the early 1800's.

A few small urban menageries were already established when the Zoological Society of Philadelphia (chartered in 1859) opened its zoological garden in 1874. Most of these urban menageries eventually closed, but a few, such as those at Lincoln Park in Chicago and Central Park in New York City, continued and eventually became modern zoological gardens. Throughout the rest of the world, menageries were developing into zoological gardens, although often hindered by local economies and politics.

Robert Warington and Philip H. Gosse first developed the modern aquarium during the early 1850's in England. Gosse also worked with the Zoological Society of London to establish the first public aquarium at the London Zoo in 1853. Other public aquariums, along with the home aquarium craze, swept Europe and the United States soon after.

The turn of the century brought about a tremendous increase in the number of zoos and, to a lesser extent, aquariums that lasted up through World War I. It was a period during which zoos and aquariums improved their programs in conservation, animal husbandry, research, and education. Beginning in the 1890's, conservation of wildlife became an important concern in the United States and the European colonies. Europe had been dealing with conservation issues for many centuries, but these other regions saw their seemingly limitless resources quickly disappear. The New York Zoological Park (the Bronx Zoo), along with other United States zoos, played a significant role in conserving the American bison, which had become extinct in the wild. European zoos did likewise, saving the European bison (wisent), Père David's deer, and Przewalski's horse from extinction.

Animal husbandry research improved when the Penrose Research Laboratory opened at the Philadelphia Zoo about 1901-1905. In situ field research began at the New York Zoological Park with the inception of its Department of Tropical Research in 1916. Exhibition techniques received further attention when Hagenbeck's Tierpark (in Stellingen, Germany) opened in 1907. This was an important event in the trend toward moated, open exhibits (rather than buildings), ecological exhibits (rather than systematic arrangements), and mixed species exhibits (rather than single species exhibits). Hagenbeck's Tierpark featured panorama exhibits based on zoogeographic themes, with a series of back-to-back moated displays designed in such a way that, from the visitor's perspective, the animals appeared to be together in one space.

World War I affected zoos because of a loss of employees to the war effort, a loss of revenues to operate the facilities, a loss of paying visitors, difficulty in finding food for the animals, and a loss of some animals. After recovering from the social and economic impacts of this war there was another surge in the number of zoos and aquariums up through World War II. As zoos and aquariums increased in numbers, the professional management of these institutions improved and became more organized.

During the 1930's, a studbook for the European wisent was established, the first of many species-specific wild animal studbooks. As of 1997, there were 150 mammal, bird, and reptile international studbooks and world registers. In 1887, the Verband Deutscher ZooDirektoren (Association of German Zoo Directors) formed in Germany, the first of several early professional associations. In the United States, the American Association of Zoological Parks and Aquariums (now the American Zoo and Aquarium Association) formed in 1924. In 1999 there were forty-six national and regional associations.

World War II repeated the problems faced during the previous war but to a much greater extent, because in addition to the previous problems, there was more physical destruction of European zoos. The physical, social, and economic damage from this war took longer to correct than did the first war's. Improvements began in earnest as soon as the war ended, however, and the postwar period became a time of scientific advances, improved technology, better animal husbandry, new exhibit designs, improved education, more intense conservation programs, and professionalism.

Modern Zoos and Aquariums

Many new zoos and aquariums were built in the decades after World War II, and many older zoos and aquariums were renovated. In addition, many advances were made in areas important to animal husbandry, such as veterinary medicine, chemical immobilization and transportation, animal nutrition, reproductive biology, conservation techniques, biotechnology, materials and exhibit design, and water management technology for aquariums.

Zoo staff training became more formal and systematic beginning in the 1950's. The work had become a profession, and the required knowledge had increased, making formal training a necessity. In 1959, a zoo school was established at the Wrocław Zoo, Poland, as well as at several German zoos in the 1960's and 1970's. The American Zoo and Aquarium Association published a zookeeper training manual in 1968 and began a series of training classes in 1975. In 1972, the first of sev-

Wild Animals as Diplomatic Gifts

Animals have always been used as diplomatic gifts and tribute. Because wild animals are difficult to capture, ship, and maintain, they have been coveted luxury items. Rarely seen exotic animals, especially the large mammals, were impressive prizes in royal collections. King Manuel I of Portugal sent his rare Indian rhinoceros as a gift to Pope Leo X in 1515, hoping to influence the Pope's decisions on the placement of the demarcation line dividing Portugal's and Spain's colonial possessions. Muhammad Ali of Egypt provided giraffes to Paris, London, and Vienna in 1826 in order to secure their governments' favor when he waged war against their ally, Greece. In less dramatic ways, kings stayed on the good side of fellow rulers with gifts, including animals. Subordinates to rulers also provided wild animal gifts to their rulers as favors. If a ruler was very interested in an animal collection, he often used diplomatic envoys and other government officials to obtain particular species. Just about every country has a national collection, to which wild animal gifts are sent. In the United States, the National Zoological Park in Washington, D.C., has received living animals presented to the president since it was established in 1889. Even today, China still uses giant pandas as diplomatic gifts, although such gifts are now accompanied with a mandate to contribute to panda conservation programs.

Zoo Biology

Until recently, there has been little training needed or given at zoos. Most zoo employees learned their work through word-of-mouth from experienced workers. During this time, very little was understood about wild animals or any of the fields of study now associated with wildlife husbandry. Knowledge about wild animal care has evolved and grown along with the knowledge in those sciences relevant to this care. As more was learned about species' needs in the wild, animal behavior, animal health, nutrition, population biology, other zoological studies, and the scientific and professional aspects of zookeeping emerged. Heini Hediger, former director of the Bern, Basel and Zürich zoos, reviewed and explained this growing base of knowledge in a series of books written from the 1940's to the 1960's. Hediger's concept was known as zoo biology, a practical and scientific approach to wildlife husbandry that laid the foundation for much of today's studies and animal management. There is now a journal with the same name *Zoo Biology*, which encourages the study and publication of information related to this field. There are also numerous training programs for zookeepers and other zoo employees, both within zoos and independently at community colleges. While taking care of wild animals is fun, it is also a professional and a scientifically managed business.

eral academic programs in zookeeper training began at the Santa Fe Community College in Gainesville, Florida.

Professional associations increased as well. The American Association of Zoo Veterinarians formed in 1946, the American Association of Zoo Keepers formed in 1967, and the Association of British Wild Animal Keepers was founded in 1972. Since then, several other segments of the zoo and aquarium work force have formed professional associations.

Conservation efforts intensified as the seriousness of the endangered species problem increased. More attention was paid to endangered species and environmental problems in the 1960's and 1970's, particularly after activities were held at many zoos and aquariums for the first Earth Day on April 22, 1970. Government laws and regulations concerning endangered species and wildlife importation increased significantly during these decades as well. Conservation efforts at zoos and aquariums included the establishment of international and regional studbooks, regional species survival programs, taxon advisory groups, conservation assessment and management plans, International Union for Conservation of Nature and Natural Resources (IUCN) species survival commission action plans, fauna interest groups, breeding consortia, scientific advisory groups, species survival plans, and, as of 1997, over 1,200 conservation research studies at American zoos and aquariums.

Recent trends include a popular increase in the number of new aquariums, the development of more naturalistic exhibits, participation in in situ conservation research, development of frozen zoos, and the use of biotechnology to bring back extinct species. Zoos and aquariums have evolved over the past five thousand years into important cultural and conservation institutions. This evolutionary process will continue into the future.

—*Vernon N. Kisling, Jr.*

See also: Breeding programs; Cloning of extinct or endangered species; Domestication; Ecology; Endangered species; Genetics; Population genetics; Reproductive strategies; Urban and suburban wildlife; Wildlife management.

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GLOSSARY

Abdomen: The part of the body between the thorax and the pelvis, containing the viscera; the posterior part of an arthropod (such as an insect or crustacean).

Abiotic: The physical part of an ecosystem or biome, consisting of climate, soil, water, oxygen, and carbon dioxide availability, and other physical components.

Ablation: The technique of removing a gland to determine its function and observe what effects its removal will precipitate.

Absorption: The movement of nutrients out of the lumen of the gut into the body.

Abundance: In ecology, the number of organisms living in a particular environment.

Acceleration: The appearance of an organ earlier in a descendant's development than in the ancestor, as a result of an acceleration of development in ontogeny.

Acclimatization: A process by which animals are adapted to new environmental conditions.

Accommodation: Changing the shape of the eye's lens in order to keep objects at different distances focused on the retina.

Acetylcholine: A neurotransmitter produced by a nerve cell that enables a nerve impulse to cross a synapse and reach another nerve or muscle cell.

Acid rain: An excessive release of nitrogen oxides or sulfur dioxide as the result of the burning of primarily fossil fuels; these combine with water to form nitric or sulfuric acids that dissolve into rainfall.

Acidosis: A body fluid pH of less than 7.4 at 37 degrees Celsius.

Actin: One of the two major types of contractile proteins; it forms the thin myofibrils of the sarcomere.

Active or wide foraging: Moving about in search of prey.

Aculeus: The sting, either a single or double hollow barb that delivers the venom to prey.

Adaptation: In evolutionary biology, a heritable structure, physiological process, or behavioral pattern that gives an organism a better chance of surviving and reproducing; in physiology, the decrease in the size of the response of a sense organ following continuous application of a constant stimulus.

Adaptive radiation: The rapid evolution of new species following invasion of a new geographic region or ecological niche, or exploitation of a new ecological opportunity.

Adenosine triphosphate (ATP): The primary energy storage molecule in cells of all organisms; links energy-producing reactions with energy-requiring reactions.

AER. *See* **Apical ectodermal ridge (AER)**.

Aerobic: Requiring free oxygen; any biological process that can occur in the presence of free oxygen.

Aerobic metabolism: A set of chemical reactions that require oxygen to make ATP, as opposed to anaerobic metabolism, which does not require oxygen.

Aggression: A physical act or threat of action by one individual that reduces the freedom or genetic fitness of another.

Aging: A process common to all living organisms, eventually resulting in death or conclusion of the life cycle.

Agnatha: A class of vertebrates that includes all forms in which jaws are not developed; the group to which the earliest vertebrates belong.

Airfoil: The wing of a flying animal or airplane that the provides lift and/or thrust needed for flight.

Alates: Recently molted winged adult termites.

Alkalosis: A body fluid pH greater than 7.4 at 37 degrees Celsius, the opposite of acidosis.

Allele: Alternative version of a single gene, located at the same position on a chromosome, that can be expressed as a new physical trait in organisms.

Allele frequency: The relative abundance of an allele in a population.

Allelochemic: A general term for a chemical used as a messenger between members of different species; allomones and kairomones are allelochemics, but hormones and pheromones are not.

Allogrooming: Mutual grooming or grooming between two individuals.

Allomone: A chemical messenger that passes information between members of different species, resulting in an advantage to the sender.

Alloparenting: Performance of parenting duties by an individual not the parent of the offspring (though usually a relative).

Allopatric: Populations of organisms living in different places and separated by a barrier that prevents interbreeding.

Allozyme: One of two or more forms of an enzyme determined by different alleles of the same gene; usually analyzed by gel electrophoresis.

Altricial: Animals born in a helpless state and completely dependent on the parent(s).

Altruism: A behavior that increases the fitness of the recipient individual while decreasing the fitness of the performing individual.

Alveoli: The milk-producing areas within the mammary glands.

Alveolus: The thin-walled, saclike lung structure where gas exchange takes place.

American Sign Language (ASL): An American system of communication for the deaf that employs hand gestures and facial expressions.

Amino acid: An organic molecule with an attached nitrogen group that is the building block of polypeptides.

Amniote: Animals with eggs in which embryos develop within fluid-filled membranes (the amnion), allowing eggs to be laid on land; amniotes include reptiles, birds, and mammals.

Amphistyly: The mechanism by which the jaws of sharks are suspended from, but not directly fused to, the skull.

Amplexus: A form of pseudocopulation seen in amphibians, where the male mounts and grasps the female so that their cloacae are aligned, and eggs and sperm are released into the water in close proximity and at the same time.

Amygdala: Subcortical brain structure related to emotional expression.

Anabolism: A series of chemical reactions that builds complex molecules from simpler molecules using energy from ATP.

Anaerobic metabolism: Metabolism in the absence of oxygen that leads to the production of lactic acid, a strong acid.

Analogue: An individual structure shared by two or more species that is of only superficial similarity; thus, it is not indicative of a common ancestor.

Anatomy: The science of the structure of organisms and their parts.

Androgens: The general term for a variety of male sex hormones made by the testes, such as testosterone and dihydrotestosterone, responsible for male secondary (anatomical) sex characteristics and masculine behavior.

Angle of attack: The angle at which an airfoil meets the air passing it.

Animal husbandry: Care and welfare of domestic animals.

Anisogamy: Reproduction using gametes unequal in size or motility.

Anosmia: The clinical term for the inability to detect odors.

Antagonism: Any type of interactive, interdependent relationship between two or more organisms that is destructive to one of the participants.

Antennae: A pair of segmented sensory appendages located above the mouth parts.

Anterior pituitary gland: The front portion of the pituitary gland, which is attached to the base of the brain; the source of luteinizing hormone (LH) and follicle-stimulating hormone (FSH).

Anthropogenic disturbance: A change (usually a reduction) in population size caused by human activities.

Anthropomorphism: Attributing human characteristics or states of mind to animals.

Antibody: Protein produced by lymphocytes, with specificity for a particular antigen.

Antidiuretic hormone (ADH): A hormone produced in the hypothalamus that controls reabsorption of water in the loop of Henle.

Antigen: A chemical that stimulates the immune system to respond in a very specific manner.

Antipredator benefits: Benefits that come from actions that protect individuals from being killed.

Antlers: Branched, temporary horns made of solid bone, shed and regrown yearly.

Aorta: The major arterial trunk, into which the left ventricle of the heart pumps its blood for transport to the body.

Apes: Large, tailless, semierect anthropoid primates, including chimpanzees, gorillas, gibbons, orangutans, and their direct ancestors—but excluding humans and their direct ancestors.

Apical ectodermal ridge (AER): A thickened ridge of ectodermal (outer tissue) cells that appears along the distal edge of the limb as it first begins its development as a limb bud.

Aposematic coloration: Bright warning coloration that toxic species use to advertise their distastefulness to would-be predators.

Appendicular skeleton: One of two main divisions of vertebrate skeletal systems, composed of the bones of the pelvic girdle, the shoulders, and the limbs.

Apterous: Insects without wings, such as fleas.

Aquaculture: The artificial growth of animals or plants that live in the water; the culture of something living in water.

Arachnid: A class of arthropods with jointed legs and hard external skeleton that includes mites, scorpions, spiders, and ticks.

Arboreal: Living in trees.

Archenteron: The primitive gut cavity formed by the invagination of the blastula; the cavity of the gastrula.

Arteriole: The finest branch of an artery.

Artery: A blood channel with thick muscular walls which transports blood from the heart to various parts of the body.

Arthropods: Invertebrate animals having jointed legs, a chitinous exoskeleton, and a ventral nerve cord; includes crustaceans, insects, and arachnids.

Artiodactyls: Hoofed mammals with even numbers of toes.

Asexual reproduction: Reproduction without the union of male and female sex cells.

Assortative mating: A type of nonrandom mating that occurs when individuals of certain phenotypes are more likely to mate with individuals of certain other phenotypes than would be expected by chance.

Asthenosphere: The region below the lithosphere where rock is less rigid than that above and below it.

Astragalus: A pulley-shaped bone between the legs and ankles of antelopes.

Atoll: A remnant horseshoe or ring-shaped barrier reef surrounding a sunken island.

ATP. *See* **Adenosine triphosphate (ATP)**.

Atria: The two chambers of the heart, which receive venous blood from the body (via the right atrium) or oxygenated blood from the lungs (left atrium).

Auditory nerve: The cranial nerve that conducts sensory impulses from the inner ear to the brain.

Australopithecines: Nonhuman hominids, commonly regarded as ancestral to humans.

Autotomy: The self-induced release of a body part.

Autotrophs: Organisms that have the ability to make their own food from inorganic substances; also known as primary producers.

Axial skeleton: A main division of vertebrate skeletal systems, made up of the bones of the skull, the vertebral column, the ribs, and the sternum.

Axon: That part of a nerve cell through which impulses travel away from the cell body.

Baleen: Whalebone mouth plates that capture and strain small food animals eaten by baleen whales.

Banding: Technique for studying the movement, survival, and behavior of birds by means of identification tags.

Barrier reef: A reef that is separated from land by a lagoon.

Basal metabolic rate (BMR): The rate of metabolism measured when the animal is resting and has had no meals for twelve hours; used to compare different species.

Basilar membrane: The flexible partition connected to the cochlea along which are attached neural hair cells.

Batesian mimicry: An evolutionary trend in which an edible species mimics the form of a distasteful species to avoid predation.

Behavior: An animal's movements, choices, and interactions with other animals and its environment.

Behavioral ecology: The systematic study of the strategies animals use to overcome environmental problems and the adaptive value of those strategies.

Behavioral thermoregulation: Maintaining relatively constant body temperature by shuttling between warm and cool microhabitats.

Behaviorism: The school of psychology that focuses on the investigation of overt behaviors and rejects allusion to inner processes as a means of explaining behavior.

Benthos: The area of the ocean floor; organisms associated with the sea bottom.

Bet-hedging: A reproductive strategy in which an organism reproduces on several occasions rather than focusing efforts on a single or few reproductive events.

Bifurcation: The division of a Y-shaped and connected mesenchymal structure into a single proximal chondrogenic focus and two distal chondrogenic foci; this can lead to the formation of separate chondrification centers in a developing digit.

Big game: Large animals, usually mammals such as deer or predators such as mountain lions; some wildlife departments may list other animals as big game.

Bilateral symmetry: An arrangement of body parts of an organism down a central axis which, when divided down the midline, produce right and left mirror images.

Bile salts: Organic compounds derived from cholesterol that are secreted by the liver into the gut lumen and that emulsify fats.

Binocular vision: The ability to utilize image information from both eyes to form a single image with depth information.

Binomial nomenclature: The two-word system used for naming every individual species.

Bioclimatic zone: A zone of transition between differing yet adjacent ecological systems.

Biodiversity: Variety of life found in a community or ecosystem; includes both species richness and the relative number of individuals of each species.

Biogenetic law: Ernst Haeckel's term for his generalization that the ontogeny of an organism recapitulates the adult stages of its ancestors (recapitulation).

Biological clock: A timekeeping mechanism that is endogenous (a part of the animal) and capable of running independently of exogenous timers such as day-night cycles or seasons, although the clock is normally set by them.

Biological magnification: The increasing accumulation of a toxic substance in progressively higher feeding levels.

Biological rhythm: A cyclical variation in a biological process or behavior, often with a duration that is approximately daily, tidal, monthly, or yearly.

Biology: The science of life and living organisms.

Bioluminescence: Production of visible light by living organisms.
Biomass: The weight of organic matter in an environment or ecosystem, often expressed in terms of grams per square meter per year.
Biome: A terrestrial ecosystem that occupies an extensive geographical area and is characterized by a specific type of plant community, such as deserts.
Biosphere: The sum of all the occupiable habitats for life on earth.
Biostratigraphy: The dating of rocks using fossils.
Biotechnology: Methods used to manipulate biological processes (such as reproduction).
Biotic: The living part of an ecosystem or biome, consisting of all organisms.
Bipedal: Walking on only two feet, as humans do.
Biserial dermal armor: Bony plates running along side of the vertebral column.
Bivalve: A mollusk having two shell halves.
Blastema: A region of surviving, proliferating cells at the edge of a damaged tissue.
Blastula: An early stage of an embryo which is shaped like a hollow ball in some animals and a small, flattened disc in others; contains a cavity called the blastocoel.
Blood: The fluid connective tissue within blood vessels that carries raw materials to cells and carries products and wastes from them.
Blood vessels: Membranous tubes through which blood flows; arteries carry blood from the heart, veins carry blood to the heart, and capillaries are tiny vessels in which exchange takes place.
Blubber: Thick layer of fat under the skin.
BMR. *See* **Basal metabolic rate (BMR)**.
Body mass: The average weight of females of a species, expressed in kilograms.
Boltrun: Mole burrow tunnel used as an emergency exit.
Bond: The tie or relationship between opposite-sex partners in a pair bond.
Bonding behaviors: Behavior patterns that establish, maintain, or strengthen the pair bond.
Bone: The dense, semirigid, calcified connective tissue which is the main component of the skeletons of all adult vertebrates.
Book lungs: A system of blood-filled diverticula that are surrounded by air pockets located in a chamber called the atrium.
Brachiation: A form of locomotion in which the body is held suspended by the arms from above; also called arm-swinging.
Bridge: The portion of the shell that connects the carapace to the plastron.
Bristles: Specialized feathers that protect the nostrils.
Bronchus (*pl.* bronchi): An individual tube that is part of a lung and leads to one of the smaller lung parts.
Brood: All the immature insects within an insect colony, including eggs, larvae, and, in the Hymenoptera, the pupal stage; also, to cover young with the wings.
Brood-parasite. *See* **Nest-parasite**.
Brood pouch: A temporary external pouch created by folding the skin of the abdomen together; used to carry young as they continue to develop.
Browser: An animal that feeds on leaves and twigs from trees.
Brucellosis: Cattle disease caused by brucellae bacteria.
Budding: A form of asexual reproduction that begins as an outpocketing of the parental body, resulting in either separation from or continued connection with the parent, forming a colony.
Bulla: Hollow bony area.
Burrowing insectivore: An insect-eating animal that usually lives in nests formed by digging holes or tunnels in the ground.

Calcareous: A material composed primarily of calcium compounds.
Calcification: Calcium deposition, mostly as calcium carbonate, into the cartilage and other bone-forming tissue, which facilitates its conversion into bone.
Calorie: The traditional unit of heat; one calorie

is the amount of heat required to raise the temperature of one gram of water 1 degree Celsius.

Camouflage: Patterns, colors, and/or shapes that make it difficult to differentiate an organism from its surroundings.

Cancellous bone: Spongy bone that is composed of an open, interlacing framework of bony tissue oriented to provide maximum strength in response to normal strains and stresses.

Canine teeth: Four elongated, pointed teeth that grasp and kill prey.

Capillaries: The very fine vessels in various tissues, which connect arterioles with venules; it is here that respiratory gases, nutrients, and wastes are exchanged between blood and tissues.

Carangiform swimming: A method of swimming where the tail is moved while the body is held rigid.

Carapace: Hard case covering the back of an animal, such as the chitinous outer covering of a crustacean shell or insect exoskeleton, or the portion of the shell that covers a turtle's back.

Carbohydrate: An organic molecule containing only carbon, hydrogen, and oxygen in a 1:2:1 ratio; often defined as a simple sugar or any substance yielding a simple sugar upon hydrolysis.

Carbonic anhydrase: An enzyme used in the mineralization process to convert carbon dioxide to bicarbonate.

Cardiac output: The amount of blood ejected by the left ventricle into the aorta per minute.

Carnassial teeth: Pairs of large, cross-shearing teeth designed to sheer flesh; the characteristic that unites all members of the order Carnivora.

Carnivore: A member of the meat-eating order Carnivora, which includes dogs, cats, weasels, bears, and their relatives.

Carrion: Corpses of dead animals.

Carrying capacity: The maximum number of animals that a given area can support indefinitely.

Cartilage: A soft, pliable typically deep-lying tissue that constitutes the endoskeletons of primitive vertebrates, such as sharks, as well as the embryonic skeletons and jointing structures of adult higher vertebrates.

Caste: One of the recognizable types of individuals within an insect colony, such as queens, workers, soldiers, and males or drones; usually these individuals are physically and behaviorally adapted to perform specific tasks.

Castoreum: A secretion from the castor glands of beavers, used in scent marking.

Catabolism: A series of chemical reactions that break down complex molecules into simple components, usually yielding energy.

Catarrhini: A primate group including Old World monkeys, apes, and humans, with reduced tails and only two pairs of premolar teeth.

Catastrophism: A scientific theory which postulates that the geological features of the earth and life thereon have been drastically affected by natural disasters of huge proportions in past ages.

Caudal fin: The tail fin of fishes, which supplies the forward thrust in locomotion.

Cecum: Structure in the digestive tract that aids in digestion and water retention.

Cell-mediated immunity: Production of lymphocytes that specifically kill cells with foreign antigens on their surfaces.

Cellular respiration: The release of energy in organisms at the cell level, primarily by the use of oxygen.

Cellulose: Fibrous polysaccharide that chiefly constitutes the cell walls of plants.

Celsius: A scale for measuring temperature in which freezing is zero degrees and boiling is one hundred degrees, abbreviated C.

Centrum: The spool-shaped body of a vertebra.

Cephalothorax: Combined head and thorax of an arthropod.

Cercal organs: Tufts of hair supplied with nerves, located on insect's abdomens, which respond to aerial sounds.

Cetaceans: Plant-eating marine mammals, such as whales, dolphins, and porpoises.
CFCs. *See* **Chlorofluorocarbons (CFCs)**.
Chelate: Pincerlike.
Chelicerae: Appendages with pincers.
Chemical pollutants: Harmful chemicals manufactured and released to the environment; normally referring to those that contaminate ecosystems.
Chemoreceptor: Specialized nervous tissue that senses changes in pH (hydrogen ions) and oxygen.
Chemotaxis: An oriented response toward or away from chemicals.
Chitin: A transparent, horny substance of invertebrate exoskeletons.
Chlorofluorocarbons (CFCs): A group of very stable compounds used widely since their development in 1928 for refrigeration, coolants, aerosol spray propellants, and other uses; once risen in stratosphere, they cause ozone depletion.
Chlorophyll: One of several forms of photoactive green pigments in plant cells that is necessary for photosynthesis to occur.
Cholera: Gastrointestinal diseases.
Chondrification: The process by which undifferentiated connective cells transform into chondrocytes (cells that make cartilage) and begin forming extracellular matrix.
Chordates: A phylum of organisms characterized by the presence of a notochord, a dorsal nerve cord, and gill slits.
Chorion: The outer cellular layer of the embryonic sac of reptiles, birds, and mammals; the term was coined by Aristotle.
Chromatophores: Pigment-producing cells.
Chromosome: A molecule of DNA that contains a string of genes, which consist of coded information essential for all cell functions, including the creation of new life; chromosomes are passed from one generation to the next by the gametes.
Ciliated: Bearing short, hairlike organelles on the surface of cells, used for motility.
Circadian rhythm: A physiological or behavioral cycle that occurs in a twenty-four-hour pattern.
Circular muscle: Muscle fibers that run in a circular pattern around the body perpendicular to the long axis of the body.
Clade: A group of animals and their common ancestor.
Cladistics: A method of analyzing biological relationships in which advanced characters of organisms are used to indicate closeness of origin.
Clasper: A modification of the pelvic fins in male sharks and rays which acts as the male sexual organ in internal fertilization of the female.
Class: The taxonomic category composed of related genera; closely related classes form a phylum or division.
Classification: The arranging of organisms into related groups based on specific relationships.
Clavicle: The collarbone, connecting the top of the breastbone to the shoulder.
Cleavage: The process by which the fertilized egg undergoes a series of rapid cell divisions which result in the formation of a blastula.
Cleidoic egg: A shelled egg equipped with internal membranes that make terrestrial reproduction possible.
Cline: A gradual, continuous variation from one population of a species to the next that is related to differences in geography.
Cloaca: A bodily opening at the end of the gut into which both the waste disposal and reproductive systems open; the common opening through which the products of the urinary, intestinal, and reproductive systems are expelled from the body.
Clock sense: An inherent awareness of time or time intervals used, for example, to compensate for celestial movements in navigation.
Clone: An organism that is genetically identical to the original organism from which it was derived.
Closed circulation: A circulation system made

of arteries, capillaries, and veins that returns blood flow back to the heart.

Clutch: Number of eggs in the nest.

Cnidocyte: Specialized cells on the body or tentacles of jellyfish that contain nematocysts.

Coalitions: Short-term alliances designed to gain access to a contested resource, often by fighting.

Cochlea: The vertebrate neural organ which transduces sound waves into nerve impulses.

Coelenteron: The fluid-filled gastrovascular cavity of Cnidarians.

Coelom: The body cavity of higher invertebrates and vertebrates, where mesodermal tissues enclose a fluid-filled space.

Coevolution: Joint evolutionary change caused by the close interaction of two or more species; each species serves as the natural selection agent for the other species.

Cognition: Transformation and elaboration of sensory input.

Cognitive ethology: Scientific study of animal intelligence.

Cohort: A group of organisms of the same species, and usually of the same population, that are born at about the same time.

Cold-blooded: Referring to animals whose body temperatures equal the temperature of their surroundings.

Collagen: A fibrous protein very plentiful in bone, cartilage, and other connective tissue.

Collembola: Primitive, wingless insects.

Colony: A cluster of genetically identical individuals formed asexually from a single individual.

Colostrum: The precursor to milk that is formed in the mammary gland during pregnancy and immediately after birth of the young.

Commensalism: A type of coevolved symbiotic relationship between different species that live intimately with one another without injury to any participant.

Commitment: The "decision" by an embryonic cell to develop in a certain way, which may be reversed if the cell is removed from its normal surroundings.

Community: A population of plants and animals that live together and interact with one another through the processes of competition, predation, parasitism, and mutualism, making up the biotic part of an ecosystem.

Compact bone: A dense type of bone, often termed lamellar bone, formed of a calcified bone matrix having a concentric ring organization.

Comparative anatomy: The branch of natural science dealing with the structural organization of living things.

Comparative psychology: The branch of psychology that uses comparative studies of animals as a means of investigating phenomena such as learning and development.

Competition: Interactions among individuals that attempt to utilize the same limited resource.

Compound eyes: Eyes that are made up of multiple lenses or light detectors.

Conditioning: The behavioral association that results from the reinforcement of a response with a stimulus.

Connective tissue: Any fibrous tissue that connects or supports body organs.

Consort pair: A temporarily bonded pair within a polygamous group; also called consortship.

Conspecific: A member of the same species.

Constriction: A method of killing prey using increasingly tight coils around the body to trigger stress-induced cardiac arrest.

Consumer: An organism that eats other organisms.

Consumer food chain: A simplified description of the grazing and predator/prey relationships within an ecosystem.

Continental drift: Theory that the continents have moved slowly apart from an early landmass, explaining why many species appear to be closely related while separated by wide expanses of ocean.

Continuous growth: Growth in a population in which reproduction takes place at any time during the year rather than during specific time intervals.

Contractile vacuole: The excretory organ of several one-celled organisms.

Controlling site: A sequence of nucleotides generally fifteen to sixty nucleotides long, to which a transcriptional activator or repressor binds.

Convection: A transfer of heat from one substance to another with which it is in contact.

Convergent evolution: The process by which unrelated animals tend to resemble one another as a result of adaptations to similar environments.

Copulation: Mating; the insertion of the male's penis into the female's vagina to fertilize her ova.

Core temperature: Internal body temperature around the heart, brain, and spinal cord.

Corona radiata: The layers of follicle cells that still surround the mammalian egg after ovulation.

Corpora allata: A gland in insects that synthesizes and secretes juvenile hormone (JH).

Corpus luteum (pl. corpora lutea): The structure on the ovary that is formed from the follicle after the egg has been released; it secretes progesterone.

Cortex: The main part of a hair, made of pigment-containing cells, surrounding a central medulla.

Costal grooves: Parallel grooves or folds on the side of a salamander's body.

Countercurrent exchanger: The process where a medium (air or water) flowing in one direction over a tissue surface encounters blood flowing through the tissue in the opposite direction; this improves the gas diffusion by maintaining a concentration gradient.

Countercurrent mechanism: A heat exchange system in which heat is passed from fluid moving in.

Countershading: A form of crypsis involving dark coloration on top and light coloration on the underside.

Coverts: Feathers covering the bases of the large feathers of the wings and tail.

Crepuscular: Active after sunset and in early morning.

Crest: Tuft of feathers on the head.

Critical period: A very brief period of time in the development of an animal during which certain experiences must be undergone; the effects of such experiences are permanent.

Crop: A specialized part of a bird's digestive system that holds and softens food.

Crossbridge: A structure seen in electron micrographs of contracted muscle; the point of attachment of a myosin "head" to actin.

Cross-pollination: The transfer of pollen grains and their enclosed sperm cells from the male portion of a flower to a female portion of another flower within the same species.

Crown: External tooth surface above gums.

Crustaceans: Lobsters, shrimps, crabs, and barnacles.

Cryptic coloration: Any color pattern that blends into the background.

Ctenoid scales: Scales with comblike serrations on rear edge, found on many bony fishes.

Cuckold: A partnered male who is helping his mate to raise offspring which are not genetically his own.

Cud: Food regurgitated and chewed a second time after its initial ingestion.

Cuspid: A tearing tooth found in the mouth of a carnivorous animal.

Cuticle: The outer arthropod exoskeleton consisting of several layers of secreted organic matter, primarily nonliving chitin; or the outermost layer of a hair, made of scales.

Cuttlefish: A squidlike marine mollusk, eaten by Odontoceti.

Cycloid scales: Thin, flat bony scales with a smooth surface; rounded in shape, found on herrings, minnows, trout, and other primitive teleosts.

Cyclostomes: The modern agnathans, comprising lampreys and hagfish.

Cyst: A secreted covering that protects small invertebrates from environmental stress.

Cytoplasm: The living portion of the cell that is contained within the cell membrane.

Darwinism: Branching evolution brought about by natural selection.

Death: The cessation of all body and brain functions.

Decapods: Animals with ten appendages (from Greek *deca*, "ten," plus *poda*, "foot or leg").

Decomposers: Microbes such as fungi and bacteria that digest food outside their bodies by secreting digestive enzymes into the environment.

Deep sea: Water depths below six hundred feet, also below penetration of light.

Definitive host: The host in which a symbiont (the organism living within the host) matures and reproduces.

Delayed implantation: An extended period after fertilization when an embryo stops developing, before it attaches to the uterine wall and resumes embryonic development.

Deme: A local population of closely related living organisms.

Dendroclimatology: The study of tree-ring growth as an indicator of past climates.

Denning: The period of winter sleep during which a bear does not eat, drink, urinate or defecate.

Density: The number of animals present per unit of area being sampled; for example, ten mice per hectare or five moose per square kilometer.

Density-dependent growth: Growth in a population in which the per capita rates of birth and death are scaled by the total number of individuals in the population.

Density-dependent population regulation: The regulation of population size by factors or interactions intrinsic to the population; the strength of regulation increases as population size increases.

Dental battery: Unit of teeth in the upper and lower jaws consisting of the cutting teeth and the rows of replacements below them.

Dental comb: Forward-projecting lower incisors and canines that are used for grooming and feeding.

Dental formula: The types of teeth in one quarter of the mouth, expressed as the ratio of incisors to canines to premolars to molars.

Dentine: The ivory portion of a tooth or scale; dentine or dentinelike substances such as cosmine are found in the scales of most fishes.

Dentition: Referring to the teeth.

Deoxyribonucleic acid (DNA): The genetic material of cells, having the molecular form of a twisted double helix that is linked by purine and pyrimidine base pairs; carries the inherited traits and controls for cell activities.

Dermis: Layer beneath the epidermis, primarily connective tissue but also containing nerves and blood vessels.

Determination: An event in organismal development during which a particular cell becomes committed to a specific developmental pathway.

Detritus feeders: An array of small and often unnoticed animals and protists that live off the refuse of other living beings, such as molted shells and skeletons, fallen leaves, wastes, and dead bodies.

Deuterostomes: Echinoderms, hemichordates, and chordates, a group linked by features of cell development including retention of the blastopore as anus.

Dewlap: Loose fold of skin hanging from the throat of some cattle.

Diapause: A resting phase in which metabolic activity is low and adverse conditions can be tolerated; also, an interruption in embryonic development.

Diapsids: A group of reptiles in which the temporal region of the skull is characterized by two openings, a supratemporal opening and an infratemporal opening.

Diastole: Period of heart muscle relaxation and declining pressure.

Differentiation: The process during

development by which cells obtain their unique structure and function.

Diffusion: The net movement of molecules from an area of high concentration to one of lower concentration as a result of random molecular movements; the passive movement of a gas across a membrane from a region of high pressure to one of low pressure: the process by which larger organic nutrients are broken down to smaller molecules in the lumen of the gut.

Digit: A finger, toe, or related bony animal structure.

Digitigrade: Walking on the toes, with the heel raised.

Dilution effects: The reduction in per capita probability of death from a predator due to the presence of other group members.

Dimorphism: Existence of two distinct forms within a species.

Dingo: The wild dog brought to Australia by the aborigines.

Dioecious: Having two separate sexes, namely male and female.

Diploid: A cell containing two sets of chromosomes, usually one derived from the father and one derived from the mother; the normal condition of all cells except reproductive ones.

Diplosomite: Millipede trunk segment, formed by the fusion of two body segments.

Discrete growth: Growth in a population that undergoes reproduction at specific time intervals.

Discrete signals: Signals that are always given in the same way and indicate only the presence or absence of a particular condition or state.

Disharmonic: Ecologically unbalanced.

Disjunct: Pertaining to the geographic distribution pattern in which two closely related groups are widely separated by areas that are devoid of either group.

Dispersal: The movement of organisms from one geographic area to another; movements may be the result of an animal's own efforts or the consequence of being passively transported by natural or human-mediated means; dispersal is limited by barriers.

Display: A social signal, particularly a visual signal, exchanged between animals.

Disruptive coloration: Use of stripes, spots, or blotches to break up the body outline and blend into a complex background.

Distal: Occurring near the outer end of a limb.

Distemper: Viral disease affecting respiration.

Diurnal: Awake and functional during the daylight hours.

Divergence: The evolution of increasing morphological differences between an ancestral species and offshoot species caused by differing adaptive pressures.

Diversity: The number of taxa (classification groups) associated with a particular place and time.

Domestication: A process by which animals are adapted biologically and behaviorally to a domestic (human) environment in order to tame and manipulate them for the benefit of humans.

Dominance: The physical control of some members of a group by other members, initiated and sustained by hostile behavior of a direct, subtle, or indirect nature.

Dominance hierarchy: A social system, usually determined by aggressive interactions, in which individuals can be ranked in terms of their access to resources or mates.

Dominance social behavior: Organization around a dominant leader, whom the rest of the group follows.

Dominant: Requiring only one copy of a gene for expression of the trait.

Dominant species: A species in a community that acts to control the abundance of its competitors because of its large size, extended life span, or ability to acquire and hold resources.

Dopamine: Neurotransmitter involved in movement and reward systems.

Dorsal: At the hind (posterior) end of a living organism.

Drag: A force that acts in the opposite direction of the movement of a body through a fluid medium; sources of drag vary but include friction and pressure suction.

Drone: A fertile male social insect.

Drumming: Type of nonvocal communication produced by banging bill on a hollow tree trunk or other noise-producing object.

Dryopithecines: Extinct Miocene-Pliocene apes (sometimes including *Proconsul*, from Africa) found in Europe and Asia; their evolutionary significance is unclear.

Dung showering: Behavior by bulls to show dominance over other males.

Duodenum: The first part of the small intestine, where it joins the stomach.

Eccrine gland: A type of sweat gland that helps maintain body temperature; the glands are located on the palms and soles, forehead, neck, and back.

Ecdysis: Molting; the process of removing (escaping from) the old exoskeleton.

Ecdysone: A hormone that triggers both molting and metamorphosis in insects as well as in many other species of animals.

Echolocation: The ability of animals to locate objects at a distance by emitting sound waves which bounce off an object and then return to the animal for analysis.

Eclipse plumage: The drab plumage of male birds following the postbreeding molt, in which their bright courtship feathers are replaced by dull earthy feathers that provide inconspicuous coloring.

Ecological niche: The sum of environmental conditions necessary for the survival of a population of any species, including food, shelter, habitat, and all other essential resources.

Ecology: The study of the interactions between animals and their environment.

Ecomorph: Species of different phyletic origins (at most distantly related) with similar structural and behavioral adaptations to similar niches.

Ecosystem: A biological community and the physical environment contained in it.

Ectoderm: The outermost of the three fundamental tissue types that appear during the development of most animals; it will form the skin and all of its derivatives, nervous tissue, and many other tissues.

Ectoparasite: A parasitic organism that attaches to the host on the exterior of the body.

Ectotherm: An animal that depends on environmental heat sources, usually solar radiation, to maintain body temperature.

Ediacarian fauna: A diverse assemblage of fossils of soft-bodied animals that represents the oldest record of multicellular animal life on earth; also called Ediacaran fauna.

Effector: That part of a nerve which transmits an impulse to an organ of response.

Egg tooth: A hard, calcified structure on the tip of the bill of a bird embryo that is used to help the bird break its shell during hatching.

Ejaculation: The process of expelling semen from the male body.

Elapids: A snake classification which includes cobras and rattlesnakes that have short, fixed front fangs.

Elasmobranch: The classificatory subbranch of sharks and rays.

Electroencephalogram (EEG): A chart of brain wave activity as measured by electrodes glued to the surface of the skull.

Electron transport chain: A series of electron carrier molecules found in the membrane of mitochondria; oxygen is used and ATP is made at this site.

Electrophoresis: A technique for separating molecules when they are placed in an electrical field; the separation is usually based on their charge and weight.

Electroreceptors: Sensors in the bill of the platypus that detect the weak electric field given off by animals.

Elfin forest: A stunted forest growing at high elevations in warm, moist climates.

Elytra: Rigid front wings of beetles that cover the second, functional pair of wings.

Embryo: A fertilized egg as it undergoes divisions from one cell to several thousand cells, but before the individual is completely differentiated into a fetus.

Embryo polarity genes: Genes whose expression in maternal cells results in products being stored in the egg that establish polarity, such as the anterior-posterior axis, after fertilization.

Embryology: The study of the development of individual animals.

Embryonic induction: The point at which one embryonic tissue signals another embryonic tissue to develop in a certain way.

Emergent vegetation: Aquatic vegetation that grows tall enough to be visible above the water.

Emigration: The movement of animals out of an area; one-way movement from a habitat type.

Encounter effects: The reduction in the probability of death from a predator due to a single group of N members being more difficult to locate than an equal number of solitary individuals.

Endangered species: A species of animal or plant that is threatened with extinction.

Endemic: Belonging to or native to a particular place.

Endocannibalism: A form of human cannibalism in which members of a related group eat their own dead.

Endocrine glands: Glands that produce hormones and secrete them into the blood; the hypothalamus of the brain, the pituitary gland, and the testes are all endocrine glands.

Endocrine system: An array of ductless glands scattered throughout the mammalian body that produce and secrete hormones directly into the bloodstream.

Endocuticle: Usually the thickest layer of the cuticle, found just outside the living epidermal cell layer and made of untanned proteins and chitin.

Endogenous: Refers to rhythms that are expressions of only internal processes within the cell or organism.

Endometrium: An inner, thin layer of cells overlying the muscle layer of the uterus.

Endoparasitic: A parasitic organism that attaches to an interior portion of the host's body.

Endoskeleton: The type of skeleton that is found beneath the musculature of an animal's body; it provides mechanical support for the body as a whole, some protection for vulnerable internal organs and tissues, and sites for muscle attachment.

Endotherm: An animal that, by its own metabolism, maintains a constant body temperature (warm-blooded); birds and mammals are endotherms.

Energy pyramid: A graphical representation of the energy contained in succeeding trophic levels, with maximum energy at the base (producers) and steadily diminishing amounts at higher levels.

Enterocytes: The cells that line the lumen of the small intestine.

Entrainment: The synchronization of one biological rhythm to another rhythm, such as the twenty-four-hour rhythm of a light-dark cycle.

Environment: All the external conditions that affect an organism or other specified system during its lifetime.

Environmental constraints: The physical demands placed upon any species by its surroundings that ultimately determine the success or failure of its adaptations and consequently its success as a species; also called pressures.

Enzyme: A protein that acts as a catalyst under appropriate physiological conditions to break down bonds of a large protein, fat, or carbohydrate.

Epicuticle: The outermost and thinnest layer of the arthropod cuticle, composed mainly of the hardened protein cuticulin.

Epidermis: The outer, protective layer of epithelial cells in the skins of vertebrates.

Epifauna: Animals that live on the sea floor.

Epihyal bone: A hyoid bone whose presence or absence determines whether a cat generally purrs or roars.

Epiphragm: Covering or sealing membrane.

Epithelium: The tissue that covers and lines all exposed surfaces of an organism, including internal body cavities such as the viscera and blood vessels.

Equids: Members of the horse family (Equidae) including horses, asses (including the donkey), zebras, and their crosses (including the mule and the hinny).

Erection: The process of enlargement and stiffening of the penis because of increased blood volume within it.

Esophagus: The part of the oral cavity (pharynx) that transfers morsels to the stomach; it is usually a long, muscular tube with no digestive function other than transport.

Essentialism: The Platonic-Aristotelian belief that each species is characterized by an unchanging "essence" incapable of evolutionary change.

Estivation: Similar to hibernation; period of reduced activity or dormancy triggered by dry and/or hot environmental conditions.

Estrogen: A hormone secreted by the ovary and placenta for development of the uterus.

Estrus cycle: Hormonally controlled changes that make up the female reproductive cycle in most mammals; ovulation occurs during the estrus (heat) period.

Ethology: The study of an animal's behavior in its natural habitat.

Eukaryote: A higher organism, whose cells have their genetic material in a membrane-bound nucleus and possess other membrane-bound organelles.

Euryhaline: The ability of an organism to tolerate wide ranges of salinity.

Eusocial: A social system with a single breeding female; other members of the colony are organized into specialized classes (exemplified by bees, ants, and termites).

Evolution: A process, guided by natural selection, that changes a population's genetic composition and results in adaptations.

Evolutionarily stable strategy: A behavioral strategy that will persist in a population because alternative strategies, in the context of that population, will be less successful.

Evolutionary zoology: The study of the mechanisms of evolutionary change and the evolutionary history of animal groups.

Ewe: Female sheep.

Ex situ: Conservation and research out of the animal's natural environment (at a zoo).

Exocannibalism: A form of human cannibalism in which unrelated humans are eaten.

Exocuticle: A thick middle layer in the cuticle made up of both chitin and rigid, tanned proteins termed sclerotin.

Exogenous: Rhythms that originate outside the organism in the environment.

Exoskeleton: A jointed and segmented, relatively thin, hard covering made up of chitin and protein that surrounds and protects the entire inner body in most arthropods.

Exotic species: Organisms that are not naturally found in a place but have been artificially introduced, whether by accident or intentionally.

Exponential growth: A pattern of population growth in which the rate of increase becomes progressively larger over time.

External fertilization: The union of eggs and sperm in the environment, rather than in the female's body.

External genitals: The external reproductive parts of the female.

Extinct: No longer found anywhere on earth.

Extirpated: Not found in an immediate local area but found elsewhere on earth.

Extracellular fluid: The fluid outside cell membranes, including fluid in spaces between cells (interstitial), in blood vessels (plasma), in lymph vessels (lymph), and in the central nervous system (cerebrospinal).

Facial disk: The distinctive concentric circles of feathers that encircle the eyes of owls, helping direct sound toward the ears.

Fahrenheit: A scale for measuring temperature in which freezing is 32 degrees and boiling is 212 degrees, abbreviated F.

Fangs: Enlarged teeth that are hollow like a hypodermic needle or grooved to facilitate the injection of venom.

Fast muscle: Muscle cells that respond quickly to nervous impulses; in invertebrates, these muscle fibers have short sarcomeres and a low ratio of thin to thick myofibrils.

Fate map: A map of determined, but undifferentiated, tissue by which specific cell regions can be identified as giving rise to specific adult structures.

Fecundity: The number of offspring produced by an individual.

Feedback: In endocrinology, this usually refers to one hormone controlling the secretion of another that stimulates the first, usually in the form of negative feedback, in which the second hormone inhibits the first.

Female: An organism that produces eggs, the larger of two different types of gametes.

Fenestration: A latticework of openings on the sides of the skull.

Feral: Referring to domestic animals that have reverted to a wild or semiwild condition, such as cats, dogs, or caged birds that have been released or escaped and now survive in the wild.

Fertilization: The process by which the egg and sperm unite to form the zygote.

Fetus: A differentiated but undeveloped individual with organ systems usually identifiable as a member of a species.

Fibula: The smaller of two bones between the knee and ankle.

Field observations: Observing behavior in naturalistic settings.

Filtration: The process of diffusion of plasma from the blood to the glomerulus and nephron.

Fin-fold theory: Theory that fins initially evolved as long folds of tissue extending around the body.

Fire ecology: An ecosystem that depends on periodic fires to clear underbrush; the seeds of many plants in such an ecosystem require fire in order to germinate.

Fission: The division of an organism into two or more essentially identical organisms; an asexual process.

Fitness: The ability of an organism to produce offspring that, in turn, can reproduce successfully; the fitness of organisms increases as a result of natural selection.

Fixed action pattern: A complex motor act involving a specific, temporal sequence of component acts.

Flagellate: A protozoan that uses long, whiplike structures called flagella for locomotion.

Flagellum: A long cell extension used in locomotion.

Fledgling period: Period after hatching, during which a nestling grows flight feathers and learns to fly.

Flehmen: Behavior involving curling and wrinkling of lips and nostrils, with the activation of the Jacobson's organ.

Flipper: Finlike structures of marine mammals that have evolved from the forelimbs of their terrestrial ancestors.

Fluid: A substance, either liquid or gas, that flows or conforms to the outline of its container.

Flyway: An established route that migratory birds take between their wintering and nesting grounds.

Follicle: The saclike organ from which a hair grows; its blood vessels nourish the hair.

Food chain: An abstract chain representing the links between organisms, each of which eats and is eaten by another.

Food pyramid: Diagram representing organisms of a particular type that can be supported at each trophic level from a given input of solar energy in food chains and food webs.

Food web: A network of interconnecting food chains representing the food relationships in a community.

Fossil: A remnant, impression, or trace of an animal or plant of a past geological age that has been preserved in the earth's crust.

Four-fin system: The combined activity of paired fins in some bony fishes that makes them highly maneuverable.

Fovea: Specific area with an exceptionally dense concentration of light-sensitive cells in eyes of animals.

Fratricide: Deliberate killing of one sibling by another sibling.

Free-living: An organism that does not have to spend a portion of its life cycle attached to another organism.

Free-running: Denotes a rhythm that is not entrained to an environmental signal such as a light-dark cycle.

Frenulum: A spinelike device that connects the front and hind wings in moths.

Frequency: The number of repetitions of a rhythm per unit time, such as a heart rate of seventy beats per minute.

Frequency-dependent predation: Predation on whichever species is most common in a community; a frequency-dependent predator will switch prey if necessary.

Frill: An elaborate crest at the back of the skull used for visual display but not for protection.

Frontal bone: The bone which, vertically, makes up the forehead and is important, horizontally, to formation of the top (roof) of the orbital and nasal cavities.

Frozen zoo: Frozen tissue bank maintained at a zoo that contains wild animal tissue and reproductive samples for use in future breeding programs.

Functional response: The rate at which an individual predator consumes prey, dependent upon the abundance of that prey in a habitat.

Funnel: An opening in a cephalopod mantle, providing oxygen and propulsion.

Furcula: Fused clavicles, the wishbone of birds.

Fusion-fission community: A society whose members are of both sexes and all ages, which can form and dissolve subgroupings.

Game: Economically important animals, usually birds or mammals; it includes those taken for recreation or products and those that damage human property.

Gamete: A haploid sex cell that contains one allele for each gene; sperm and egg cells are gametes that fuse to form a diploid zygote.

Ganoid scales: Heavy, dense scales containing ganoine found in primitive bony fishes.

Gap rule genes: Expressed in the zygote, these genes divide the anterior-posterior axis of fruit flies into several regions.

Gastroliths: Stones found in the gut region that aided in the digestion of coarse plant food.

Gastronomic: Pertaining to the art of fine dining.

Gastrula: The stage of development during which the endoderm (gut precursor) and the mesoderm (muscle and connective tissue precursor) are internalized.

Gastrulation: The transformation of a blastula into a three-layered embryo, the gastrula; initiated by invagination.

Gelding: Castrated male, usually a horse.

Gemmule: An asexual reproductive structure that becomes a new sponge.

Gene: A sequence of approximately one thousand to ten thousand DNA nucleotide pairs on a chromosome that encodes a messenger ribonucleic acid (mRNA) for eventual protein production.

Gene flow: The movement of genes from one population to another through migration and hybridization between individuals belonging to adjacent populations.

Gene pool: The array of alleles for a gene available in a population; it is usually described in terms of allele or genotype frequencies.

Generalized: Not specifically adapted to any given environment.

Genetic code: The three-nucleotide base sequences (codons) that specify each of the twenty types of amino acids; there can be more than one codon for a particular amino acid.

Genetic diversity: The total number and distribution of alleles and genotypes in a population; a population with a very high genetic diversity would have many alleles and genotypes, all evenly distributed or with approximately equal frequency.

Genetic drift: Change in gene frequencies in a population owing to chance.

Genital tubercle: A small swelling or protuberance toward the front of an embryo's genital area; it is destined to become the penis tip or clitoris.

Genitalia: The external sex structures.

Genome: All the genes of one organism or species.

Genotype: The complete genetic makeup of an organism, regardless of whether these genes are expressed.

Genotype frequency: The relative abundance of a genotype in a population; to calculate, count the number of individuals with a given genotype in the population and divide by the total number of individuals in the population.

Genus (pl. genera): A group of closely related species; for example, *Felis* is the genus of cats, and it includes the species *Felis catus* (the domestic cat) and *Felis couguar* (the cougar or mountain lion).

Geoffroyism: An early theory of evolution in which heritable change was thought to be directly induced by the environment.

Geographically isolated: Living in different habitats.

Geological periods: The twelve divisions in successive layers of sedimentary and volcanic rocks, which are differentiated by the distinctive fossils present within each division; because of many recently discovered fossils and careful dating, the beginning and ending dates for these periods tend to vary somewhat among different references.

Germ layers: The embryonic layers of cells which develop in the gastrula—ectoderm, mesoderm, and endoderm.

Gestation: Duration of pregnancy.

Gigantothermy: A form of metabolism in which internal temperature is maintained by the large mass of the animal.

Gill: An evaginated organ structure where the membrane wall turns out and forms an elevated, protruding structure; typically used for water respiration.

Gill rakers: Sievelike strainers found upon the gill arches of whale sharks, used to filter food from water taken in though the mouth.

Gilt: A young female pig that has not produced a litter.

Gizzard: A part of a bird's stomach that uses ingested pebbles (gastroliths) to grind up food.

Gland: A tissue composed of similar cells that produce a hormone.

Global extinction: The loss of all members of a species; that is, extinction whereby all populations of a species disappear or are eliminated.

Glomerulus (pl. glomeruli): A capsule fitting around capillary blood vessels that receives the filtrate from the blood and passes it into the tubule.

Gnathostomata: All vertebrates in which jaws are developed.

Gonad: The organ responsible for production of gametes—the testis in the male, the ovary in the female.

Gonadotropin: A hormone that stimulates the gonads to produce gametes and to secrete other hormones.

Gonochorism: Sexual reproduction in which each individual is either male or female, but never both; the opposite of hermaphroditism.

Gorget: Patch of feathers between the bird's throat and breast.

Gracile: Slender and light-framed, as opposed to robust.

Gradualism: The idea that transformation from ancestor to descendant species is a slow, gradual process spanning millions of years.

Granular glands: One of many kinds of glands in the skin of amphibians; granular glands secrete toxins for defense from predators.

Gray matter: The part of the central nervous system primarily containing neuron cell bodies and unmyelinated axons.

Grazer: An organism that feeds primarily on grasses.

Greenhouse effect: The process by which certain gases, such as carbon dioxide and methane, trap sunlight energy in atmosphere as heat, resulting in global warming as more gases are released to atmosphere by human activities.

Gregarious: Forming groups temporarily or permanently.

Growth: The increased body mass of an organism that results primarily from an increase in the number of body cells and secondarily from the increase in the size of individual cells.

Guanine: A chemical deposited in the skin of freshwater eels as they return to the sea.

Gulper: A fish that captures and ingests its prey in one swallow.

Gymnosperm: A plant whose seeds are borne on seed scales arranged in cones.

Habitat: The physical environment, usually that of soil and vegetation as well as space, in which an animal lives.

Habitat selection: Process of choosing a home range, territory, nesting site, or feeding site on the basis of specific features of the habitat that the raptor is best adapted to exploit.

Hand: Ten-centimeter (four-inch) measuring unit.

Haplodiploidy: Sex determination found in the Hymenoptera, where males arise from unfertilized eggs and females from fertilized eggs.

Haploid: Having one chromosome of each type; gametes (eggs or sperm) are usually haploid.

Harem: A group of breeding females controlled by a single male.

Haversian systems: Narrow tubes surrounded by rings of bone, called lamellae, that are found within compact bones of animals having endoskeletons; the tubes contain blood vessels and bone.

Heart: A discrete, localized pumping structure within the circulatory system.

Heat: That part of the estral cycle when the female is receptive to male copulatory behavior.

Heliotherm: An animal that uses heat from the sun to regulate its body temperature.

Hemimetabolous: Incomplete metamorphosis in which juveniles resemble wingless adults.

Hemoglobin: A protein in vertebrate red blood cells that carries oxygen and carbon dioxide.

Hemolymph: The transport fluid of organisms with open circulation systems in which there is no clear distinction between blood and intercellular tissue fluid.

Hemotoxin: A substance that causes blood vessel damage and hemorrhage.

Herbivores: Animals that eat plants and show specializations of teeth and digestive tracts to do so.

Heritability: The extent to which variation in some trait among individuals in a population is a result of genetic differences.

Hermaphrodite: A single organism that produces both eggs and sperm.

Hermatypic coral: Reef-building coral species, belonging to the Cnidarian order of Scleractinia.

Heterocercal tail: A tail in which the spine extends into the upper lobe, giving a distinctly sharklike impression.

Heterochrony: Any phenomenon in which there is a difference between the ancestral and descendant rate or timing of development.

Heterodont: Having two or more types of teeth, such as molars and incisors.

Heterotroph: An organism that requires the ingestion of food for survival.

Heterozygote: A diploid organism that has two different alleles for a particular trait; a person with blood type A could be heterozygous by having an A allele and an O allele.

Hexapod: Six-footed; a general term for an insect.

Hibernacula: The winter habitats of brown bats.

Hibernation: A sustained period of torpor (lack of activity) where an animal reduces its metabolic rate.

Hierarchy: A social structure in which animals are dominated by those higher on the linear ladder.

Higher insects: Generally larger insects with increasing levels of morphological complexity.

Home range: Geographic area used by an individual, pair, or group for their daily, seasonal, and sometimes their yearly activities; the defended portion of the home range is called a territory.

Homeobox: One of 180 nucleotide pairs that code for a protein called the homeodomain, found in such diverse organisms as insects, frogs, and humans; they are known to influence body plan formation in fruit flies.

Homeosis: A process that results in the formation of structures in the wrong place in an organism, such as a leg developing in place of a fly's antenna.

Homeostasis: The dynamic balance between body functions, needs, and environmental factors which results in internal constancy.

Homeotherm: An animal that maintains a constant, steady body temperature.

Homeotic selector genes: Genes that determine the identity and developmental fate of segments established in fruit flies by a hierarchy of genes.

Hominid: An anthropoid primate of the family Hominidae, including the genera *Homo* and *Australopithecus*.

Homocercal tail: A type of tail at which the spine ends at the base of the tail, which consists of two equal lobes.

Homodont: Having teeth all of the same type.

Homologue: An individual structure shared by two or more different species that is indicative of a common ancestor.

Homozygote: A diploid organism that has two identical alleles for a particular trait; a person with blood type A would be homozygous if he had two A alleles.

Hormone: A blood-borne chemical signal, either protein or steroid, from one area of the body to another.

Horn: Hard, smooth, keratinous material forming an external covering.

Hornet: A social wasp.

Host: By convention, the larger of two species involved in a symbiotic association.

Humans: Hominids of the genus *Homo*, whether *Homo sapiens sapiens* (to which all varieties of modern humans belong), earlier forms of *Homo sapiens*, or such presumably related types as *Homo erectus* and the still earlier (and more problematic) *Homo habilis*.

Humidity: The amount of water vapor in the air, often considered with temperature (as in relative humidity).

Humoral immunity: Production of antibodies specifically reactive against foreign antigens, carried in body fluids (humors).

Hybrid: An organism resulting from the crossing of two species.

Hybrid vigor: The tendency of hybrids to be larger and more durable than their parent species; also called heterosis.

Hydrologic cycle: Earth's cycle of evaporation and condensation of water, which produces rain and maintains oceans, rivers, and lakes.

Hydrostatic skeleton: A system in which fluid serves as the support by which muscles interact.

Hygroscopic: Able to retain moisture.

Hyoid bones: Series of connected bones at the base of the tongue.

Hyperdactyly: A condition whereby the number of digits is increased above the normal five to create a wing.

Hypermorphosis: A phenomenon in which the rate and initiation of growth in the descendant are the same as in the ancestor but in which the cessation of development takes place later.

Hyperosmotic: A solution with a higher osmotic pressure and more osmotically active particles than the solution with which it is being compared.

Hyperphalangy: A condition whereby the number of phalanges is increased in each digit.

Hyperventilation: An increase in the flow of air or water past the site of gas exchange (lung, gill, or skin).

Hypoosmotic: A solution with a lower osmotic pressure, fewer osmotically active particles relative to the same volume, than the solution with which it is being compared.

Hypophysis: The pituitary gland, or master gland, which produces and secretes at least eight protein hormones influencing growth, metabolism, and sexual development.

Hypothalamus: A brain region just below the cerebrum that interconnects the nervous and endocrine systems of mammals, thereby controlling most hormone production and many body functions.

Hypoxia: From two Latin words, *hypo* and *oxia*, meaning "low oxygen."

Ichnology: The study of trace fossils.

Imaginal disk: Flat sheets of cells within an insect larva; these cells will change shape during metamorphosis and form the external structures of the adult.

Immigration: The movement of animals into an area; a one-way movement into a habitat type.

Imprinting: A specialized form of learning characterized by a sensitive period in which an association with an object is formed.

Impulse: A message traveling within a nerve cell to another nerve cell or to a muscle cell.

In situ: Conservation and research in the animal's natural habitat.

In situ hybridization: A technique used to visualize the location of specific DNA or RNA sequences; typically, a radioactively tagged sequence of nucleic acids is paired (hybridized) to a complementary sequence of nucleic acids.

Inbreeding: Mating between relatives, an extreme form of positive assortative mating.

Incisors: Teeth that are located in the front of the mouth and whose function is to tear, hold, and cut the prey.

Indicator species: A species monitored by biologists as a means of ascertaining the health of the ecosystem in which it lives.

Industrial melanism: The rapid rise in frequency of the melanic form in many moth species downwind of manufacturing sites, associated with the advent of industrial pollution.

Inertia: The property of an object with kinetic energy to move in a straight line unless acted upon by an outside force.

Infauna: Animals that live in the sea floor.

Innate: Any inborn characteristic or behavior that is determined and controlled largely by the genes.

Insectivore: A member of the order Insectivora of small, nocturnal mammals, including shrews, moles, and hedgehogs; also, any animal that feeds on insects.

Insight learning: Using past experiences to adapt and to solve new problems.

Instinct: Any behavior that is completely functional the first time it is performed.

Integumentary processes: Surface outgrowths from the cuticle, primarily rigid nonarticulated processes or movable articulated processes.

Interbreeding: The mating of closely related individuals which tends to increase the appearance of recessive genes.

Interference: The act of impeding others from using some limited resource.

Interfertile: Able to breed and produce fertile offspring.

Intermediate host: An animal species in which nonsexual developmental stages of some commensals and parasites occur.

Interneuron: A central nervous system neuron that does not extend into the peripheral nervous system and is interposed between the sensory and motor neurons.

Interstitial fluid: The fluid found in between cells.

Intestine: The part of the digestive system involved in completing the process of digestion and absorption of nutrients; usually divided into the small intestine and the large intestine, which opens to the exterior by way of the anus.

Intracellular fluid: The fluid compartment within the cell membrane.

Intrinsic rate of increase: The growth rate of a population under ideal conditions, expressed on a per individual basis.

Introgression: The assimilation of the genes of one species into the gene pool of another by successful hybridization.

Invagination: The turning of an external layer into the interior of the same structure; formation of archenteron.

Invertebrates: Animals lacking an internal skeleton.

Involuntary: Functioning automatically; not under conscious control.

Iridescent: Showing the colors of the rainbow depending on light reflection.

Irruption: A sudden increase in the size of a population, usually attributed to a particularly favorable set of environmental conditions.

Isogamy: Reproduction in which all gametes are equal in size and motility.

Isosmotic: A solution having the same osmotic pressure, the same number of osmotically active particles relative to the same volume, as the solution with which it is being compared.

Ivory: A white or honey-colored, bony substance.

Jacobson's organ: A sense organ in the mouth, which detects reproductive chemical signals.

Juvenile hormone (JH): A species-specific hormone which controls whether a molt will produce a larger larva or initiate metamorphosis.

K strategy: A reproductive strategy typified by low reproductive output; common in species living in areas having limited critical resources.

Kairomone: A chemical messenger that passes information between members of different species, resulting in an advantage to the receiver.

Keratin: A tough, fibrous major component of hair, feathers, nails, hooves, horns, and scales.

Keystone species: A species that determines the structure of a community, usually by predation on the dominant competitor in the community.

Kin selection: A phenomenon by which acts of altruism can help pass on genes for altruism by improving the survival of kin and their offspring.

Kinetic skull: A highly moveable arrangement of bones that allows independent action of the snout and jaws on both sides.

Kingdom: The broadest category of organisms; the system currently used recognizes five kingdoms—Monera, Protista, Fungi, Animalia, and Plantae.

Knuckle-walking: Terrestrial locomotion, in which the animal walks on the knuckles of the forelimbs and soles of the hind feet.

Krill: Small, shrimplike sea creatures.

Labial folds: The paired ridges of tissue on either side of the embryo's genital area, which become penis and scrotum in males and labia in females.

Labium: The sheath that contains the slender, styletlike mouthparts of the mosquito, including the mandibles, maxillae, and hypopharynx.

Lactation: The process of producing and delivering milk to the young; also, the time period during which milk is produced.

Lactogenesis: The synthesis of milk within the mammary gland.

Lacunae: Small spaces among tissue cells through which hemolymph flows in open circulatory systems.

Lamarckism: An early evolutionary theory in which voluntary use or disuse of organs was thought to be capable of producing heritable changes.

Lamellae: Any one of several structures in the context of gas-exchange organs, usually found in gills; or, toothlike structures in the beak, forming a strainer that permits birds to retain food particles while still enabling water to flow from the closed mouth.

Laminate structure: Having a layered shell, as in the exoskeletons of crustaceans and the valves of clams.

Larva: The reproductively immature feeding stage in the development of many species of animals, including those insects which undergo complete metamorphosis.

Larynx: The vocal mechanism of mammals, consisting of a structure of cartilage at the upper end of the trachea containing the vocal folds.

Lazarus taxa: Groups that apparently disappear during a mass extinction only to appear again later.

Lecithotrophy: Nutrition of developing offspring from yolk reserves within the egg.

Lek: A territory used by a certain animal for mating.

Lepidotrichia: Modified scales that form the supporting rays of the fins of bony fishes.

Leptocephalus: The larval form of most eel species, bearing little resemblance to the adult eel environment.

Leptospirosis: Bacterial infection of spirochetes spread by urine.

Lexigrams: Symbols associated with objects or places in keyboard communication experiments with primates.

Lichens: Organisms formed by algae and fungi that are a source of food for tundra animals.

Life cycle: The sequence of development beginning with a certain event in an organism's life (such as the fertilization of a gamete), and ending with the same event in the next generation.

Life expectancy: The probable length of life remaining to an organism based upon the average life span of the population to which it belongs.

Life span: The maximum time between birth and death for the members of a species as a whole.

Life table: A chart that summarizes the survivorship and reproduction of a cohort throughout its life span.

Lift: An aerodynamic force created through differential flow above and below a structure.

Limb bud: Thickened epithelial cells along the lateral body fold that are underlain by mesoderm, creating a paddle-shaped extension from the trunk.

Limbic system: Brain structures related to the regulation of emotions.

Lipid: An organic molecule, such as a fat or oil, composed of carbon, hydrogen, oxygen, and sometimes phosphorus, that is nonpolar and insoluble in water.

Lipophilic: Fat soluble or water insoluble.

Litter: The offspring produced in a single birth; also referred to as a clutch.

Liver: An organ derived from the gut that secretes bile; it is connected to the gut by a duct through which its secretions enter the gut.

Local extinction: The loss of one or more populations of a species, but with at least one population of the species remaining.

Locomotion: The ability of an organism to move from one place to another as needed.

Logistic growth: A pattern of population growth that involves a rapid increase in numbers when the density is low but slows as the density approaches the carrying capacity.

Long-term pair bond: Pair-bonding that continues beyond a single reproductive period.

Longitudinal muscle: Muscle fibers that run along the longitudinal or anterior-posterior axis of the body.

Loop of Henle: A slender hairpin turn in the tubule where most adjustment of the water balance of the body occurs.

Lower chordates: A group within the Chordata that shows chordate characteristics in the larvae but is separated from vertebrates by the lack of a skeleton.

Luciferase: One of a group of enzymes that catalyzes the oxidation of a luciferin.

Luciferin: One of a group of organic compounds that emits visible light when oxidized.

Lumen: The central opening through the digestive tract, which is continuous from the mouth to the anus.

Lung: A concave inpocketing of the body wall of an animal (in contrast with a gill); lungs occur in air-breathing animals.

Lymphatic vessels: Very thin tubes that carry water, proteins, and fats from the gut to the bloodstream.

Lymphocyte: White blood cell that produces either cell-mediated or humoral immunity in response to foreign antigens.

Macroevolution: Large-scale evolutionary processes that result in major changes in organisms and allow them to change rapidly, occupy new adaptive niches, or develop novel body plans.

Macrophage: An animal that feeds on whole plants or animals or their parts; these can be carnivores, herbivores, or omnivores; or, a mature phagocytic cell that works with lymphocytes in destroying foreign antigens.

Madreporite: A fine-meshed sieve that opens from the sea water into the water vascular system of the echinoderms.

Male: An organism that produces sperm, the smaller of two different types of gametes.

Malphigian tubule: The primitive excretory organ of insects.

Mammary glands: The milk-producing glands found in all mammals.

Mandible: The hard part of a jaw or beak.

Mane: Long, thick hair growing from the neck.

Mantle: The outermost living tissue of mollusks; it makes shells, mother-of-pearl, and pearls.

Marked: An individual animal that is identifiable by marks that may be either man-made, such as metal bands or tags, or natural, such as the pattern of a giraffe.

Marsupial: A pouched mammal that gives birth to embryonic young that complete development in a pouch, attached to the mother's nipples.

Marsupium: Abdominal pouch containing mammary glands, which shelters the offspring of marsupials until they are fully developed.

Mass extinction: An event in which a large number of organisms in many different taxa are eliminated; there have been five such events in the history of life that resulted in the disappearance of more than 75 percent of all species.

Master control gene: A gene that single-handedly triggers the formation of an organ or structure.

Mate choice: The tendency of members of one sex to mate with particular members of the other sex.

Mate competition: Competition among members of one sex for mating opportunities with members of the opposite sex.

Maternal: Referring to the female parent.

Matrilines: Several generations of adult females all related by common descent from one female ancestor.

Matrix: Proteins or protein-chitin polymers that act as nucleation sites for mineralization in exoskeletons, or for the production of nails or claws.

Matrotrophy: Nutrition of developing offspring directly from the mother.

Maxillary: Retaining to the upper jawbone.

Medulla: The innermost layer of a hair.

Medusa (*pl.* medusae): Adult umbrella- or bell-shaped forms of jellyfish, with mouth facing downward.

Meiosis: Reduction division of the genetic material in the nucleus to the haploid condition; it is the process used by animal cells to form the gametes, during which the genes from the two parents are mixed.

Melanistic: Having dark coloration of skin and hair.

Melanophore: A melanin-containing cell.

Menagerie: A French word for zoos first used in the early 1700's to describe the keeping (and later exhibition) of animals.

Menstrual cycle: A series of regularly occurring changes in the uterine lining of a nonpregnant primate female that prepares the lining for pregnancy.

Mesenchyme: Embryonic undifferentiated connective tissue, derived from mesoderm, that will eventually give rise to all forms of connective tissue in the adult.

Mesoderm: The middle layer of the three fundamental tissue layers that appear during development; it will give rise to mesenchymal cells, muscles, bones, and blood.

Mesoglea: Gelatinous material lying between the inner and outer layers of a jellyfish.

Mesozoic era: A period of geologic time between 70 and 225 million years ago; subdivided into the Cretaceous, Triassic, and Jurassic periods.

Metabolic rate: The rate (expressed as calories per minute) at which an animal produces and consumes energy.

Metabolism: The conversion of carbohydrates, proteins, or fats into chemical energy that can be used to accomplish work and generate heat.

Metamorphosis: An abrupt change from a larval body form, accompanied by many physiological changes in the determination, differentiation, and distribution of cells, into an adult body form.

Metazoa: Organisms which are multicellular.

Microevolution: Small-scale evolutionary processes resulting from gradual substitution of genes and resulting in very subtle changes in organisms.

Microphages: Animals that feed on small microscopic particles suspended in water or deposited on bottom sediments.

Migration: The movement of individuals resulting in gene flow, changing the proportions of genotypes in a population.

Migratory animals: Animals that move from one place to another for feeding or breeding.

Milk ejection: Also known as milk letdown, this is the reflex response of the mammary gland to suckling of the nipple; the hormone oxytocin mediates this reflex.

Mimicry: The resemblance of one species (the model) by one or more other species (mimics), such that a predator cannot distinguish among them.

Mitochondria: Self-replicating units in a cell that are responsible for the metabolic generation of energy for cell processes; these structures are used to estimate the relationships between groups of organisms; the more similar the DNA, the more closely related the groups.

Mitosis: The process of cellular division in which the nuclear material, including the genes, is distributed equally to two identical daughter cells.

Modality: A specific type of sensory stimulus or perception, such as taste, vision, or hearing.

Molars: Flat, stout teeth used for grinding food.

Molecule: The smallest part of a chemical compound.

Mollusks: A phylum of aquatic invertebrates, usually shelled, such as clams, mussels, and squid.

Molting: The process of replacing exoskeletons or feathers.

Monogamy: A mating system in which one male pairs with one female.

Monophyletic: A group of species that is believed to have a common ancestor; thus, the species are all members of a clade.

Monotreme: A primitive mammal, such as the platypus and spiny anteater, which lays eggs and has other archaic features.

Morphogenesis: The development of form, including the overall form of the organism and the form of each organ and tissue.

Morphology: The scientific study of body shape, form, and composition; includes gross morphology, which examines entire structures or systems, such as muscles or bones; histology, which examines body tissues; and cytology, which focuses on cells and their components.

Mortality rate: The number of organisms in a population that die during a given time interval.

Morula: A solid ball or mass of cells resulting from early cleavage divisions of the zygote.
Mosaic development: The process whereby early embryonic cells are determined by the cytoplasm they receive from the egg; also called determinate development.
Motor neuron: A nerve cell that transmits impulses from the central nervous system to an effector such as a muscle cell.
Motor unit: A motor neuron together with the muscle cells it stimulates.
Mouth: The anterior part of the digestive system, used for ingesting food; it leads into the oral cavity, which opens into the esophagus.
Mucosa: The lining of the inner wall of the gut facing the lumen.
Mucus: A secretion of the salivary glands and other parts of the digestive system which lubricates passages; also covers the internal nasal structures to aid in humidification, warming, and particle filtration.
Müllerian ducts: The embryonic ducts that will become the female oviducts or Fallopian tubes, uterus, and vagina.
Multicellular organisms: Organisms consisting of more than one cell; there are diverse types of cells, specialized for different functions and generally organized into tissues and organs.
Musk: Bad-smelling liquids made to mark territory or for self defense.
Musth: Aggressive rutting behavior during elephant mating.
Mutation: A change in the nucleotide sequence of a gene or of a controlling site; changes in genes alter the protein, whereas changes in controlling sites determine where and how much of a protein is produced; usually refers to genetic change significant enough to alter the appearance or function of the organism.
Mutualism: A type of commensalism in which both symbiotes benefit from the association in terms of food, shelter, or protection.
Muzzle: The area around the nose and mouth of an animal.
Myelinated axon: An axon surrounded by a glistening sheath formed when a supporting cell has grown around the axon.
Myocarditus: Inflammation of the heart muscle.
Myoepithelial cells: The specialized cells within the mammary gland that surround the alveoli and contract to force milk into the ducts during milk ejection.
Myosin: One of the two major contractile proteins making up the thick myofibrils.
Myrmecology: The study of ants.

N: A standard abbreviation for the size of an actual population; if $\hat{n}$, it is an estimated value.
Nacre: Shiny, pearly lining of some mollusk shells; mother of pearl.
Nasohypophysial opening: An opening in the head of modern agnathans leading to a sac that aids in olfaction.
Natality rate: The number of individuals that are born into a population during a given time interval.
Natural selection: The process of differential survival and reproduction that leads to heritable characteristics that are best suited for a particular environment.
Navigation: To follow or control the course of movement from the place of origin to a specific destination.
Nekton: An aquatic organism that has the ability to swim.
Nematocyst: Poison sting cell.
Nematode: A long, cylindrical worm; some are parasitic.
Neoteny: Either the retention of immature characteristics in the adult form or the sexual maturation of larval stages; it results in new kinds of adult body plans.
Neotropical fauna: The geographic faunal region that includes Central and South America.
Nephridia: Excretory tubules specialized for excretion and osmoregulation, with an external opening and with or without an internal opening.

Nephron: Tubular structures in the kidneys that extract filtrate, reabsorb nutrients and other valuable substances, and secrete wastes.
Nerve: A cordlike bundle of sensory and/or motor axons in the peripheral nervous system.
Nest box programs: Construction and placement of nest boxes in suitable habitat to provide nesting platforms for specific birds of prey.
Nest-parasite: Also called brood-parasite; an individual (or species) that lays its eggs in the nest of another individual (or species) and does no parenting at all.
Neural integration: Continuous summation of the incoming signals acting on a neuron.
Neural spine: A projection extending off the upper side of a vertebra.
Neurobiology: The study of the biology of the brain.
Neuroethology: The study of behavior as it relates to brain functions.
Neurons: Complete nerve cells that respond to specific internal or external environmental stimuli, integrate incoming signals, and sometimes send signals to other cells.
Neurosecretory cells: Specialized neurons capable of manufacturing and releasing hormones (neurosecretions or neurosecretory hormones) and discharging them directly into circulation.
Neurotoxin: A substance that damages the nervous system, most often nerves that control breathing and heart action.
Neurotransmitter: A signaling molecule that provides neuron-to-neuron communication in animal nervous systems; some double as hormones.
Neurulation: The process by which the embryo develops a central nervous system; formation of a neural plate and subsequent closure of the plate to form a neural tube.
Niche: An organism's role in its habitat environment, such as food producer, decomposer, parasite, plant eater (herbivore), meat-eater (carnivore).
Nidifugous birds: Ground-nesting birds.
Nipple: The raised area on the surface of the skin over the mammary gland that contains the duct openings.
Nocturnal: Active at night.
Nomadic: Moving about from place to place according to the state of the habitat and food supply.
Nomenclature: The part of systematics that deals with establishing a valid name for a species, according to specific guidelines.
Nonrapid eye movement (NREM) sleep: Sleep characterized by relaxed muscles and slow brain waves.
Nonruminating: Digesting grasses without chewing cud.
Notochord: A dorsal, flexible, rodlike structure extending the length of a vertebrate's body; serves as an axis for muscle attachment.
Nuclear ribosomal deoxyribonucleic acid: Nuclear DNA that codes for the ribosomal DNAs.
Nuclear transfer: The insertion of genetic material from a donor cell to a recipient cell; in reproductive technologies the recipient cell is an egg cell from which the nucleus has been removed.
Nucleic acid: An organic acid chain or sequence of nucleotides, such as DNA or RNA.
Nucleus (pl. nuclei): A central cell structure that controls the activity of the cell because of the genetic material it contains; or, a cluster of neuron cell bodies within the central nervous system.
Numerical response: The abundance of predators dependent upon the abundance of prey in a habitat.
Nutrient: A nourishing food ingredient.
Nutrient cycle: A description of the pathways of a specific nutrient (such as carbon, nitrogen, or water) through the living and nonliving portions of an ecosystem.
Nymph: The sexually immature feeding stage in the development of those insects which undergo incomplete metamorphosis.

Occipital condyle: Ball-shaped bone that connected the back of the skull to the fused upper vertebrae of the spine.

Olfaction: The sense of smell.

Olfactory receptors: Receptor organs which have very high sensitivity and specificity and which are "distance" chemical receptors.

Ommatidium: Individual unit of the multifaceted compound eye.

Omnivore: An animal that eats both plant material and animal material.

Ontogenetic trajectory: A model of development represented as a graph on which the y axis is an abstract representation of morphology and the x axis is time; initiation of growth, rate of growth, and cessation of growth are shown.

Ontogeny: The successive stages during the development of an animal, primarily embryonic but also postnatal.

Oogenesis: Gamete formation in the female; it occurs in the female gonads, or ovaries.

Open circulation: An open-ended sinus or arterial vessel system in which the circulation system does not return blood or hemolymph directly back to the heart.

Opportunistic omnivore: An animal who includes a variety of plant and animal material in its diet, depending on the availability of different foodstuffs.

Opposable: Capable of rotation so that the fingerprint surface of the thumb or big toe approaches the corresponding surfaces of other fingers or toes.

Opsin: A membrane-bound protein or pigment, which absorbs light.

Optic nerve: The main nerve taking information from the eyes to higher processing areas.

Optimum temperature: The narrow temperature range within which the metabolic activity of an animal is most efficient.

Order: A group of closely related genera; in mammals, orders are the well-recognized major groups, such as the rodents, bats, whales, and carnivores.

Organelle: A subcellular structure found within the cytoplasm that has a specialized function.

Organism: Any form of life.

Orientation: An inherent sense of geographical location or place in time.

Orienting reflex: An unspecific reflex reaction caused by a change in the quantity or quality of a stimulus; it will disappear or decrease after repeated presentations of the stimulus.

Ornithischia: One of the two main dinosaur groups, characterized by a pelvis in which the pubis is swung backward.

Ornithology: The scientific study of birds.

Ornithopods: Bipedal, herbivorous dinosaurs.

Os: Bone.

Osculum: An opening through which a sponge ejects water.

Osmoconformer: An organism whose internal osmotic pressure approximates the osmotic pressure of its environment; such an organism is also referred to as poikilosmotic.

Osmoregulation: The regulation of the ratio between all dissolved particles, regardless of their chemical nature as ions or molecules, and water.

Osmoregulator: An organism that maintains its internal osmotic pressure despite changes in environmental osmotic pressure; such an organism is also referred to as euryosmotic.

Ossicles: The small bones of the middle ear.

Osteichthyes: The taxonomic class in which the bony fishes are placed; contains species related to the ancestors of higher vertebrates.

Osteoblast: A bone cell which makes collagen and causes calcium deposition.

Osteogenesis: The total biological process by which bone is formed within the body; the process involves the action of osteoblasts and is also called ossification.

Ostium: A surface pore through which water enters a sponge.

Otolith: A dense mineral frame supported by sensory hair cells immersed in aqueous fluid; used in the auditory system of lower animals to detect acceleration.

Oval gland: The poison gland in the scorpion telson.

Ovarian diverticulum: Used to house embryos and to obtain nutrients via absorptive cells among viviparous species.

Ovary: The female gonad that is the source of eggs to be fertilized and hormones to maintain pregnancy.

Oviduct: A narrow, hollow tube which takes the newly ovulated egg from the ovary, provides the site for fertilization, and transports the new embryo to the uterus.

Oviparity: Production of shelled eggs by females.

Oviphagy: A mode of reproduction in which embryo sharks develop in the maternal uterus and feed on unfertilized eggs produced by the mother.

Ovipositor: A tube that extends from the female's body for depositing eggs.

Ovum (pl. ova): The female reproductive cell (gamete); a mature egg cell.

Owl pellets: Compacted packets of undigested prey that is regurgitated; owl pellets may be used to determine food habits.

Oxytocin: Hormone involved with pleasure during bonding.

Ozone layer: The ozone-enriched layer of the upper atmosphere that filters out some of the sun's ultraviolet radiation, which causes skin and other types of cancer.

Pacemaker: A specialized group of cardiac muscle cells in the right atrium which initiates the heartbeat; also called the sinoatrial node.

Paedomorphosis: The appearance of youthful characters of ancestors in later ontogenetic stages of descendants.

Pair bond: Close relationship between a male and female for breeding purposes.

Pair-bonding: Prolonged and repeated mutual courtship display by a monogamous pair, serving to cement the pair bond and to synchronize reproductive hormones.

Pair-rule genes: Segmentation genes of fruit flies that divide the anterior-posterior axis into two-segment units.

Paleontology: The branch of geology that deals with prehistoric forms of life through the study of fossil animals, plants, and microorganisms.

Paleozoic era: Time period from 570 to 245 million years ago, which comprises the Cambrian, Ordovician, Silurian, Devonian, Carboniferous, and Permian periods.

Palp: Oral sensory organs of arthropods.

Palynology: The study of pollen and spores; also called paleopalynology.

Pancreas: An organ derived from the gut that secretes digestive enzymes; it is connected to the gut by a duct through which its secretions enter the gut.

Papillae: Sharp, curved projections on the tongue.

Paramyosin: A structural protein associated with myosin myofibrils and thought to support them.

Parapodia: Paired lateral projections on each side of most segments, variously modified for locomotion, respiration, or feeding.

Parasite: Any organism that lives on or in other living organisms and obtains its food from them.

Parasite-mix: All the individuals and species of symbiotes living in a host concurrently.

Parthenogenesis: Asexual reproduction from unfertilized gametes, producing female offspring only.

Partial pressure: The pressure exerted by a specific gas in a mixture of gases such as the atmosphere; it is analogous to concentration.

Patagium: A soft, flexible membrane.

Patch reef: A small, isolated reef that is typically found in lagoons.

Pathogens: Bacterium or viruses which cause diseases.

Pectines: Comblike structures on the ventral surface of the scorpion that are used in chemoreception.

Pectoral and pelvic girdles: Skeletal structures that form a structural base for attachment of the paired fins in fishes, connecting them to the rest of the body's skeleton.

Pectoral fin: One of a pair of fins just behind the head of a fish, where arms of terrestrial vertebrates are attached.

Pedicle: A small bone spur from which an antler grows (for example, in deer).

Pedipalps: Clawlike appendages that are used to catch and hold prey.

Pelage: A mammal's fur coat.

Pelagic: The area of open water in the oceans; organisms that occur in the water column.

Pelvic fins: Paired fins found either near the tail end of the fish body or below the pectoral fins; related to the hindlimbs of higher vertebrates.

Peptide: A chemical combination of certain amino acids.

Peramorphosis: A group of phenomena in which descendant morphologies exceed the ancestral morphologies either in the rate at which they develop or in the length of time during which development occurs.

Perineal: Located between scrotum and anus in males or the equivalent region in females.

Period: The length of one complete cycle of a rhythm; ultradian rhythms are shorter than twenty hours, circadian rhythms are about twenty-four hours (twenty to twenty-eight hours), and infradian rhythms are longer than twenty-eight hours.

Periodicity hypothesis: The proposal that mass extinctions have occurred approximately every 26 million years over the past 250 million years.

Periosteum: The fibrous membrane which covers all bones except at points of articulation, containing blood vessels and many connections to muscles.

Perissodactyls: Ungulates having an odd number of toes.

Permeability: The tendency to permit the movement of a gas across a membrane.

Persistent organic pollutants (POPs): Chemicals that remain in the environment for a very long time and can be found at long distances from where they are used or released; they are nearly all of human origin.

Perspiration: A watery fluid exuded by sweat glands that contains small quantities of salts, urea, and uric acid.

pH: The negative logarithm of the hydrogen ion concentration, with higher hydrogen ion concentrations indicating lower pH; the pH scale goes from 0 to 14, with a pH of 7 being neutral, values below 7 indicating acidity, and values above 7 indicating alkalinity.

Phagocytosis: Obtaining food by engulfing it.

Phalanges: The free toes of the foot; some can be modified to claws, hoofs, or nails.

Phanerozoic era: An era of geologic time beginning approximately 544 million years ago at the start of the Paleozoic era, when animals with mineralized skeletons became common.

Pharynx: Lower part of vocal tract, connecting the mouth and nasal cavities to the larynx.

Phasic receptors: Receptors that adapt quickly to a stimulus.

Phasmid: Sense organs located in the tail region of roundworms that are important for detecting chemical signals in the environment.

Phenotype: The visible or outward expression of the genetic makeup of an individual.

Pheromone: A chemical produced by one member of a species that influences the behavior or physiology of another member of the same species.

Photoperiod: The measure of the relative length of daylight as it relates to the potential physiological responses that exposure to daylight evokes.

Photoperiodism: The responses of an organism to seasonally changing day length that cause altered physiological states, such as flowering or nonflowering in plants and reproductive seasons in animals.

Photophore: A light-emitting organ consisting of a lens, reflector, and light-emitting photogenic cells.

Photoreceptor: A cell containing membranes that house light-sensitive pigments.

Photosynthesis: The process by which green plants and algae use sunlight as energy to convert carbon dioxide and water into energy-rich compounds such as glucose.

Phylogenetics: The study of the developmental history of groups of animals.

Phylogeny: The evolutionary history of taxa, such as species or groups of species; order of descent and the relationships among the groups are depicted.

Phylum (pl. phyla): The taxonomic category of animals and animal-like protists that is contained within a kingdom and consists of related classes.

Physiology: The study of the functions, activities, and processes of living organisms.

Phytophagous: Animals, also referred to as herbivorous, that feed on plants.

Phytoplankton: Small, aquatic free-floating plants.

Pigments: A variety of colored substances which impart color to feathers.

Pinna (pl. pinnae): The external ear of an animal.

Pinnipeds: Flipper-footed marine mammals, such as sea lions, fur seals, true seals, walruses.

Pit viper: A poisonous snake, such as a rattlesnake, which detects its prey via paired heat-sensing pits in its head.

Pitch: The frequency of sound; the higher the frequency, the greater its pitch.

Placenta: Structure that connects a fetus to the mother's womb; indicative of internal gestation of young.

Placodermi: Extinct class of fishes characterized by dense armor plating made of dermal bone.

Placoid denticles: Toothlike scales found in sharks and rays.

Plankton: Floating or weakly swimming plants and animals, usually very small in size.

Plantigrade: Walking on the sole, with the heel touching the ground.

Planula: Free-swimming, ciliated jellyfish larva.

Plastron: The portion of the shell that protects a turtle's belly (venter).

Plate tectonics: Often referred to as continental drift; the modern theory assumes that the current position of continents and oceans are the consequence of dynamic forces that involve land masses "floating" on the earth's molten core.

Pleistocene era: A period from about 1.8 million years ago to the last 100,000 years, characterized by alternating glacial and interglacial cycles; during the glacial periods ice sheets many miles deep covered as much as a third of the earth's surface.

Pleurocoel: Chamber formed in the centrum of a vertebra to reduce its weight.

Plexus: A group of nerve cells and their connections to one another.

Plumage: The feathers of birds.

Podites: The parts of the jointed appendages of arachnids.

Poikilotherm: Cold-blooded or ectothermic; any organism having a body temperature that varies with its surroundings; in general, reptiles, amphibians, fish, and invertebrates.

Polyestrous: Multiple sexual heats or periods of sexual excitement.

Polygamy: A mating system in which one male mates with several females (polygyny) or one female mates with several males (polyandry).

Polymorphism: The occurrence of two or more structurally or behaviorally different individuals within a species.

Polyp: Immature cylindrical forms of jellyfish with mouth facing upward.

Polyphyletic: A group of species believed not to have a common ancestor; thus, they are not members of a clade but are probably a product of convergent evolution.

Population: A group of individuals of the same species that live in the same location at the same time.

Population analysis: The study of factors that influence growth of biological populations.

Population density: The number of individuals in a population per unit area or volume.

Population regulation: Stabilization of population size by factors such as predation and competition, the relative impact of which depends on abundance of the population in a habitat.

Pore canals: Sites that house the cytoplasmic extensions of the crustacean hypodermis.

Positional information: A concept by which differentiating cells organize themselves to produce a particular tissue type based upon cell-to-cell interactions.

Postdisplacement: A form of paedomorphosis in which the initiation of growth in a descendant occurs later than in the ancestor, ensues at the ancestral rate, and ceases at the ancestral point.

Postnuptial molt: Replacement of feathers following the mating season.

Precambrian era: The earliest chapter of the earth's history, covering the time interval between the formation of the earth, about 4.6 billion years ago, and the beginning of the Cambrian period, about 570 million years ago.

Precocial: The condition of being strong and relatively well developed at birth or hatching, and thus not particularly dependent upon parental care.

Predation: The act of killing and consuming another organism.

Predentary bone: Keeled and pointed bone that terminated the lower jaw.

Predisplacement: A form of peramorphosis in which the initiation of growth in a descendant occurs earlier than in the ancestor, ensues at the ancestral rate, and ceases at the ancestral point.

Preening: A bird's act of grooming itself by cleaning and straightening its feathers.

Prehensile: Adapted for seizing or grasping.

Primary consumer: An organism that get its nourishment from eating primary producers, which are mostly green plants and algae.

Primary emotions: Emotions related to innate motivations.

Primary feathers: Flight feathers on the outer joint of the wing.

Primary production: The energy assimilated by green plants and stored as organic tissue.

Primates: A group of mammals including apes, chimpanzees, monkeys, humans, lemurs, and tarsiers.

Primer pheromone: A chemical substance that affects behavior by altering physiology and is therefore not rapid in its effects.

Primitive: Referring to a feature that reflects an ancestral condition, rather than those that represent more recent evolutionary changes (derived).

Principle of antithesis: The observation that signals communicating opposite meaning tend to be expressed using displays having opposite characteristics.

Prismatic layer: The outer crystalline layer of the molluscan shell.

Proboscis: A coiled, springlike sucking tube or "tongue" used to drink nectar.

Producers: Green plants and chemosynthetic organisms that can produce food from inorganic materials.

Progenesis: A form of paedomorphosis in which the initiation of growth in a descendant occurs at the same time as in the ancestor, ensues at the ancestral rate, but ceases earlier than at the ancestral point.

Progesterone: The hormone essential for maintenance of pregnancy that is secreted by the corpus luteum.

Proglottid: A body segment of a tapeworm that contains a set of reproductive organs, usually both ovaries and testes.

Prokaryote: An organism that has no internal membranes in its cells; the only membrane in a prokaryote is the cell membrane.

Prolactin: A hormone responsible for secretions of milk from the mammary glands of mammals and from the crops of birds.

Promiscuity: A mating system in which sexual partners do not form lasting pair bonds, where their relationship does not persist beyond the time needed for copulation and its preliminaries.

Prosimians: A group of primates that retain some primitive characteristics absent in higher primates.

Protandry: The condition of starting out male with the potential to become female.

Protective mimicry: Use of both color and form to mimic an inanimate feature of the environment.

Protein: An organic molecule containing carbon, hydrogen, oxygen, nitrogen, and sulfur and composed of large polypeptides in which over a hundred amino acids are linked together; proteins are the chief building blocks of cellular structures.

Protein hormone: A hormone type composed of protein, a long chain of amino acids encoded by a gene.

Prothoracic gland: The gland where ecdysone is made in insects.

Prothoracicotropic hormone (PTTH): A hormone made in the brain of insects which stimulates the prothoracic gland to make ecdysone.

Protists: Members of the kingdom Protista; the greater number are unicellular but, unlike bacteria, possess a nucleus and chromosomes.

Protogrammar: Word coined to signify the early foundation for grammar development found in primates.

Protogyny: The condition of starting out female with the potential to become male.

Protostomes: Annelids, mollusks, flatworms, and arthropods, a group linked by features of cell development including retention of the blastopore as the mouth.

Protozoa: Single-celled, animal-like organisms; all are eukaryotic (the cells have nuclei and other internal structures).

Proximal: Occurring near the base end of a limb.

Pseudocoel: A fluid-filled body cavity that is bounded by mesodermal muscle on the outside and endodermal epithelium on the internal boundary.

Pseudopods: Cytoplasmic extensions of a protozoan's body, used for locomotion and the engulfing of food.

Pubis: One of the three bones that make up the pelvis (the others are the ischium and ilium).

Pugmarks: Pawprints.

Punctuated equilibrium: The idea that new species form during relatively short (a few generations) speciation events and then persist for millions of years unchanged until they go extinct.

Pupa: Intermediate stage between the larval and adult stages of the life cycle, during which metamorphosis occurs.

Pyramid of numbers: A graph that plots the size of animals against the number of individuals, generally yielding a pyramidal shape when the X axis is shifted to the middle of the figure.

Quadrat: A sample plot of a specific size and shape used in one method of determining population size or species diversity.

Quadruped: Animal with four feet.

Quills: Sometimes referred to as spines; modified guard hairs; quills have barbed tips which can work themselves deeper into flesh once they have penetrated.

r strategy: A reproductive strategy involving high reproductive output; found often in unstable or previously unoccupied areas.

Rabies: Viral disease of the nervous system.

Radial sesamoid: Forefoot wrist bone.

Radial symmetry: An arrangement of body parts of an organism like the pieces of a pie around an imaginary central axis.

Radiochronometry: The determination of the age of an object using radioactive isotope decay rates.

Radioisotopes: Unstable elements that decay into stable forms at a constant rate, which are used to determine how long ago volcanic rocks solidified.

Radula: A tonguelike, toothed organ used to grind food or drill holes in shells of prey.

Rami: The branches of an arthropod limb or appendage.

Random genetic drift: The random change of gene frequencies because of chance, especially in small populations.

Random mating: The assumption that any two individuals in a population are equally likely to mate, independent of the genotype of either individual; this is equivalent to saying that all the gametes of all the individuals in a population are placed into a large pool, from which gametes are paired at random.

Rapid eye movement (REM) sleep: Sleep characterized by fast brain waves, during which dreaming typically occurs.

Recapitulation: The repetition of phylogeny in ontogeny or of the ancestral adult stages in the embryonic stages of descendants.

Recaptured: A previously marked animal that is either seen, trapped, or collected again after its initial marking.

Receptive field: The area upon or surrounding the body of an animal that, when stimulated, results in the generation of a response in the sense organ.

Receptor: A nerve ending specialized for the reception of stimuli; or, a protein molecule on or in a cell that responds to the hormone by binding to it and initiating a series of events that form the response.

Receptor cells: Sensory cells within sense organs that are directly responsible for detecting stimuli.

Receptor molecule: A molecule on the cell membranes of target tissues that binds to the hormone molecule and initiates the action of the hormone.

Receptor potential: A change in the distribution of electric charge across the membrane of a receptor cell in response to the presentation of a stimulus.

Recessive: Requiring two copies of a gene for the trait to be expressed.

Reciprocal relationship: Any type of coevolved, highly interdependent relationship between two or more species.

Reciprocal sacrifice: One explanation for acts of altruism among unrelated animals; an individual sacrifice is made under the assumption that a similar sacrifice may in turn aid the individual in the future.

Rectrices: Tail feathers.

Reflex arc: The entire nerve path involved in a reflex action.

Regulative development: The process whereby early embryonic cells are determined by their interactions with other cells; also called indeterminate development.

Releaser: A stimulus that releases a sequence of reflexes that always occur in the same order and manner.

Releaser pheromone: A chemical that generates an immediate and more or less predictable behavioral response in another member of the same species.

Remnants: Nesting material not deliberately placed in nest by birds.

Reproductive mode: A combination of life-history characteristics, including egg-deposition site and type of parental care.

Reproductive strategy: A set of traits that characterizes the successful reproductive habits of a group of organisms.

Reproductive success: The number of offspring produced by one individual relative to other individuals in the same population.

Reproductives: Sexually mature males and females.

Reptile: A class of vertebrates characterized by cleidoic eggs, dry scaly skin, a single bone in the middle ear, and several bones in each jaw.

Reservoir host: A host species other than the one of primary interest in a given research study.

Resilience stability: Stability exhibited by a community that changes its structure when disturbed but returns to its original structure when the disturbance ends.

Resource: A requirement for life, such as space for living, food (for animals), or light (for plants), not including conditions such as temperature or salinity.

Resource defense: The control of a resource indirectly or directly.

Resource-holding potential: The ability of an individual to control a needed resource relative to other members of the same species.

Respiration: The utilization of oxygen; in air-breathing vertebrates, the inhalation of oxygen and the exhalation of carbon dioxide.

Respiratory medium: The water or air that contains the oxygen used by an animal to carry out biochemical reactions.

Respiratory pigment: A protein that “supercharges” the body fluid (blood) with oxygen; the oxygen can bind to the pigment and then be released.

Respiratory surface: The gill, lung, or skin site at which oxygen is taken up from the air or water into the animal, with the release of carbon dioxide at the same time and site.

Restriction: Reduction of the developmental potency of a cell.

Retardation: The appearance of an organ later in the development of a descendant than in the ancestor as a result of a slowing of development.

Reticulate: Netlike covering of scales on legs.

Retina: The light-sensitive membrane at the back of the eye.

Reynolds numbers: The results of a formula that takes into account the velocity of an object, its characteristic length divided by the dynamic viscosity of the fluid.

Ribonucleic acid (RNA): A long, single-stranded molecule that amplifies, transports, and expresses the coded information in DNA.

Ribosomes: Small cytoplasmic particles that function in protein synthesis.

Ritualization: An evolutionary process that formalizes the context and performance of a display so that its meaning is clear and straightforward.

RNA. *See* **Ribonucleic acid (RNA)**.

Rostral bone: Keeled and pointed bone that terminated the upper jaw.

Royal jelly: The protein- and hormone-rich food that worker bees feed queen larvae.

Rudimentary: Short or small.

Ruminant: A herbivore that chews and swallows food which enters its stomach, is partly digested, is regurgitated and chewed again, and reenters the stomach for more digestion.

Rut: Activities associated with cervid mating behaviors.

Saggital: Bony skull top.

Salinity: A measure of the quantity of dissolved salts in seawater.

Saliva: The liquid containing enzymes secreted by the salivary glands that is injected into the host when the adult mosquito feeds.

Sampling: The process of collecting data, usually in such a manner that a statistically valid set of data can be acquired.

Saprovore: Any organism that consumes dead or decaying plant or animal matter.

Sarcomere: The fundamental unit of contraction within a muscle cell; repeating bands of actin and myosin.

Sarcoplasmic reticulum: Membrane-bound sacs that surround the myofibrils of muscle cells and which store and release calcium ions.

Saurischia: One of the two main dinosaur groups, characterized by a pelvis in which the pubis points forward.

Sauropods: Large, quadrupedal herbivorous dinosaurs that lived from the Early Jurassic to the end of the Cretaceous.

Scale of being: An arrangement of life-forms in a single linear sequence from lower to higher; also called a chain of being.

Scavenger: An animal that feeds on the dead carcasses of other animals.

Schema (pl. schemata): An innate releasing mechanism; a neural process that programs an animal for receiving a particular sign stimulus and causes a specific behavioral response.

Sclerotin: A hard, horny protein constituent of the exocuticle found in arthropods such as insects; it is superficially similar to vertebrate horn or keratin.

Scutellate: Overlapping of platelike or shieldlike scales.

Secondary emotions: Emotions with a strong social component.

Secondary feathers: Flight feathers on the inner wing.

Secondary metabolite: A biochemical that is not involved in basic metabolism, often of unique chemical structure and capable of serving a defensive role for the organism.

Secondary palate: The palate forming a shelf in the mouth that places the internal nares far back in the throat.

Segment polarity genes: Segmentation genes of fruit flies that divide the anterior-posterior axis into individual segments.

Segmentation: The division of a structure into linearly arranged segments; it can lead to the formation of somites, or it can lead to the formation of separate chondrification centers in a developing digit.

Segmentation genes: These include the gap rule, pair-rule, and segment polarity genes; they establish anterior-posterior segmentation in fruit flies without specifying segment identity.

Selection: A process that prevents some individuals from surviving and propagating while allowing others to do so.

Selective pressure: Evolutionary factors that favor or disfavor the genetic inheritance of various characteristics of a species.

Semen: Fluid produced by the male reproductive system that contains the sperm.

Semiochemical: A chemical messenger that carries information between individual organisms of the same species or of different species; pheromones and allelochemics are semiochemicals, but hormones are not.

Sensilla: Hairlike structures associated with nerves that act as mechanoreceptors and chemoreceptors.

Sensitive period: A period during which a given event produces a stronger effect on development or in which a given effect can be produced more rapidly than it can earlier or later.

Sensitization: An arousal or an alerting reaction which increases the likelihood that an organism will react; also, a synonym for loss of habituation with increased intensity of response.

Septa: A thin, muscular tissue used to separate segments into a series of ringlike cavities.

Septum: The bony structure that divides the nose into two sections.

Sequential hermaphrodite: Species or individual with the potential to change from one sex to the other.

Sequester: To store a material derived from elsewhere. In defenses, some predators sequester defensive properties from their prey to defend themselves from their own predators.

Sessile: An organism incapable of moving from its point of origin.

Setae: A needlelike, chitinous structure of the integument, used for locomotion; also, hairlike organs arising from the cuticle that are typically sens.

Sex hormones: Hormones (androgens in males, estrogens in females) associated with sex characteristics and sexual behavior.

Sex-limited traits: Features that are only expressed in one sex.

Sex pheromone: A volatile chemical released into the air by females to attract males.

Sex-role reversal: Generally used to refer to species in which the male does most of the parenting.

Sexual dimorphism: A difference in structure or behavior between males and females.

Sexual reproduction: Reproduction in which genes are exchanged between individuals.

Sexual selection: The process that occurs when inherited physical or behavioral differences among individuals cause some individuals to obtain more matings than others.

Sexual swelling: An estrogen-induced water retention that causes reddening and swelling in the perineal region and around the buttocks.

Shaft: Long, central spine of the feather; or, the main hair part, made of dead cells arranged in a complex fashion.

Shedding: A process through which organisms lose and replace their external covering.

Siblicide: Infanticide committed by the siblings of the individual killed.

Signal: Information transmitted through sound, such as bird calls, or through sight, such as body posture.

Signal pheromone: Nearly a synonym of releaser pheromone, but used with mammals to remove the suggestion of a programmed response and to indicate a more complex response.

Silurian era: A geological period from about 440 million years ago to about 400 million years ago; the first jawed fishes appeared during this period.

Simultaneous hermaphroditism: The condition of being simultaneously male and female.

Sinuses: Larger spaces, thought to represent through channels, for hemolymph in open circulatory systems, sometimes bound by membranes.

Siphon tube: Tube that extends from the rear of the larval abdomen at the air water interface and allows the larva to breath air.

Sit-and-wait foraging: Sitting in one place, waiting, and attacking prey as they move.

Slotting: The separation of primary feathers at the tip of the wings.

Slow muscle: Muscle cells that respond slowly to nervous impulses; in invertebrates, these muscle fibers have long sarcomeres and a high ratio of thin to thick myofibrils.

Snailing: The process in which the free-swimming larva (miracidium) of flukes utilizes the tissue of a snail as an intermediate host.

Social grooming: An activity maintaining social interaction, whereby debris is removed from a primate's hair.

Social wasp: A wasp living in a large colony.

Sociality: The tendency to form and maintain stable groups.

Sociobiology: The study of the biological basis of the social behavior of animals.

Soldiers: Large workers who defend the colony and often raid other colonies.

Solitary: Lives alone.

Somite: A condensation of mesoderm on either side of the notochord (a rod extending the length of the embryo), whose three different cell populations will differentiate during cellular migration into various types of connective tissue, muscles, and other structures and tissues.

Sound frequency: The distances between crests of sound waves measured in hertz.

Sound intensity: The loudness of a sound directly related to the amplitude of the sound waves measured in decibels.

Speciation: The formation of new species as a result of geographic, physiological, anatomical, or behavioral factors that prevent previously interbreeding natural populations from breeding with each other any longer.

Species: A group of animals capable of interbreeding under normal natural conditions; the smallest major taxonomic category.

Species selection: The idea that species are independent entities with their own properties, such as birth (speciation) and death (extinction); a higher level of selection above that of natural selection is postulated to take place on the species level.

Species-specific: A behavior or trait that characterizes members of a species, is innate, and is exclusive to that species.

Specific metabolic rate: The rate of metabolism per unit body mass (calories per gram per hour).

Spectacle: Transparent scale covering the eye as a replacement for the eyelid; occurs in some lizards and all snakes.

Spermaceti: A waxy substance in heads of sperm whales; usable for candles, ointments, lubricants, and cosmetics.

Spermatogenesis: Gamete formation in the male; it occurs in the male gonads, or testes.

Spermatophore: A tiny, mushroomlike structure deposited by a male salamander for transferring sperm to a female during courtship.

Spermiogenesis: The structural and functional changes of a spermatid that lead to the formation of a mature sperm cell.

Sphincter: A ring of muscle that can close off a portion of the gut.

Spicule: A needlelike structure that is part of a sponge skeleton.

Spindle: In a muscle, the bundle of nuclear fibers formed during one stage of mitosis.

Spiracles: Openings on the outside of the insect abdomen that lead to breathing tubes.

Spongin: A fibrous skeletal material in soft sponges.

Stasis: The long-term stability and lack of change in fossil species, often spanning millions of years of geologic time.

Status badge: A visual feature that, based on its size or color or some other variation, indicates the social status of the bearer.

Stegosaurs: Quadrupedal, herbivorous dinosaurs with vertical bony plates along their backbones.

Stem cell: A determined, undifferentiated cell that is hormonally activated and changes into a specific cell type.

Stenohaline: The inability of an organism to tolerate wide ranges of salinity.

Stereoscopic vision: Vision with good depth perception.

Stereotyped behavior: An unlearned and unchanging behavior pattern that is unique to a species.

Steroid: A hormone that is made from cholesterol.

Stimulus: Any environmental cue that is detected by a sensory receptor and can potentially modify an animal's behavior.

Stomach: The part of the digestive system where mechanical breakdown of food is completed and chemical digestion begins.

Strategy: A behavioral action that exists because natural selection favored it in the past (rather than because an individual has consciously decided to do it).

Stratigraphy: In geology, a sequence of sedimentary or volcanic layers, or the study of them; indispensable for dating specimens.

Striated muscle: Voluntary or skeletal muscle, capable of conscious ennervation.

Strong acid: An acid that dissociates almost completely into its component ions; hydrochloric acid, for example, dissociates almost completely into hydrogen ions and chloride ions.

Studbook: A record-keeping system that provides information on an animal's lineage.

Submersible: A vessel, like a submarine, that can operate with or without occupants.

Subspecies: A group or groups of interbreeding organisms that are distinct and separated from similar related groups but not fully reproductively isolated.

Subungulates: Nonhoofed mammals that support their weight on more than the terminal phalanges; some, such as elephants and hyraxes, have pads under their metatarsals, others, such as the sirenians, have forelimbs modified into flippers.

Succession: Change in a plant or animal community over time, with one kind of organism or plant being replaced by others in a more or less predictable pattern.

Survivorship: The pattern of survival exhibited by a cohort throughout its life span.

Sustained annual yield: The harvest of no more animals than are produced, so that the total population remains the same.

Swim bladder: An internal organ evolved from the gut that allows a fish to regulate its vertical position in the water column (maintain its balance); also called an air bladder.

Symbiosis: A type of coevolved relationship between two species in which both participants benefit; a type of mutualism.

Sympatric: Populations of organisms living in the same place, not separated by a barrier that would prevent interbreeding.

Synapse: The point of contact between adjacent neurons, where nerve impulses are transmitted from one to the other.

Synchronization: Causing events to occur simultaneously.

Syrinx: The vocal mechanism of birds, consisting of one or more membranous structures at the lower end of the trachea, where the windpipe divides into two bronchial tubes leading to the lungs; the membranes vibrate due to pressure differences when air streams across their surfaces.

Systematics: The subdivision of biology that deals with the identification, naming, and classification of organisms and with understanding the evolutionary relationships among them.

Systemic: Referring to a group of organs that function in a coordinated and controlled manner to accomplish some end, such as respiration.

Systolic pressure: The pressure in blood vessels when the ventricles of the heart contract.

Tadpole: The larval stage of frogs and toads.

Tagmatization: Functional specialization of groups of segments.

Talons: The long, curved, and sharply pointed claws of a bird of prey; used for slashing and killing, holding and carrying of prey, and for defense.

Tapetum: Membrane layers.

Taphonomy: The study of the processes that lead to fossilization.

Target cells: Cells that contain hormone receptors.

Target organ: A specific body part that a particular hormone directly affects.

Taxon (*pl.* taxa): The basic unit of taxonomy; any of the categories of classification to which an organism may be assigned.

Taxonomy: A classification scheme for organisms based primarily on structural similarities; taxonomic groups consist of genetically related animals.

Teat: An elongated form of nipple that contains one duct opening.

Tectonic plate: Tectonic plate theory suggests that the earth's surface is composed of a number of oceanic and continental plates which have the ability to move slowly across the earth's asthenosphere.

Teleosts: Members of the infraclass Teleostei, the most advanced of the ray-finned fishes; they compose the vast majority of living bony fish species.

Tentacles: A long flexible arm or projection.

Terrestrial: Living on land.

Territorial behavior: The combination of methods and actions through which an animal or group of animals protects its territory from invasion by other species.

Tetrapods: Four-legged vertebrates (amphibians, reptiles, birds, and mammals).

Thanatocoenosis: An assemblage of fossil species from a particular environment; a fossilized community; compare to "biocoenosis," an assemblage of living species.

Thermogenesis: The generation of heat in endotherms by shivering or increased oxidation of fats.

Thermoregulation: The process by which animals maintain body temperatures within a certain range.

Theropoda: "Beast foot"; dinosaurs that lived from the Late Triassic to the terminal Cretaceous extinction event; most predatory and carnivorous dinosaurs belong to this group.

Thoracic: Related to the middle section of the body of arthropods, which are generally subdivided into a head, thorax, and abdomen; both thorax and abdomen may have several segments.

Thorax: The middle section of insects from which the legs and wings protrude.

Threat display: A territorial behavior exhibited by animals during defense of a territory, such as charging, showing bright colors, and exaggerating body size.

Threatened species: Animals or plants so few in number that they may soon be endangered and then extinct.

Thrust: The forward force that is developed by engines, rotors, or moving wings, which pushes airplanes, helicopters, or flying animals and which opposes drag.

Tissue: A group of cells with a similar structure and their intercellular matrix, which work together to accomplish a specific function.

Tonic receptors: Receptors that typically show little or no adaptation to a continuously applied stimulus.

Torpid: Dormant, numb, sluggish in action.

Totipalmate: Having all four toes fully webbed.

Totipotent: The ability of a cell to develop into any kind of cell in the body.

Toxin: Any substance, such as the venom in snakes or spiders, that is toxic to an animal.

Tracheal system: The respiratory system of insects and other terrestrial invertebrates; it consists of numerous air-filled tubes with branches extending into tiny channels in direct contact with body cells.

Tract: A cordlike bundle of parallel axons within the central nervous system.

Trait: A genetically inherited characteristic.

Transdetermination: An event by which a determined, undifferentiated cell changes its determination, thereby giving rise to a different tissue type.

Transduction: The translation of a stimulus's energy into the electrical and chemical signals that are meaningful to the nervous system.

Triploid: Having three of each chromosome; an abnormal state which is unable to produce normal haploid gametes.

Trophallaxis: The exchange of bodily fluids between nestmates, either by regurgitation or by feeding on secreted or excreted material.

Trophic hormones: Hormones that stimulate another endocrine gland.

Trophic level: A level in a food chain or food web at which all organisms consume the same general types of food.

Tropomyosin: A double-stranded protein that lies in the grooves of actin myofibrils, blocking actin from attachment to myosin.

Troponin: A globular protein composed of three subunits; one subunit binds calcium ions, and another draws tropomyosin away from actin, which allows myosin to form crossbridges constituting the third subunit.

True horn: The permanent horns found in animals such as cattle, sheep, and goats.

Tubule: The long, slender part of the nephron that is the location of almost all kidney function.

Turbinates: Bony structures that define the internal nasal anatomy.

Turbulence: Flow that is chaotic and may create stall conditions through the loss of lift.

Twitch: A rapid muscular contraction followed by relaxation that occurs in response to a single stimulus.

Tympanic membrane: Eardrum or other surface which serves the purpose of converting sound waves into mechanical vibration.

Ungulate: A hoofed mammal from the order Artiodactyla (pigs, cattle, antelope, and their relatives) or from the order Perissodactyla (horses, rhinoceroses, tapirs, and their relatives).

Unguligrade: Walking on the tips of the toes.

Unicellular: Consisting of only one cell.

Uniformitarianism: The belief that the earth and its features are the result of gradual biological and geological processes similar to the processes that exist today.

Uniramous: Having only one rami; antennae appear as a single, nonbifurcated structure.

Upper Paleolithic era: The era from 30,000 B.C.E. to 3500 B.C.E., when humans first began to affect European wildlife populations.

Urea: A substance formed from by-products of protein metabolism and excreted by the kidney.

Urogenital groove: A slitlike opening behind the genital tubercle that will become enclosed in the penis but remain open in females.

Uterus: The hollow, thick-walled organ in the pelvic region of females that is the site of menstruation, implantation, development of the fetus, and labor.

Valves: Specialized, thickened groups of muscle cells in the heart chambers, major arterial trunks, arterioles, and veins which prevent backflow of blood.

Vane: Flat, broad web emerging from opposing sides of the feather shaft.

Vascular papilla: A protuberance having a blood supply.

Vector: Transmits pathogens from one host to another.

Vein: A tubelike, elastic channel with thin walls enforced with smooth muscles and valves that transport oxygen-poor blood; veins start as fine venules in tissues connected with capillary beds.

Velvet: A hairy skin richly endowed with blood vessels that covers developing antlers.

Venom: A toxic substance that must be injected (instead of ingested) to immobilize or kill prey.

Ventilation: The movement of the respiratory medium to and across the site of gas exchange.

Ventricle: The right and left chambers of the heart, which pump blood into pulmonary and systemic circulation, respectively.

Vertebrates: A subphylum of the phylum Chordata that includes all animals with backbones, and thus all animals possessing endoskeletons.

Vestigial: An organ that is no longer biologically useful.

Vibrissae: Stiff hairs, whiskers, or bristles projecting as feelers from the nose and the head, used to provide positional information to an animal.

Vicariance: An event involving the erection of a barrier to dispersal that splits the distribution of an organism and facilitates the differential evolution of the geographically separated descendants.

Viscera: Any internal body organ, such as intestines or entrails.

Viscosity: The stickiness of a fluid created by internal forces as molecular attractions.

Visual cortex: The part of the cerebral cortex concerned with vision.

Visual predation: Catching prey (such as insects) by sighting them visually, judging their exact position and distance, and pouncing on them.

Vitamin: An organic nutrient that an organism requires in very small amounts and which generally functions as a coenzyme.

Vitelline envelope: The protective layers that form around the egg while it is still in the ovary.

Vivaria: A Latin word for a structure housing living animals, first used by the Romans to describe the places holding elephants and other animals for their shows.

Viviparous: Characterized by live birth (as opposed to egg-laying).

Vocal folds: Small, laminated sheets of muscle which meet at the front of the larynx; they are open for breathing, and are brought together to vibrate for voiced sounds.

Volatiles: Chemical compounds that are vapor or gas at environmental temperatures or that readily release many of their molecules to the vapor phase.

Voluntary: Capable of being consciously controlled.

Warm-blooded: Referring to animals whose body temperatures are maintained at a constant level by their own metabolisms.

Warning coloration: The bright colors seen on many dangerous and unpalatable organisms that warn predators to stay away.

Weak acid: An acid that does not dissociate to a great extent; carbonic acid, for example, dissociates to produce some ions, but most of the molecules remain in their original forms.

White matter: The part of the central nervous system primarily containing myelinated axon tracts.

Wildlife: All living organisms; traditionally, the term included only mammals and birds that were hunted or considered economically important.

Wildness: Characteristics that define the biological and behavioral life of a species in the wild.

Wing loading: Ratio of weight to lifting area of wing; birds with large wings and light weight, such as the swallow-tailed kite, have a low wing loading, while birds with small wings and large, heavy bodies, such as pheasant or turkey, have a high wing loading.

Wolffian ducts: An embryonic duct system that becomes the internal accessory male structures that carry the sperm.

Workers: Sterile, wingless female social insects.

Xenotransplantation: The transplantation of organs from one species to another.

Zeitgeber: "Time giver" in German, also referred to as a synchronizer or entraining agent; most often the light-dark cycle, noise, feeding, or, for humans, societal factors.

Zona pellucida: Mammalian protective layer analogous to the vitelline envelope.

Zone fossils: Fossils that characterize a period of time and can be used to provide a relative date for a rock.

Zone of polarizing activity (ZPA): A region at the posterior base of the limb bud that seems to influence the distal development of pattern in a developing limb.

Zoo: An English abbreviation of the term "zoological garden"; first used in the early 1800's to describe the early British zoos, it tended to replace the word menagerie in the 1900's.

Zoogeography: The study of the distribution of animals over the earth.

Zoonoses: Diseases transmissible from animals to humans.

Zygodactyl: Having two toes pointing backward and two toes pointing forward.

Zygote: The single cell formed when gametes from the parents (ova and sperm) unite; a one-celled embryo.

ANIMAL TERMINOLOGY

Animal	*Male*	*Female*	*Young*	*Group of Animals*
aardvark	—	—	pup	—
alligator	bull	cow	hatchling	congregation, pod, bask
alpaca	—	—	cria	herd, flock
American pronghorn	buck	doe	fawn	herd
anteater	—	—	pup	—
antelope	buck	doe	calf	herd
ape	male	female	baby	shrewdness
armadillo	male	female	pup	—
ass	jack	jenny	foal	herd, band, pace
baboon	male	female	infant	tribe
badger	boar	sow	kit, cub	cete
bat	male	female	pup, battling	colony
bear	boar	sow	cub	sloth, sleuth
beaver	male	female	pup, kitten	lodge, colony
bee	drone	queen, worker	larva	hive, swarm, bike, drift, grist
bird	cock	hen	hatchling, nestling, chick	dissimulation, fleet, flight, flock, parcel, pod, volery, drove, brace
boar	boar	sow	piglet, shoat, farrow, boarlet	singular, sounder
buffalo	bull	cow	calf	gang, herd
butterfly	male	female	caterpillar, larva, pupa, chrysalis	swarm, rabble, army (caterpillars)
camel	bull	cow	calf	flock
cat	tomcat	queen	kitten, kit, kittling, cub	clutter, clowder, litter, kindle, pounce
cheetah	male	female	cub	—
chicken	rooster	hen	chick, pullet (female), cockrell (male)	flock, brood (hens), clutch or peep (chicks)
chinchilla	—	—	—	herd
clam	—	—	larva	bed
cockroach	—	—	nymph	—
codfish	male	female	codling, hake, sprag, sprat	school
cormorant	cock	hen	chick	gulp
cow	bull	cow, heifer	calf	herd, drove, drift, mob
coyote	dog	bitch	pup, whelp	pack, rout

Animal	*Male*	*Female*	*Young*	*Group of Animals*
crane	cock	hen	chick, craneling	sedge, siege, herd
crocodile	bull	cow	crocklet	bask, congregation
crow	cock	hen	chick	murder, muster, horde
deer	buck, stag, hart	doe, hind	fawn, knobber, brockett	herd, mob, bevy
dinosaur	bull	cow	hatchling, juvenile	herd (plant-eaters), pack (meat-eaters)
dog	dog	bitch	pup	kennel, pack (wild dogs), litter
dolphin	bull	cow	pup, calf	pod, herd, school
donkey	jack, jackass	jennet, jenny	colt, foal	drove, herd
dove	cock	hen	chick	flight, piteousness
duck	drake	duck	duckling	badelynge, brace, bunch, flock, paddling, raft, team, flush
eagle	male	female	fledgling, eaglet	aerie, convocation, jubilee
echidna	—	—	puggle	—
eel	male	female	elver	swarm
elephant	bull	cow	calf	herd, parade, memory
elk	bull	cow	calf	herd, gang
falcon	tercel, terzel	falcon	chick	—
ferret	hob	jill	kit	business
finch	cock	hen	chick	charm
fish	male	female	fry, fingerling, alevin	draft, run, school, shoal, nest
flamingo	—	—	—	stand
fly	—	—	maggot	cloud, swarm
fox	reynard, dog	vixen	kit, cub, pup	skulk, leash, earth
frog	male	female	tadpole, pollywog, froglet	army
gerbil	buck	doe	pup	horde
giraffe	bull	doe, cow	calf	herd, corps, tower, group
gnat	male	female	larva	cloud, horde
gnu	bull	cow	calf	herd
goat	buck, billy	doe, nanny	kid, billy	trip, tribe, herd, flock
goldfish	male	female	—	charm
goose	gander	goose	gosling	flock, gaggle, skein, wedge, brood
gorilla	male	female	infant	band
grasshopper	male	female	nymph	swarm
grouse	cock	hen	chick, cheeper	covey, pack
guinea pig	buck	doe	pup	group
gull	cock	hen	chick	colony
hamster	buck	doe	pup	horde

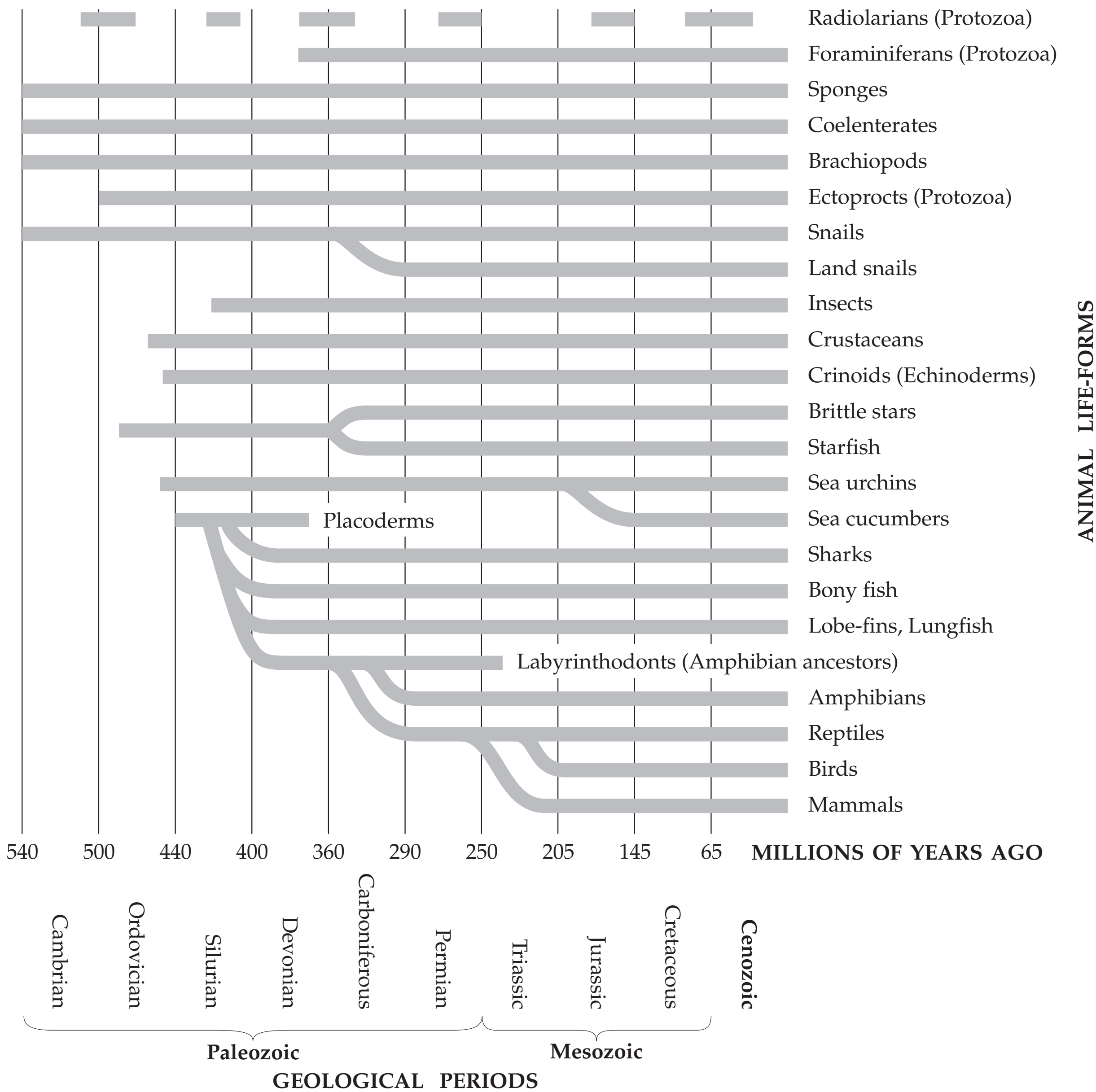
Animal	*Male*	*Female*	*Young*	*Group of Animals*
hare	buck	doe	leveret	down, husk, warren
hawk	tiercel	hen	eyas	aerie, cast, kettle, boil
hedgehog	boar	sow	piglet, pup	array
heron	cock	hen	chick	sedge, siege
herring	male	female	sprat	army
hippopotamus	bull	cow	calf	herd, bloat
hog	boar	sow	shoat, farrow	drove, herd, litter
hornet	male	female	larva	nest
horse	stallion, stud	mare, dam	foal, colt (male), filly (female)	stable, harras, herd, team, string, field
hound	dog	bitch	pup	cry, mute, pack, kennel
hummingbird	cock	hen	chick	charm
hyena	male, dog	female, bitch	cub, pup	clan, crackle
hyrax	buck	doe	bunny	bury
jay	cock	hen	chick	band, party, scold
jellyfish	—	—	ephyna	smack
kangaroo	buck, boomer, jack	doe, flyer, jill, roo	joey	troop, mob, herd
koala	male	female	joey	—
lark	cock	hen	chick	exaltation
lemur	male	female	infant	group
leopard	leopard	leopardess	cub	leap, prowl
lion	lion	lioness	cub	pride
llama	male	female	cria	herd
locust	—	—	—	host, swarm
louse	male	female	nymph	colony, infestation
magpie	cock	hen	chick	tiding, tribe, charm, gulp, flock, murder
mallard	drake	duck	duckling	flush, sord, brace
mole	male	female	pup	labor
monkey	male	female	infant	troop, cartload
moose	bull	cow	calf	herd
mosquito	male	female	nymph	swarm
mouse	buck	doe	pup, pinkie, kitten	horde, mischief
mule	jack	hinney	foal	barren, pack, span
nightingale	cock	hen	chick	watch
opossum	jack	jill	joey	passel
ostrich	cock	hen	chick	flock
otter	male, dog	female, bitch	whelp, pup, cub	family, raft, bevy, romp
owl	male	female	owlet	parliament

Animal	*Male*	*Female*	*Young*	*Group of Animals*
ox	steer, bull	cow	stot, calf	drove, herd, yoke, team
oyster	—	—	spat	bed
panda	boar	sow	cub	—
parrot	cock	hen	chick	company, flock
partridge	cock	hen	chick, cheeper	covey
peafowl	peacock	peahen	peachick	muster, ostentation, pride
penguin	male	female	chick	rookery, colony, parcel, huddle
pheasant	cock	hen	chick	brood, nye, bouquet, nide, nest
pig	boar	sow	piglet, shoat, farrow, suckling	drove, drift, herd, litter, sounder
pigeon	cock	hen	squab, squeaker	flock, kit
polar bear	boar	sow	cub	pack
porcupine	boar	sow	pup, porcupette	prickle
porpoise	bull	cow	calf	herd, pod, school
prairie dog	boar	sow	pup	coterie, town
quail	cock	hen	chick	bevy, covey, drift
rabbit	buck	doe	kitten, bunny, kit	colony, drove, leash, nest, trace, warren, down, husk, trip, bury
raccoon	boar	sow	cub	nursery
rat	buck	doe	pup, pinkie, kitten	horde, mischief
raven	cock	hen	chick	congress, unkindness
reindeer	bull	cow	calf	herd
rhinoceros	bull	cow	calf	crash
salmon	—	—	parr, smolt, grilse	school, run, shoal
sand dollar	male	female	larva, pluteus, juvenile	—
sea urchin	male	female	larva, pluteus, juvenile	—
seal, sea lion	bull	cow	pup	herd, pod, rookery, harem, colony, crash
shark	bull	female	pup, cub	school, shiver
sheep	buck, ram	ewe, dam	lamb, lambkin, lambling, cosset	drift, drove, flock, herd, mob, trip
skunk	—	—	kit	surfeit
snake	male	female	snakelet, neonate, hatchling	bed, nest, pit
snipe	cock	hen	chick	wisp, walk
sparrow	cock	hen	chick	host
spider	male	female	spiderling	—
squirrel	buck	doe	pup, kit, kitten	dray, scurry
starfish	male	female	larva, pluteus, juvenile	—
stork	cock	hen	chick	mustering
swallow	cock	hen	chick	flight
swan	cob	pen	cygnet, flapper	bevy, game, herd, team, wedge

Animal	*Male*	*Female*	*Young*	*Group of Animals*
tapir	male	female	calf	—
termite	male	female	larva	swarm, colony
tiger	tiger	tigress	cub, whelp	ambush, streak
toad	male	female	tadpole, toadlet	knot
trout	male	female	fry, fingerling	hover
turkey	tom	hen	poult	rafter, gang
turtle	male	female	hatchling	bale, nest
turtle dove	—	—	chick	pitying
viper	male	female	snakelet	nest
vulture	cock	hen	chick	colony
wallaby	jack	jill	joey	mob
walrus	bull	cow	cub, pup	pod, herd
wasp	drone	queen, worker	larva	colony
weasel	dog, buck, jack, hob	bitch, doe, jill	kit	gang
whale	bull	cow	calf	gam, grind, herd, pod, school
wolf	dog	bitch	pup, whelp	pack, rout
wombat	jack	jill	joey	mob, warren
woodpecker	male	female	chick	descent
wren	cock	jenny	chick	flock, herd
yak	bull	cow	calf	herd
yellow jacket	drone	queen, worker	larva	colony
zebra	stallion	mare	colt, foal	herd, crossing

TIME LINE

The evolutionary diagram presented below, based on fossils and taxonomic studies, indicates a branch-like bush. All currently living groups are at the tips of the branches. The arrangement of animal groups in classifications on the evolutionary tree thus indicates not only how the groups are related to one another but also when the linkages occurred.



CLASSIFICATION TABLE

The scientific groupings of the animal world on which microbiologists and zoologists more or less agree are shown in their Latin, not vernacular, designations. They indicate both evolutionary history—how the animal kingdom developed over time—as well as the relationships among groups. In the seventeenth and eighteenth centuries, when these classifications were first compiled by Carolus Linnaeus (1707-1778) and others, structure and appearance were used as the most important basis. After Charles Darwin (1809-1882) propounded his theory of natural selection, animals were understood to have evolved and changed during long periods of geological time, with one kind of animal giving rise to another. Thus, it was only after the mid-nineteenth century that the arrangement of animal groups in a classification was expected to indicate how the groups were related to one another in this historical and evolutionary sense.

The following list, taken from *The New Larousse Encyclopedia of Animal Life* (1980), begins with the oldest animal form, phylum Protozoa, and proceeds to the most recent, phylum Chordata. Whether the phylum includes a large number of members or fewer than a dozen, all share many features that both unite them and mark them as distinct from all other fauna. Subordination in the classification of phyla—the primary divisions of the animal kingdom—is indicated by differences in degrees of indentation. Thus, where applicable, each phylum in the kingdom Animalia is broken down according to subphylum, superclass, class, subclass, superorder, order, infraclass, suborder, superfamily, family, section, and group. Since the number of animal species, from microscopic one-celled protozoans to humans, is estimated to be well over one million and perhaps over two million, and new ones are still being discovered, the lowest levels of classification, namely, genus and species, as well as subgenus and subspecies, are necessarily omitted. Thus, *Canis lupus* for wolf or *Canis familiaris* for dog (all varieties), from the family Canidae, will not appear because the numbers would be unmanageable.

—Peter B. Heller

PHYLUM PROTOZOA
- Class Mastigophora
  - Subclass Phytomastigophora
    - Order Phytomonadida
    - Order Euglenoidida
    - Order Cryptomonadida
    - Order Chrysomonadida
    - Order Dinoflagellata
  - Subclass Zoomastigophora
    - Order Protomonadida
    - Order Polymastigida
    - Order Trichomonadida
    - Order Opalinida
- Class Sarcodina
  - Subclass Rhizopoda
    - Order Rhizomastigida
    - Order Amoebina
    - Order Testacida
    - Order Foraminifera
    - Order Heliozoida
    - Order Radiolarida
- Class Sporozoa
  - Subclass Gregarinomorpha
    - Order Archigregarinida
    - Order Eugregarinida
      - Suborder Cephalina
      - Suborder Acephalina
  - Subclass Coccidiomorpha
    - Order Eucocciida
      - Suborder Adeleidea
      - Suborder Eimeriidea
      - Suborder Haemosporidia
- Class Cnidosporidea
- Class Ciliata
  - Subclass Holotricha
    - Order Gymnostomatida

Suborder Rhabdophorina
Suborder Cyrtophorina
Order Suctorida
Order Trichostomatida
Order Hymenostomatida
Order Peritrichida
Order Astomatida
Subclass Spirotricha
Order Heterotrichida
Order Hypotrichida
Order Entodiniomorphida

PHYLUM MESOZOA
Order Dicyemida
Order Orthonectida

PHYLUM PORIFERA
Class Calcarea
Class Hexactinellida
Class Demospongiae
Class Sclerospongiae

PHYLUM CNIDARIA
Class Hydrozoa
Order Athecata
Family Tubulariidae
Family Clavidae
Family Corynidae
Family Bougainvilliidae
Family Hydridae
Order Thecata
Family Campanulariidae
Family Lafoeidae
Family Sertulariidae
Order Limnomedusae
Order Trachymedusae
Order Narcomedusae
Order Siphonophora
Order Hydrocorallinae
Suborder Milleporina
Suborder Stylasterina
Class Scyphozoa
Order Semaeostomeae
Order Rhizostomeae
Order Coronatae
Order Cubomedusae
Order Stauromedusae
Class Anthozoa
Subclass Octocorallia
Order Alcyonacea
Order Gorgonacea
Order Pennatulacea
Subclass Zoantharia
Order Actiniaria
Order Corallimorpharia
Order Scleractinia
Order Zoanthiniaria
Subclass Ceriantipatharia
Order Antipatharia
Order Cerianthidea

PHYLUM CTENOPHORA
Class Tentaculata
Order Cydippida
Order Lobata
Order Cestida
Order Platyctenea
Class Nuda
Order Beroida

PHYLUM PLATYHELMINTHES
Class Turbellaria
Order Polycladida
Suborder Cotylea
Suborder Acotylca
Order Tricladida
Suborder Maricola
Suborder Paludicola
Suborder Terricola
Order Protricladida
Suborder Crossocoela
Suborder Cyclocoela
Order Eulecithophora
Order Perilecithophora
Order Archoophora
Order Temnocephala
Class Monogenea
Class Digenea
Class Cestoda
Subclass Cestodaria (= Cestoda Monozoa)
Subclass Eucestoda (= Cestoda Merozoa)

PHYLUM NEMERTINA (= RHYNCHOCOELA)
- Class Anopla
  - Order Palaeonemertini
  - Order Heteronemertini
- Class Enopla
  - Order Hoplonemertini
  - Order Bdellonemertini

PHYLUM ASCHELMINTHES
- Class Nematoda
  - Subclass Aphasmida
    - Order Chromadorida
    - Order Enoplida
  - Subclass Phasmida
    - Order Rhabditida
    - Order Strongylida
    - Order Ascaridida
    - Order Tylenchida
    - Order Spirurida
- Class Rotifera
  - Order Seisonidea
  - Order Bdelloidea
  - Order Monogononta
    - Suborder Ploima
    - Suborder Flosculariacea
    - Suborder Collothecacea
- Class Gastrotricha
  - Order Chaetonotoidea
  - Order Macrodasyoidea
- Class Kinorhyncha
- Class Priapuloidea
- Class Nematomorpha
  - Order Nectonematoidea
  - Order Gordioidea

PHYLUM ACANTHOCEPHALA

PHYLUM ENTOPROCTA

PHYLUM BRYOZOA
- Class Phylactolaemata
- Class Gymnolaemata
  - Order Cyclostomata
  - Order Cheilostomata
  - Order Ctenostomata

PHYLUM PHORONIDA

PHYLUM BRACHIOPODA
- Class Inarticulata
- Class Articulata

PHYLUM MOLLUSCA
- Class Monoplacophora
- Class Amphineura
  - Subclass Polyplacophorea (= Loricata)
  - Subclass Aplacophorea
- Class Gastropoda
  - Subclass Prosobranchea
    - Order Archaeogastropoda
    - Order Neritoidea
    - Order Mesogastropoda
    - Order Neogastropoda
  - Subclass Opisthobranchia
    - Order Cephalaspidea (= Bullomorpha)
    - Order Aplysiacea (= Anaspidea)
    - Order Thecosomata
    - Order Gymnosomata
    - Order Notaspidea(= Pleurobranchomorpha)
    - Order Acochlidiacea
    - Order Sacoglossa
    - Order Acoela (= Nudibranchia)
  - Subclass Pulmonata
    - Order Basommatophora
    - Order Geophila (= Stylommatophora)
- Class Scaphopoda
- Class Bivalvia (= Lamellibrancha = Pelecypoda)
  - Subclass Protobranchia
  - Subclass Lamellibranchia
- Class Cephalopoda
  - Subclass Nautiloidea
  - Subclass Coleoidea
    - Order Sepioidea
    - Order Teuthoidea
    - Order Octopoda
    - Order Vampyromorpha

PHYLUM SIPUNCULA

PHYLUM ECHIUROIDEA

PHYLUM ANNELIDA
- Class Polychaeta
  - Family Phyllodocidae
  - Family Tomopteridae
  - Family Nephtyidae
  - Family Glyceridae
  - Family Aphroditidae
  - Family Polynoidae
  - Family Nereidae
  - Family Syllidae
  - Family Eunicidae
  - Family Amphinomidae
  - Family Ariciidae
  - Family Cirratulidae
  - Family Magelonidae
  - Family Arenicolidae
  - Family Capitellidae
  - Family Maldanidae
  - Family Spionidae
  - Family Chaetopteridae
  - Family Sabellariidae
  - Family Oweniidae
  - Family Pectinariidae (= Amphictenidae)
  - Family Ampharetidae
  - Family Terebellidae
  - Family Sabellidae
  - Family Serpulidae
- Class Oligochaeta
- Class Hirudinea

PHYLUM ARTHROPODA
- Class Onychophora
- Class Pauropoda
- Class Diplopoda
- Class Chilopoda
- Class Symphyla
- Class Insecta
  - Subclass Apterygota
    - Order Thysanura
      - Family Lepismatidae
      - Family Machilidae
    - Order Diplura
      - Family Campodeidae
      - Family Japygidae
      - Family Projapygidae
    - Order Protura
    - Order Collembola
      - Suborder Arthropleona
        - Superfamily Poduroidea
        - Superfamily Entomobryoidea
      - Suborder Symphypleona
        - Family Sminthuridae
  - Subclass Exopterygota
    - Order Ephemeroptera
      - Family Baetidae
      - Family Siphlonuridae
      - Family Caenidae
      - Family Ecdyonuridae
    - Order Odonata
      - Suborder Zygoptera
        - Family Agriidae
        - Family Coenagriidae
      - Suborder Anisozygoptera
      - Suborder Anisoptera
        - Family Aeshnidae
        - Family Libellulidae
        - Family Gomphidae
        - Family Petaluridae
    - Order Plecoptera
      - Family Eustheniidae
      - Family Pteronarcidae
      - Family Leuctridae
      - Family Capniidae
      - Family Nemouridae
      - Family Perlidae
    - Order Grylloblattodea
    - Order Orthoptera
      - Family Tettigoniidae
      - Family Stenopelmatidae
      - Family Gryllidae
      - Family Gryllotalpidae
      - Family Acrididae
      - Family Pneumoridae
      - Family Tetrigidae
      - Family Tridactylidae
      - Family Cylindrachetidae
    - Order Phasmida
      - Family Phylliidae
    - Order Dermaptera
      - Suborder Forficulina
        - Family Forficulidae
        - Family Labiidae

Family Labiduridae
Suborder Hemimerina
Suborder Arixeniina
Order Embioptera
Family Clothodidae
Family Embiidae
Order Dictyoptera
Suborder Blattodea
Suborder Mantodea
Order Isoptera
Family Mastotermitidae
Family Kalotermitidae
Family Hodotermitidae
Family Rhinotermitidae
Family Termitidae
Order Zoraptera
Order Psocoptera
Suborder Eupsocida
Family Psocidae
Family Mesopsocidae
Family Pseudocaeciliidae
Suborder Trogiomorpha
Suborder Troctomorpha
Order Mallophaga
Suborder Amblycera
Family Menoponidae
Suborder Ischnocera
Family Philopteridae
Family Trichodectidae
Suborder Rhynchophthirina
Order Siphunculata
Family Echinophthiriidae
Family Hoplopleuridae
Family Linognathidae
Order Hemiptera
Suborder Heteroptera
Section Geocorisae
Family Pentatomidae
Family Coreidae
Family Pyrrhocoridae
Family Lygaeidae
Family Tingidae
Family Reduviidae
Family Nabidae
Family Anthocoridae
Family Cimicidae
Family Miridae
Family Saldidae
Section Amphibicorisae
Family Gerridae
Family Veliidae
Family Hydrometridae
Section Hydrocorisae
Family Naucoridae
Family Belostomatidae
Family Nepidae
Family Notonectidae
Family Corixidae
Suborder Homoptera
Section Auchenorrhyncha
Family Cicadidae
Family Cicadellidae
Family Membracidae
Family Cercopidae
Group Fulgoroidea
Family Delphacidae
Section Sternorrhyncha
Group Aphidoidea
Family Psyllidae
Family Coccoidae
Family Pseudococcidae
Family Aleyrodidae
Order Thysanoptera
Suborder Terebrantia
Suborder Tubulifera
Subclass Endopterygota
Order Neuroptera
Suborder Megaloptera
Family Sialidae
Family Corydalidae
Family Raphidiidae
Suborder Plannipennia
Family Sisyridae
Family Hemerobiidae
Family Chrysopidae
Family Mantispidae
Family Myrmeleontidae
Family Ascalaphidae
Order Mecoptera
Family Panorpidae
Family Bittacidae
Order Lepidoptera

Suborder Zeugloptera
Family Micropterygidae
Suborder Monotrysia
Family Eriocraniidae
Family Hepialidae
Family Incurvariidae
Suborder Ditrysia
Family Sesiidae
Family Tinaeidae
Family Gracillariidae
Family Plutellidae
Family Orneodidae
Family Cossidae
Family Psychidae
Family Zygaenidae
Family Tortricidae
Family Eucosmidae
Family Olethreutidae
Superfamily Pyralidoidea
Family Galleriinae
Family Crambinae
Family Phycitinae
Family Pyralidae
Family Pyraustinae
Family Lasiocampidae
Family Saturniidae
Family Bombycidae
Family Nymphalidae
Family Lycaenidae
Family Pieridae
Family Papilionidae
Family Hesperiidae
Family Geometridae
Family Sphingidae
Family Noctuidae
Family Notodontidae
Family Lymantriidae
Family Arctiidae
Order Trichoptera
Family Rhyacophilidae
Family Hydroptilidae
Family Hydropsychidae
Family Phryganeidae
Family Limnephilidae
Family Leptoceridae
Order Diptera
Suborder Nematocera
Family Tipulidae
Family Psychodidae
Family Culicidae
Family Cecidomyiidae
Family Bibionidae
Family Mycetophilidae
Family Simuliidae
Family Chironomidae
Suborder Brachycera
Family Stratiomyidae
Family Rhagionidae
Family Tabanidae
Family Asilidae
Family Bombyliidae
Family Empididae
Family Dolichopodidae
Suborder Cyclorrhapha
Family Syrphidae
Family Phoridae
Section Acalyptratae
Family Agromyzidae
Family Psilidae
Family Tephritidae
Family Chloropidáe
Section Calyptratae
Family Oestridae
Family Calliphoridae
Family Tachinidae
Family Muscidae
Family Hippoboscidae
Order Siphonaptera
Order Hymenoptera
Suborder Symphyta
Family Xyelidae
Family Siricidae
Family Diprionidae
Family Pergidae
Family Orussidae
Family Tenthredinidae
Suborder Apocrita
Section Parasitica
Family Ichneumonidae
Family Braconidae
Family Cynipidae
Superfamily Chalcidoidea

Family Trichogrammatidae
Family Mymaridae
Family Agaontidae
Superfamily Proctotrupoidea
Family Scelionidae
Family Platygasteridae
Section Aculeata
Family Dryinidae
Family Chrysididae
Family Scoliidae
Family Tiphiidae
Family Formicidae
Family Pompilidae
Family Vespidae
Family Sphecidae
Family Prosopidae
Family Andrenidae
Family Megachilidae
Family Apidae
Order Coleoptera
Suborder Adephaga
Family Carabidae
Family Cicindelidae
Family Paussinae
Family Haliplidae
Family Dytiscidae
Family Gyrinidae
Suborder Archostemata
Suborder Myxopbaga
Family Cupedidae
Suborder Polyphaga
Family Hydrophilidae
Family Histeridae
Family Silphidae
Family Staphylinidae
Family Passalidae
Family Lucanidae
Family Geotrupidae
Family Scarabaeidae
Family Elateridae
Family Buprestidae
Family Cantharidae
Family Lampyridae
Family Dermestidae
Family Anobiidae
Family Cleridae
Family Nitidulidae
Family Coccinellidae
Family Tenebrionidae
Family Meloidae
Family Cerambycidae
Family Chrysomelidae
Family Curculionidae
Family Scolytidae
Order Strepsiptera
Class Crustacea
Subclass Cephalocarida
Family Hutchinsoniellidae
Subclass Branchiopoda
Order Anostraca
Order Notostraca
Order Conchostraca
Order Cladocera
Family Daphniidae
Subclass Mystacocarida
Subclass Copepoda
Order Calanoida
Family Diaptomidae
Family Centropagidae
Order Cyclopoida
Family Cyclopidae
Family Notodelphyidae
Order Harpacticoida
Order Caligoida
Order Monstrilloida
Order Lernaeoida
Subclass Branchiura
Subclass Ostracoda
Order Myodocopa
Order Cladocopa
Order Platycopa
Order Podocopa
Subclass Cirripedia
Order Thoracica
Order Rhizocephala
Order Ascothoracica
Subclass Malacostraca
Superorder Phyllocarida
Order Leptostraca
Superorder Hoplocarida
Order Stomatopoda
Superorder Syncarida

Order Anaspidacea
Order Stygocaridacea
Order Bathynellacea
Superorder Peracarida
Order Spelaeogriphacea
Order Thermosbaenacea
Order Mysidacea
Suborder Lophogastrida
Suborder Mysida
Order Tanaidacea
Order Isopoda
Suborder Asellota
Family Asellidae
Suborder Flabellifera
Family Limnoriidae
Family Sphaeromidae
Family Anthuridae
Suborder Gnathiidea
Suborder Valvifera
Suborder Phreatoicidea
Suborder Oniscoidea
Family Ligiidae
Family Armadillidiidae
Suborder Epicaridea
Family Entoniscidae
Family Bopyridae
Order Amphipoda
Suborder Hyperiidea
Suborder Gammaridea
Family Gammaridae
Family Talitridae
Suborder Caprellidea
Family Caprellidae
Family Cyamidae
Suborder Ingolfiellida
Order Cumacea
Family Pseudocumidae
Order Euphausiacea
Order Decapoda
Suborder Natantia
Section Penaeidea
Family Penaeidae
Family Sergestidae
Family Leuciferidae
Section Caridea
Family Atyidae
Family Alpheidae
Section Stenopodidea
Family Stenopodidae
Suborder Reptantia
Section Palinura
Section Astacura
Family Homaridae
Family Astacidae
Family Parastacidae
Family Austroastacidae
Section Anomura
Family Paguridae
Family Coenobitidae
Family Lithodidae
Family Galatheidae
Family Porcellanidae
Section Brachyura
Family Dromiidae
Family Calappidae
Family Portunidae
Family Potamonidae
Family Xanthidae
Family Pinnotheridae
Family Grapsidae
Family Oxypodidae
Family Majidae
Class Arachnida
Order Scorpiones
Order Pseudoscorpiones
Order Opiliones
Order Acari
Family Eriophyidae
Order Palpigradi
Order Uropygi
Order Schizomida
Order Amblypygi
Order Araneae
Suborder Orthognatha (= Mygalomorpha)
Suborder Labidognatha (= Araneomorpha)
Family Araneidae (= Argiopidae)
Family Theridiidae
Family Agelenidae
Family Thomisidae
Family Lycosidae
Family Salticidae
Order Solifugae (= Solpugida)

Order Ricinulei
Class Merostomata
Class Pycnogonida

PHYLUM PENTASTOMIDA

PHYLUM TARDIGRADA

PHYLUM CHAETOGNATHA

PHYLUM POGONOPHORA

PHYLUM ECHINODERMATA
Class Asteroidea
Class Ophiuroidea
Class Echinoidea
Class Holothuroidea
Class Crinoidea

PHYLUM CHORDATA
Subphylum Hemichordata
Class Enteropneusta
Class Pterobranchia
Subphylum Urochordata
Class Ascidiacea
Class Thaliacea
Class Larvacea
Subphylum Cephalochordata
Subphylum Vertebrata
Superclass Agnatha
Class Cephalaspidomorphi
Order Petromyzoniformes
Class Pteraspidomorphia
Order Myxiniformes
Superclass Gnathostomata
Class Chondrichthyes
Superorder Selachimorpha
Order Heterodontiformes
Order Hexanchiformes
Order Lamniformes
Family Rhincodontidae
Family Orectolobidae
Family Odontaspidae
Family Lamnidae
Family Scyliorhinidae
Family Carcharinidae
Family Sphyrnidae
Order Squaliformes
Family Squalidae
Family Pristiophoridae
Family Squatinidae
Superorder Batoidimorpha
Family Pristidae
Family Rhinobatidae
Family Torpedinidae
Family Rajidae
Family Dasyatidae
Family Potamotrygonidae
Family Myliobatidae
Family Mobulidae
Subclass Holocephali
Order Chimaeriformes
Family Chimaeridae
Family Rhinochimaeridae
Family Callorhynchidae
Class Osteichthyes
Subclass Dipneusti
Order Ceratodiformes
Order Lepidosireniformes
Family Lepidosirenidae
Family Protopteridae
Subclass Crossopterygii
Order Coelacanthiformes
Family Latimeriidae
Subclass Brachioptergyii
Family Polypteridae
Subclass Actinopterygii
Order Acipenseriformes
Family Acipenseridae
Family Polyodontidae
Order Semionotiformes
Family Lepisosteidae
Order Amiiformes
Family Amiidae
Order Osteoglossiformes
Order Mormyriformes
Order Clupeiformes
Family Clupeidae
Family Engraulidae
Order Elopiformes
Order Anguilliformes
Order Notacanthiformes

Order Salmoniformes
- Suborder Esocoidei
- Suborder Salmonoidei
- Suborder Argentinoidei
- Suborder Stomiatoidei

Order Gonorynchiformes

Order Cypriniformes
- Suborder Characoidei
- Suborder Cyprinoidei

Order Siluriformes

Order Myctophiformes

Order Polymixiiformes

Order Percopsiformes

Order Gadiformes

Order Batrachoidiformes

Order Lophiiformes

Order Indostomiformes

Order Atheriniformes
- Suborder Exocoetidei
- Suborder Cyprinodontoidei
- Suborder Atherinoidei

Order Lampridiformes

Order Beryciformes

Order Zeiformes

Order Syngnathiformes

Order Gasterosteiformes

Order Synbranchiformes

Order Scorpaeniformes
- Suborder Scorpaenoidei

Order Dactylopteriformes

Order Perciformes
- Suborder Percoidei
- Suborder Mugiloidei
- Suborder Sphyraenoidei
- Suborder Polynemoidei
- Suborder Labroidei
- Suborder Blennioidei
- Suborder Icosteoidei
- Suborder Ammodytoidei
- Suborder Gobioidei
- Suborder Acanthuroidei
- Suborder Scombroidei
- Suborder Stromateoidei
- Suborder Anabantoidei
- Suborder Channoidei
- Suborder Mastacembeloidei

Order Gobiesociformes

Order Pleuronectiformes
- Family Psettodidae
- Family Citharidae
- Family Bothidae
- Family Pleuronectidae
- Family Soleidae
- Family Cynoglossidae

Order Tetraodontiformes
- Family Balistidae
- Family Ostraciontidae
- Family Tetraodontidae
- Family Diodontidae
- Family Molidae

Class Amphibia
- Order Apoda [sometimes Gymnophiona]
    - Family Caeciliidae
- Order Caudata (= Urodela)
    - Suborder Cryptobranchoidea
        - Family Hynobiidae
        - Family Cryptobranchidae
    - Suborder Ambystomatoidea
        - Family Ambystomatidae
    - Suborder Salamandroidea
        - Family Salamandridae
        - Family Amphiumidae
        - Family Plethodontidae
        - Family Proteidae
    - Suborder Sirenoidea
        - Family Sirenidae
- Order Anura (= Salientia)
    - Suborder Amphicoela
        - Family Ascaphidae
    - Suborder Opisthocoela
        - Family Pipidae
        - Family Discoglossidae
        - Family Rhinophrynidae
    - Suborder Anomocoela
        - Family Pelobatidae
        - Family Pelodytidae
    - Suborder Diplasiocoela
        - Family Ranidae
        - Family Rhacophoridae
        - Family Microhylidae
        - Family Phrynomeridae
    - Suborder Procoela

- Family Pseudidae
- Family Bufonidae
- Family Atelopidae
- Family Hylidae
- Family Leptodactylidae
- Family Centrolenidae

Class Reptilia
- Order Rhynchocephalia
- Order Testudines (= Chelonia)
  - Family Testudinidae
  - Family Emydidae
  - Family Kinosternidae
  - Family Platysternidae
  - Family Chelydridae
  - Family Chelidae
  - Family Trionychidae
  - Family Chelonidae
  - Family Dermochelidae
  - Family Pelomedusidae
  - Family Carrettochelyidae
- Order Crocodylia (= Loricata)
  - Family Gavialidae
  - Family Crocodylidae
  - Family Alligatoridae
- Order Squamata
  - Suborder Sauria (= Lacertilia)
    - Family Gekkonidae
    - Family Agamidae
    - Family Iguanidae
    - Family Lacertidae
    - Family Teiidae
    - Family Helodermatidae
    - Family Varanidae
    - Family Chamaeleonidae
    - Family Scincidae
    - Family Cordylidae
    - Family Anguidae
    - Family Amphisbaenidae
  - Suborder Serpentes (= Ophidia)
    - Family Boidae
    - Family Typhlopidae
    - Family Colubridae
    - Family Elapidae
    - Family Viperidae
    - Family Crotalidae
    - Family Hydrophidae

Class Aves
- Order Struthioniformes
- Order Rheiformes
- Order Casuariiformes
  - Family Dromaiidae
  - Family Casuariidae
- Order Apterygiformes
- Order Tinamiformes
- Order Sphenisciformes
- Order Gaviiformes
- Order Podicipediformes
- Order Procellariiformes
  - Family Diomedeidae
  - Family Procellariidae
  - Family Hydrobatidae
  - Family Pelecanoididae
- Order Pelecaniformes
  - Family Phaethontidae
  - Family Pelecanidae
  - Family Sulidae
  - Family Phalacrocoracidae
  - Family Anhingidae
  - Family Fregatidae
- Order Ciconiiformes
  - Family Ardeidae
  - Family Cochleariidae
  - Family Balaenicipitidae
  - Family Scopidae
  - Family Ciconiidae
  - Family Threskiornithidae
  - Family Phoenicopteridae
- Order Anseriformes
  - Family Anhimidae
  - Family Anatidae
- Order Falconiformes
  - Family Cathartidae
  - Family Accipitridae
  - Family Pandionidae
  - Family Falconidae
  - Family Sagittariidae
- Order Galliformes
  - Family Megapodiidae
  - Family Cracidae
  - Family Tetraonidae
  - Family Phasianidae
  - Family Numididae

Family Meleagrididae
Family Opisthocomidae
Order Gruiformes
Family Mesitornithidae
Family Turnicidae
Family Pedionomidae
Family Gruidae
Family Aramidae
Family Psophiidae
Family Rallidae
Family Heliornithidae
Family Rhynochetidae
Family Eurypygidae
Family Cariamidae
Family Otididae
Order Charadriiformes
Family Jacanidae
Family Rostratulidae
Family Haematopodidae
Family Charadriidae
Family Scolopacidae
Family Recurvirostridae
Family Phalaropodidae
Family Dromadidae
Family Burhinidae
Family Glareolidae
Family Thinocondae
Family Chionididae
Family Stercorariidae
Family Laridae
Family Rynchopidae
Family Alcidae
Order Columbiformes
Family Pteroclidae
Family Columbidae
Order Psittaciformes
Family Psittacidae
Order Cuculiformes
Family Musophagidae
Family Cucilidae
Order Strigiformes
Family Tytonidae
Family Strigidae
Order Caprimulgiformes
Family Steatornithidae
Family Podargidae
Family Nyctibiidae
Family Aegothelidae
Family Caprimulgidae
Order Apodiformes
Family Apodidae
Family Hemiprocnidae
Family Trochilidae
Order Coliiformes
Order Trogoniformes
Order Coraciiformes
Family Alcedinidae
Family Todidae
Family Momotidae
Family Meropidae
Family Leptosomatidae
Family Coraciidae
Family Upupidae
Family Phoeniculidae
Family Bucerotidae
Order Piciformes
Family Galbulidae
Family Bucconidae
Family Capitonidae
Family Indicatoridae
Family Ramphastidae
Family Picidae
Order Passeriformes
Suborder Eurylaimi
Family Eurylaimidae
Suborder Tyranni
Family Dendrocolaptidae
Family Furnariidae
Family Formicariidae
Family Conopophagidae
Family Rhinocryptidae
Family Pittidae
Family Philepittidae
Family Acanthisittidae (= Xenicidae)
Family Tyrannidae
Family Oxyruncidae
Family Pipridae
Family Cotingidae
Family Phytotomidae
Suborder Menurae
Family Menuridae
Family Atrichornithidae

Suborder Passeres (= Oscines)
Family Alaudidae
Family Hirundinidae
Family Motacillidae
Family Campephagidae
Family Pycnonotidae
Family Irenidae
Family Laniidae
Family Vangidae
Family Bombycillidae
Family Dulidae
Family Cinclidae
Family Troglodytidae
Family Mimidae
Family Prunellidae
Family Muscicapidae
Family Paridae
Family Certhiidae
Family Sittidae
Family Climacteridae
Family Dicaeidae
Family Nectariniidae
Family Zosteropidae
Family Meliphagidae
Family Emberizidae
Family Parulidae
Family Drepanididae
Family Vireonidae
Family Icteridae
Family Fringillidae
Family Estrildidae
Family Ploceidae
Family Sturnidae
Family Oriolidae
Family Dicruridae
Family Callaeidae
Family Grallinidae
Family Artamidae
Family Cracticidae
Family Ptilonorhynchidae
Family Paradisaeidae
Family Corvidae
Class Mammalia
Subclass Prototheria
Order Monotremata
Infraclass Metatheria
Order Marsupialia
Family Didelphidae
Family Dasyuridae
Family Notoryctidae
Family Peramelidae
Family Phalangeridae
Family Phascolarctidae
Family Phascolomidae
Family Macropodidae
Infraclass Theria
Order Insectivora
Family Erinaceidae
Family Soricidae
Family Tenrecidae
Family Solenodontidae
Family Talpidae
Family Chrysochloridae
Family Potamogalidae
Family Macroscelididae
Family Tupaiidae
Order Dermoptera
Order Chiroptera
Suborder Megachiroptera
Suborder Microchiroptera
Family Megadermatidae
Family Rhinolophidae
Family Vespertilionidae
Family Phyllostomatidae
Family Noctilionidae
Family Molossidae
Family Desmodontidae
Order Primates
Suborder Prosimii
Family Lemuridae
Family Cheirogaleidae
Family Lorisidae
Family Indriidae
Family Daubentoniidae
Family Tarsiidae
Suborder Anthropoidea (= Simiae)
Family Cebidae
Family Callithricidae
Family Cercopithecidae
Family Pongidae
Order Edentata
Family Myrmecophagidae

Family Bradypodidae
Family Dasypodidae
Order Pholidota
Order Lagomorpha
Family Leporidae
Family Ochotonidae
Order Rodentia
Suborder Bathyergomorpha
Suborder Hystricomorpha
Family Echimyidae
Family Dasyproctidae
Family Erethizontidae
Family Hystricidae
Family Cuniculidae
Family Dinomyidae
Family Chinchillidae
Family Caviidae
Suborder Sciuromorpha
Family Sciuridae
Family Aplodontidae
Family Castoridae
Family Geomyidae
Family Heteromyidae
Suborder Myomorpha
Family Anomaluridae
Family Pedetidae
Family Ctenodactylidae
Family Dipodidae
Family Zapodidae
Family Muscardinidae
Family Lophiomyidae
Family Spalacidae
Family Rhizomyidae
Family Muridae
Order Cetacea
Suborder Mysticeti
Family Balaenidae
Family Balaenopteridae
Family Eschrichtiidae
Suborder Odontoceti
Family Physeteridae
Family Kogiidae
Family Phocaenidae
Family Delphinidae
Family Zephiidae
Family Monodontidae
Family Platanistidae
Order Carnivora
Family Canidae
Family Ursidae
Family Procyonidae
Family Mustelidae
Family Viverridae
Family Hyaenidae
Family Protelidae
Family Felidae
Order Pinnipedia
Family Phocidae
Family Otariidae
Family Odobenidae
Order Tubulidentata
Order Proboscidea
Order Hyracoidea
Order Sirenia
Order Perissodactyla
Family Equidae
Family Tapiridae
Family Rhinocerotidae
Order Artiodactyla
Suborder Suiformes
Family Suidae
Family Tayassuidae
Family Hippopotamidae
Suborder Tylopoda
Family Camelidae
Suborder Ruminantia
Family Tragulidae
Family Cervidae
Family Giraffidae
Family Antilocapridae
Family Bovidae

GEOGRAPHICAL LIST OF ANIMALS

All Continents (except Antarctica)
Ants
Arachnids
Bats
Bees
Beetles
Butterflies
Cats
Cattle
Centipedes and millipedes
Chickens
Cockroaches
Dogs
Ducks
Eagles
Finches
Flatworms
Flies
Foxes
Frogs
Grasshoppers
Hawks
Horses
Lizards
Mice
Mollusks
Mosquitoes
Moths
Owls
Pelicans
Pigs and hogs
Quail
Rats
Roundworms
Scorpions
Sheep
Snails
Snakes
Sparrows
Spiders
Storks
Swans
Termites
Toads
Turtles and tortoises
Worms

All Oceans
Clams
Coral
Crabs
Eels
Elephant seals
Horseshoe crabs
Jellyfish
Lobsters
Mollusks
Octopuses
Otters
Oysters
Rays and skates
Sand dollars
Sea cucumbers
Sea urchins
Seahorses
Seals
Sharks
Squid
Starfish
Whale sharks
Whales, baleen
Whales, toothed
White sharks
Zooplankton

Africa
Aardvarks
Antelope
Baboons
Buffalo
Camels
Chameleons
Cheetahs
Chimpanzees
Civets and genets
Cranes
Crocodiles
Deer
Donkeys
Elephants
Flamingos
Giraffes
Goats
Gorillas
Hippopotamuses
Hyenas
Hyraxes
Leopards
Lions
Lungfish
Manatees
Meerkats
Mongooses
Monkeys
Mules
Ostriches
Parrots
Penguins
Pheasant
Porcupines
Rabbits and hares
Rhinoceroses
Shrews
Squirrels
Vultures
Weasels
Woodpeckers
Zebras

Antarctica
Penguins
Seals

Arctic
Bears
Caribou
Dolphins
Ermines
Geese
Lemmings
Mink
Moose
Polar bears
Reindeer
Sables
Shrews
Squirrels
Voles
Walruses
Wolverines
Wolves

Asia
Antelope
Bears
Buffalo
Camels
Chameleons
Cobras
Cranes
Crocodiles
Deer
Donkeys
Elephants
Elk
Ermines
Flamingos
Gibbons
Goats
Hyenas
Jerboas
Komodo dragons
Lemmings
Leopards
Lions
Marmots
Mink
Moles
Monkeys
Moose
Mules
Orangutans
Pandas
Parrots
Pheasant
Pikas
Porcupines
Pythons
Rabbits and hares
Reindeer
Rhinoceroses
Sables
Salmon
Shrews
Snow leopards
Squirrels
Tapirs
Tigers
Trout
Vultures
Wasps and hornets
Wolverines
Wolves
Woodpeckers
Yaks

Atlantic Ocean
Manatees
Porpoises
Salmon
Sponges
Trout

Australia
Camels
Cassowaries
Cranes
Crocodiles
Dingoes
Emus
Goannas
Goats
Kangaroos
Koalas
Kookaburras
Lungfish
Moles
Monitor lizards
Parrots
Penguins
Platypuses
Tasmanian devils
Wallabies
Wombats

Caribbean
Coral
Crocodiles
Flamingos
Iguanas
Manatees
Sponges

Central America
Anteaters
Armadillos
Boa constrictors
Caimans
Coatimundis
Coyotes
Cranes
Crocodiles
Deer
Donkeys
Gophers
Hummingbirds
Jaguars
Lungfish
Macaws
Manatees
Monkeys
Mules
Ocelots
Opossums
Otters
Parrots
Porcupines

Quetzals
Rabbits and hares
Raccoons
Salamanders and newts
Shrews
Skunks
Sloths
Squirrels
Tapirs
Toucans
Vultures
Wasps and hornets
Wolves
Woodpeckers

Europe
Badgers
Bears
Chameleons
Cranes
Deer
Donkeys
Elk
Ermines
Flamingos
Geese
Goats
Jerboas
Lynx
Marmots
Martens
Mink
Moles
Moose
Mules
Otters
Pheasant
Pikas
Rabbits and hares
Reindeer
Sables
Salmon
Shrews
Squirrels
Trout
Vultures
Wasps and hornets
Weasels
Wolverines
Wolves
Woodpeckers

Galápagos Islands
Finches
Iguanas
Penguins
Turtles and tortoises

Madagascar
Boa constrictors
Chameleons
Civets and genets
Lemurs
Mongooses
Parrots
Wasps and hornets

Middle East
Antelope
Baboons
Bears
Camels
Cheetahs
Cobras
Donkeys
Geese
Goats
Hyenas
Hyraxes
Jerboas
Leopards
Martens
Mules
Vultures
Wolves

North America
American pronghorns
Antelope
Armadillos
Badgers
Bears
Beavers
Bison
Caribou
Chipmunks
Condors
Coyotes
Cranes
Crocodiles
Deer
Donkeys
Elk
Fishers
Geese
Goats
Gophers
Grizzly bears
Groundhogs (woodchucks)
Hummingbirds
Iguanas
Kangaroo rats
Lynx (bobcats)
Manatees
Marmots
Martens
Mink
Moles
Moose
Mountain lions (cougars)
Mules
Muskrats
Opossums
Otters
Parrots
Pikas
Porcupines
Prairie dogs
Rabbits and hares
Raccoons
Rattlesnakes
Salamanders and newts
Salmon
Shrews
Skunks
Squirrels
Trout
Turkeys

Vultures
Wasps and hornets
Weasels
Wolverines
Wolves
Woodpeckers

Pacific Islands
Cassowaries
Coral
Crocodiles
Echidnas
Elephant seals
Goats
Iguanas
Kiwis
Mongooses
Monitor lizards
Parrots
Penguins
Pythons
Wallabies

Pacific Ocean
Porpoises
Salmon
Trout

South America
Alpacas
Anacondas
Anteaters
Armadillos
Bears
Boa constrictors
Caimans
Capybaras
Chinchillas
Coatimundis
Condors
Crocodiles
Deer
Dolphins
Donkeys
Flamingos
Hummingbirds
Iguanas
Jaguars
Llamas
Lungfish
Macaws
Manatees
Monkeys
Mules
Ocelots
Opossums
Parrots
Peccaries
Penguins
Porcupines
Pumas (cougars)
Quetzals
Rabbits and hares
Raccoons
Rheas
Shrews
Sloths
Squirrels
Tapirs
Toucans
Vicuñas
Vultures
Wasps and hornets
Wolves
Woodpeckers

BIOGRAPHICAL LIST OF SCIENTISTS

Alexander Agassiz (1835-1910). Born in Neuchâtel, Switzerland, Agassiz came to the United States in 1849 to join his father, Louis Agassiz, and was graduated from Harvard nine years later. He became a specialist in marine ichthyology. In 1865, he published *Seaside Studies in Natural History*, which he coauthored with his stepmother, Elizabeth Cabot Agassiz. He was curator of the Museum of Comparative Zoology at Harvard from 1874 to 1885, and most of his writing about marine zoology appeared in the publications of that museum.

Jean Louis Rodolphe Agassiz (1807-1873). As a student at the universities of Zürich, Heidelberg, and Munich, Agassiz, who was born on the Murtensee in Switzerland, studied natural history, giving special attention to botany. He received the Ph.D. from the University of Erlangen in 1829 and the following year received an M.D. from the University of Munich. Agassiz became an ichthyologist almost accidentally. When J. B. Spix, renowned for the collection of Amazon fish that he brought home from Brazil, died in 1826, Agassiz was chosen to complete the classification of these specimens. Besides becoming a well-respected ichthyologist, Agassiz did considerable work in tracking the course of recent glaciers. Agassiz did not accept Charles Darwin's theory of evolution, clinging to his own more conventional notion of independent creations.

John James Audubon (1785-1851). Born on the island of Saint-Domingue (now Haiti), Audubon was educated in Paris, studying art under the tutelage of Jacques-Louis David. Returning to the United States to avoid conscription, he came to live on a farm near Philadelphia. There he became intrigued by natural history and began a comprehensive study of birds, which he began to draw in remarkably accurate detail. His *Birds of America* (4 vols., 1827-1838), sold by subscription, consisted of 435 plates in color that contained 1,055 life-sized figures of birds. Between 1831 and 1839, he published, with William MacGillivray, five descriptive volumes to accompany *Birds of America* under the composite title *Ornithological Biography*. He remains the best-known American avian artist.

Henry Walter Bates (1825-1892). Usually thought of in connection with Batesian mimicry in the animal kingdom, Bates was born and spent much of his life in Britain, although he made fruitful expeditions to Brazil and other venues to observe animal behavior and to gather specimens. It was Bates who first observed in the Amazon basin that the black-banded orange-brown monarch butterfly (*Danaus plexippus*) of North America had a mimic, the viceroy (*Limentitis archippus*). The monarch develops a natural protection against predators by ingesting cardenolide toxins from the milkweed it consumes as a caterpillar, but the viceroy lacks this protection.

Comte de Buffon (Georges-Louis Leclerc; 1707-1788). A leading French naturalist of the eighteenth century, Buffon's greatest contribution to the life sciences was in establishing the field of biogeography. Practitioners in this field study not only the current geographical distribution of plants and animals but, viewing them over long periods of time, consider changes that have occurred in their geographical distribution.

This field has provoked substantial thought among scientists. Biogeography is generally credited with having been the most prominent factor in Charles Darwin's formulation of his theory of natural selection.

Rachel Carson (1907-1964). Best known for her books about the sea and pesticides, Carson, an American biologist and environmentalist who was born in Pennsylvania, gained renown with the publication of *The Sea Around Us* (1951) and *The Silent Spring* (1962), both of which warn about the effects of pesticides on the environment. Trained at The Johns Hopkins University and Woods Hole Marine Biological Laboratory, Carson became an aquatic biologist for the United States Bureau of Fisheries in 1936. In this position she learned a great deal about the environmental fragility of the sea.

Dennis Hubert Chitty (1912-). A professor emeritus at the University of British Columbia, Chitty is perhaps the world's leading authority on the fluctuating lemming populations of the world. His book, *Do Lemmings Commit Suicide? Beautiful Hypotheses and Ugly Facts* (1996), raises interesting questions about the widely held belief that lemmings are at heart suicidal.

Eugenie Clark (1922-). A native New Yorker, Clark received the Ph.D. from New York University in 1950, having done graduate study at both the Scripps Institution of Oceanography and Woods Hole Marine Biological Station prior to completing her doctorate. She served as an oceanographic chemist on an expedition to the Philippines in 1946. She recounted some of her oceanographic research in *Lady with a Spear* (1953), which was a Book-of-the-Month Club selection. Continuing to pursue her work with sharks, she contributed to P. W. Gilbert's *Sharks and Survival* (1963) and published *The Lady and the Sharks* (1969). She has made nearly twenty trips to the Red Sea to pursue her research.

Georges Cuvier (1769-1832). French comparative anatomist Cuvier is the founder of modern comparative anatomy. Regarded as the most renowned person in his field of study, he gained his reputation by departing from the natural philosophers, who tried to shape their facts to fit their preconceived notions. Cuvier permitted his generalizations to proceed from an objective consideration of the facts with which he was dealing. His *Leçons d'anatomie comparée* (5 vols., 1800-1805; lessons on comparative anatomy) brought all known anatomical data into a well-ordered system of knowledge. His later work, *Le Règne animal distribué d'après son organisation* (1817; *The Animal Kingdom, Arranged in Conformity with Its Organization*, 1827-1832), protested the idea of the scale of all living things, establishing in its place a series of types based on objective studies of the anatomy of various forms of life.

Charles Darwin (1809-1882). Possibly the most influential scientist of the nineteenth century, British-born Darwin made false starts in medicine and theology before scientists he met at Cambridge University sparked his interest in natural sciences. In 1831, an A.B. from Cambridge in hand, he sailed aboard the HMS *Beagle* on a scientific voyage around the world. On this trip, Darwin moved slowly away from the prevalent view that all living things are immutable, products of divine creation. He began to believe that species evolve by descent from other species. He expressed some such views early in *Notebooks on the Transmutation of Species* (1837), but articulated them most fully in his *On the Origin of Species* (1859).

Theodosius Dobzhansky (1900-1975). A native of Ukraine, Dobzhansky came to the United States in 1927 to work with Thomas Hunt

Morgan, an American geneticist who studied the genetics of fruit flies (*Drosophila*). In his research with fruit flies, Dobzhansky discovered that there is considerable genetic diversity among individual specimens. He demonstrated that most organisms possess one or more abnormal genes, so-called wild genes. These genes are of less immediate use than normal genes, but they are important because, as Dobzhansky's research reveals, species with large genetic loads are more adaptable than those with low genetic loads. His *Genetics and the Origin of Species* (1937) presents in detail his conclusions about genetic overload.

Gerald Malcolm Durrell (1925-1995). Born in India to British parents, Durrell, a novelist and writer of children's books, devoted much of his life to the study of nature. His book, *The Amateur Naturalist* (1982), which was made into a television series for the British Broadcasting Corporation, shows Durrell seeking out animal life in many parts of the world, while *My Family and Other Animals* (1956) is a classic memoir of family life and zoological exploration. In 1959, he founded a zoological park and shelter on the island of Jersey to care for endangered species. He is remembered for the genuine concern and respect with which he always treated animals.

Edward Forbes (1815-1854). Renowned for his research in ocean life, British zoologist Forbes advanced the field of paleontology through analyzing specimens he collected when he served as the naturalist on a voyage of HMS *Beacon* to Asia Minor. He systematically catalogued much of the sea life he encountered on this trip. His most notable books are his *History of British Starfishes* (1841) and his four-volume collaboration with Sylvanus Hanley, *History of British Mollusca* (1853).

Dian Fossey (1932-1985). Born in San Francisco, Fossey went to Rwanda in 1967 to found the Karisoke Research Centre, where she served as project coordinator from 1980 to 1983. On her first visit to Tanzania in 1963, she had impressed Louis Leakey, who offered her a position as one of his "ape girls," women who carefully observed the behavior of various primates. Fossey was assigned to observe mountain gorillas and spent much of the rest of her life doing so. She wrote about it in such books as *Gorillas in the Mist* (1983), which was made into a film by Warner Brothers and Universal Pictures in 1988. Fossey, who received a Ph.D. from Cambridge University in 1974, was active in organizing antipoaching patrols in Rwanda. Native resentment generated by this activity is presumed to have led to her murder in 1985.

Karl von Frisch (1886-1982). An Austrian zoologist, Frisch determined the means by which bees know direction and are able to communicate with other bees. As early as 1910, Frisch proved that fish can ascertain colors, shattering the long-held notion that fish and other lower animals are color-blind. His experiments with bees revealed that they can see all colors except red, as well as ultraviolet light. Observing bees through glass partitions, he discovered that they communicate by dancing and that their dances have very specific meanings. Frisch shared the 1973 Nobel Prize in Physiology or Medicine with Konrad Lorenz and Nikolaas Tinbergen.

Biruté Galdikas (1946-   ). Focusing her scholarly activity on the orangutans of Borneo and Sumatra, Galdikas, a lecturer in primatology at Simon Fraser University in Vancouver, Canada, spends most of her time on the Malay peninsula studying every aspect of orangutan life and behavior. Raised in Canada by her Lithuanian parents, Galdikas in 1971 went to Borneo, where she founded the Orangutan Research and Conservation Project in Tanjun Puting National Park. In 1986, Galdikas established the Orangutan Foundation International.

Étienne Geoffroy Saint-Hilaire (1772-1844). A French anatomist, Geoffroy Saint-Hilaire was one of the leading comparative anatomists of the nineteenth century. He sought to reduce all animal forms to a single ideal plan. He brought considerable condemnation upon himself in 1830 by contending that cephalopod mollusks developed from the same basic pattern as vertebrates, a concept that was publicly deplored by Georges Cuvier, then the most celebrated figure in the field of comparative anatomy. Geoffroy Saint-Hilaire's arguments are believed to have helped pave the way for acceptance of Charles Darwin's theories.

Jane Goodall (1934-   ). Born in London, Goodall had no formal higher education and no experience in studying animal behavior, ethology, when Louis Leakey encouraged her to observe the behavior of chimpanzees at the Gombe Stream Reserve in Tanzania in 1960. Her careful and detailed observations led to her receiving a doctorate from Cambridge University in 1965 on the basis of a thesis on chimpanzee behavior. She was the first person to report authoritatively that chimpanzees, contrary to previous speculation, are not strictly vegetarian but will track down, kill, and eat small animals. Even more important, she observed that chimpanzees can make simple tools, until then thought to be a strictly human activity. Among her books are *My Friends the Wild Chimpanzees* (1967), *In the Shadow of Man* (1971), and *The Chimpanzees of Gombe: Patterns of Behavior* (1986), her most important book.

Stephen Jay Gould (1941-   ). An American paleontologist, Gould, working from his study of fossil remains, developed his theory of punctuated equilibrium. According to Gould, fossil evidence suggests that there is seldom gradual evolution from one species to another. Rather, according to this theory, fossils show periods of relatively little change, but then a more evolved species arises quite quickly. Which species proliferate and which species become extinct is as much a matter of chance as of the ability to adapt.

Ernst Haeckel (1834-1919). This German biologist was a spirited supporter of Charles Darwin's theory of evolution espoused in 1859 in *On the Origin of Species.* Trained as a physician, Haeckel soon abandoned his medical practice and, during a soul-searching period spent in Italy, joined a scientific expedition to Messina. His publication in 1862 of the results of this expedition helped secure him a position at the University of Jena, where he served as chair of zoology from 1865 until he retired in 1909. He is best known for his recapitulation theory, now largely discredited, espousing the notion that a recapitulation of phylogeny is found in ontogeny. In simpler terms, he contends that animals, as they develop, ape the characteristics of their lineage.

Baron Alexander von Humboldt (1769-1859). This German scientist and explorer was among the most versatile naturalists of his time. Born in Berlin, Humboldt studied mining and geology at the Freiberg School of Mines. An inheritance in 1796 enabled him to pursue his scientific studies uninterruptedly. In South America, he sailed the Orinoco and the Rio Negro, systematically collecting botanical and zoological specimens. He studied the current in the Pacific Ocean that now bears his name. His major publication was the five-volume *Kosmos: Entwurf einer physischen Weltbeschreibung* (1845-1862; *Cosmos: A Sketch of a Physical Description of the Universe*, 1848-1858), which sought to explain human beings' place in the overall natural scheme.

Thomas Henry Huxley (1825-1895). Until Huxley, a British biologist, embarked on his landmark studies in paleontology, evolution, and comparative anatomy, comparative studies were pursued primarily through the deductive method. Huxley changed this practice by observing as carefully and objectively as he could and permitting his conclusions to proceed from his data. The inductive method, with his help, has become the prevailing method of scientific research.

Libbie Henrietta Hyman (1888-1969). A famed American invertebrate zoologist, Hyman challenged some of the most entrenched theories of metazoan evolution, examining closely the types of organisms that first developed a mesoderm and in flatworms formed a coelom. Hyman contended that mesodermal tissue originally appeared in a group of flatworms, suggesting, according to Hyman, that they were derived directly from the planula larvae of some other animal, giving them an ancestral relationship to all the higher animals, a revolutionary evolutionary concept.

Donald Johansen (1943-). Johansen's specialty is paleoanthropology, which has taken him to excavations all over the world. In 1974, he discovered the *Australopithecus afarensis* skeleton known as Lucy, the oldest, most complete skeleton of a human ancestor. Johansen received the Ph.D. from the University of Chicago. He has attempted to inform the general public about his field through hosting many Public Broadcasting System (PBS) series, including *In Search of Human Origins* (1995), and writing popular books such as *Lucy: The Beginnings of Humankind* (1981).

Ernest Everett Just (1883-1941). A native of Charleston, South Carolina, Just was a biologist who was particularly concerned with cell life and metabolism. He became expert in egg fertilization, artificial parthenogenesis, and cell division. He was instrumental in training many young biologists at Woods Hole Marine Biology Laboratory in Massachusetts. In 1939, his major book, *Biology of the Cell Surface*, was published. Just was the first African American zoologist to have his image featured on a United States postage stamp. Disheartened by restrictions on African Americans during the 1930's, he resided in Europe during most of that decade.

Charles J. Krebs (1936-). An American teaching at the University of British Columbia, Krebs is known for his research on the fluctuating deer mouse (*Peromyscus maniculatus*) and Townsend's vole (*Microtus oregoni*) populations near Vancouver. In 1976, Krebs began a ten-year study of snowshoe hares at Kluane Lake. Eleven years later, he embarked on a study of the dynamics of the lemming population on the Arctic coast of Canada's Northwest Territory.

Edwin Gerhard Krebs (1918-). Best known for his work on the regulation of enzyme activity, which he undertook with Edmond Fischer, Krebs was born in Lansing, Iowa. He earned an M.D. from the University of Washington in 1943, but became a professor of biochemistry rather than a practicing physician. For their work on the regulation of enzyme activity, Krebs and Fischer were awarded the 1992 Nobel Prize in Physiology or Medicine.

Schack August Steenberg Krogh (1874-1949). Born in Jutland, this Danish physiologist and zoologist is remembered mostly for his pioneering work focusing on human circulation and respiration. His strong background in physics enabled him to design the mechanical devices necessary to carry out his research. He showed how the lungs absorb oxygen and expel carbon dioxide solely by diffusion. Instruments he devised to measure blood flow and respiration during exercise led him to the important discovery that during exercise capillaries expand, permitting an increased flow of oxygenated blood to stressed muscles. For this discovery, he received the Nobel Prize in Physiology or Medicine in 1920.

Jean-Baptiste-Pierre-Antoine de Monet, chevalier de Lamarck (1744-1829). Born in Picardy, the French naturalist Jean-Baptiste Lamarck articulated the first systematic evolutionary theory in biology. He was a highly competent field botanist, but his interest in zoology grew after he was appointed professor of lower vertebrate animals at the newly founded Jardin des Plantes in 1793. He made a major contribution to the field with the publication of *Histoire naturelle des animaux sans vertèbres* (1815; natural history of invertebrate animals), which remained a standard work for half a century.

Sir Edwin Ray Lankester (1847-1929). A British embryologist in the post-Darwinian period, Lankester was active in comparative anatomical studies. Lankester was centrally concerned with the nature and development of the body cavities, notably the coelom. His pioneering work in this field led to his being knighted by King George V. He was a prolific writer and editor, whose works included *Diversions of a Naturalist* (1915) and *Great and Small Things* (1923).

Louis Leakey (1903-1972). Leakey, born in Kenya to British missionaries, spent his life in Kenya and was initiated into the Kikuyu tribe of that nation. He went to England to study at Cambridge University, from which he was graduated with first class honors in modern languages, archaeology, and anthropology. He is credited with the discovery of the first large-toothed australopithecine at Olduvai Gorge in 1955. He uncovered the first fossils of *Homo habilis* at Olduvai Gorge in 1960, claiming them as direct ancestors of modern humans. Among his many books, perhaps the most significant are *Adam's Ancestors* (1934; rev. ed. 1960), *Stone Age Races in Kenya* (1935; 2d ed. 1970), and *Olduvai Gorge, 1951-1961* (1965).

Mary Douglas Leakey (1913-1996). Born in London, Mary Leakey studied prehistoric archaeology in France before taking part in several British excavations between 1930 and 1934. Louis Leakey, impressed by her drawings of stone artifacts, sought her out. In 1936, they married, and Leakey later moved to Kenya, where she introduced modern archaeological techniques to the excavation of late Pleistocene sites at Hyrax Hill and Njoro River Cave. In 1960, she established a base camp at Olduvai Gorge, from which she directed the excavations in that area. In 1976, with the discovery of several sets of bipedal footprints at the site, Leakey found substantiation of her theory that Laetoli hominids were the earliest conclusive hominid samples found up to that time. Her *Africa's Vanishing Art: The Rock Paintings of Tanzania* (1983) is a highly significant archaeological study.

Richard Erskine Frere Leakey (1944-). The son of Louis and Mary Leakey, Richard Leakey was born in Nairobi and holds Kenyan citizenship. In 1968, he was appointed administrative director of the National Museums of Kenya, advancing to the directorship in 1974. He founded and obtained funding for the International Louis Leakey Memorial Institute for African Prehistory. An active paleontologist, Leakey has found some amazing human fossils in

Kenya, but his chief skill is as an administrator who has organized and directed international teams bent on recovering human fossils. His analyses of these fossils have been exceptionally valuable. Among his significant books are *The Making of Mankind* (1981) and *The Origins of Humankind* (1994).

Carolus Linnaeus (1707-1778). A Swedish naturalist and physician, Linnaeus devised a descriptive process for biology using standard terminology and nomenclature. Although his most renowned contributions were in botany, the methods he established and advanced are used in zoology and mineralogy as well. Linnaeus elaborated his binomial nomenclature for plants in *Species Plantarum* (1753). The tenth edition of his *Systema Naturae* (1758) introduced a similar system for animals. He sought to make his method of classification as consistent and objective as possible. A versatile man with far-ranging interests, he also wrote significantly in ethnology and geography, basing much of this writing on his travels to underdeveloped parts of Scandinavia.

Konrad Zacharias Lorenz (1903-1989). Viennese zoologist Lorenz spent most of his adult life promoting the comparative study of animal and human behavior. The father of modern ethology, the study of animal behavior, Lorenz had doctorates in both philosophy and medicine from the University of Vienna. He studied comparatively the behavior of birds, dogs, and fish, developing his theory of action-specific energy. Lorenz contended that animals' behavioral patterns are often genetically based. He studied animal behavior in relation to its adaptive survival value for the species. For this work, he shared the Nobel Prize in Physiology or Medicine in 1973.

Patrick Matthew (1790-1874). Like many British naturalists of his day, Matthew was an inveterate traveler who collected specimens in his travels and also philosophized about the origins of life and its evolution. Considered a precursor of Charles Darwin, Matthew questioned the prevailing notions about how human beings came to exist in their present form and how other forms of life adapted, seemingly in response to changing conditions. Matthew's two most noted books, both published in 1839, were *Emigration Fields, North America, the Cape, Australia, and New Zealand* and *Two Addresses to the Men of Perthshire and Fifeshire*.

Gregor Mendel (1822-1884). A Roman Catholic priest, Austrian scientist Mendel is noted for his work in heredity that began when he raised and hybridized peas in his monastery's garden, keeping careful records of them over several generations. Through his experiments, he concluded that the fertilization of an egg involved only one male sex cell. Although his vision was failing, Mendel continued his research on hawkeyes, four o'clocks, and bees. He generally did not publish his findings, although his noted article, *Versuche über Pflanzenhybriden* (1856; *Experiments with Plant Hybrids*), was published as a pamphlet and later in William Bateson's *Mendel's Principles of Heredity* (1913).

Maria Sibylla Merian (1647-1717). In 1660, Merian became the first known person to study systematically the life cycle of silkworms from caterpillars to moths. A gifted painter of flowers, Merian had no trouble selling her art work. Soon she began to add insects to her paintings. Always fascinated by insects, she began to collect caterpillars in 1674, keeping them in containers where she could watch their transformation into moths. She painted what she observed. In 1699, Merian and her daughter departed for two years in Surinam, where they both closely observed insects and other animals, painting them in immense and accurate detail.

Thomas Hunt Morgan (1866-1945). One of the leading founders of the science of modern genetics, Morgan, a native of Lexington, Kentucky, is renowned for his discovery of how chromosomes function in the transmission of heredity, a discovery for which he was awarded the 1933 Nobel Prize in Physiology or Medicine. After doctoral studies in embryology at The Johns Hopkins University, Morgan began a long career as a professor of biology, first at Columbia University, then at the California Institute of Technology. His studies centered on the fruit fly (*Drosophila melanogaster*). His collaborative study, *The Mechanism of Mendelian Heredity* (1915), contained evidence that genes too small to be seen transmit heredity and exist in the chromosomes.

Sir Richard Owen (1804-1892). Superintendent of the natural history department of the British Museum from 1856 until 1884, Owen, born in Lancaster, England, was among the great comparative anatomists of his day. His interest in vertebrate paleontology was piqued when Charles Darwin asked him in 1837 to describe a fossil specimen. Owen espoused the notion that there was an archetype or plan of organization in nature, attributing the plan of unity within diversity of animals to a creator. Although he did not completely oppose Darwin's theory of evolution, he objected to Darwin's theory of natural selection.

John Ray (1627-1705). This early British naturalist devoted himself to observing and writing about nature, trying always to do so in a systematic way. He set out to devise a taxonomy that he could apply to the classification of plants and animals. He classified plants on the basis of seed vessels, whereas he classified animals according to anatomy and habitat.

René-Antoine Ferchault de Réaumur (1683-1757). A French physicist and naturalist, Réaumur in 1731 invented a thermometer on whose temperature scale the freezing point of water was zero, as in the Celsius thermometer, and the boiling point was 80 degrees. His scientific research included work on the regeneration of crayfish and digestion in birds, particularly the role of gastric juices that he isolated. Between 1734 and 1742, he published six volumes that grew out of his extensive research on insects.

Michael Sars (1809-1869). A Norwegian biologist, Sars, professor of zoology at the Royal Frederic's University in Christiana (now the University of Oslo), carried out pioneering marine research. He observed marine mollusks carefully and finally discovered their metamorphosis. He also established the relation of crinoids to similar fossil groups. His research helped to make clear the knowledge of the alternation of generations.

Thomas Say (1787-1834). Born in Philadelphia, American naturalist Say made numerous expeditions into the Rocky Mountains as well as to Mexico, Florida, Georgia, and Minnesota in quest of insect specimens. Curator of the American Philosophical Society from 1821 to 1827, he published his major multivolume work, *American Entomology*, between 1824 and 1828. In 1824, he eloped to Robert Owen's utopian community at New Harmony, Indiana. His wife illustrated his *American Conchology* (6 vols., 1830-1834).

George B. Schaller (1933-   ). Born in Berlin, Germany, Schaller emigrated to the United States and received a B.S. in zoology and an

A.B. in anthropology from the University of Alaska in 1955. His Ph.D. is from the University of Wisconsin. Schaller is best known for studies of the mountain gorilla, the deer, and the tiger. His monumental study, *The Serengeti Lion: A Study of Predator-Prey Relations* (1972), was recipient of the 1973 National Book Award in nonfiction. Schaller has been praised for his ability to write clearly and engagingly about technical subjects. He is among the most accessible writers in field biology.

David Takayoshi Suzuki (1936-). Born in Vancouver, British Columbia, Suzuki received his education in the United States, graduating from Amherst College with an A.B. degree, and from the University of Chicago with a Ph.D. in zoology in 1961. A leading geneticist, his major research interests have been in the regulation and development of behavior, in the genetic organization of chromosomes, and in developmental and behavioral genetics. Suzuki is much concerned in his writing with the implications of his discipline for the future, as evidenced in such books as *Inventing the Future* (1989), *It's a Matter of Survival* (with Anita Gordon, 1990), and *The Sacred Balance: Rediscovering Our Place in Nature* (with A. McConnell,1997).

Nikolaas Tinbergen (1907-1988). A British zoologist born in the Netherlands, Tinbergen, along with German zoologists Konrad Lorenz and Karl von Frisch, is considered the cofounder of ethology, the study of animal behavior based on observing animals in their natural habitats. The three shared the Nobel Prize in Physiology or Medicine in 1973. Tinbergen is best known for his analyses of stimuli that cause specific behavioral responses in animals. His *The Study of Instinct* (1951) is the first real handbook of ethology. He is also known for his *Social Behavior in Animals* (1953).

Charles Henry Turner (1867-1923). Biologist Turner was born in Cincinnati, Ohio, and received a B.S. degree in 1891 and an M.S. in 1892, both from the University of Cincinnati. There he came under the influence of Professor Clarence Luther Herrick, a leader in the emerging field of psychobiology. Herrick encouraged Turner to do research and to publish. In 1907, Turner received the Ph.D. in zoology from the University of Chicago, one of the first African Americans to achieve this distinction. Turner is best known for his work on insect behavior, most notably the unique gyrations that ants make as they return to their nests. These gyrations are referred to as "Turner's circling." Turner also studied the behavior of bees, wasps, and cockroaches, determining that the latter learn by trial and error.

Alfred Russel Wallace (1823-1913). Although Charles Darwin receives much of the credit for espousing the theories of evolution and natural selection, Wallace, quite independently, embraced such notions earlier than Darwin. Born in England of Scottish parents, Wallace became interested in natural science in grammar school. With the encouragement of Henry Walter Bates, he collected and studied beetles. He accompanied Bates to Brazil in 1848, remaining there for four years. In 1854, he went to the Malay Archipelago, where he remained for eight years. There he devised an evolutionary theory. In 1855, he wrote an essay on natural selection, which he sent to Darwin. He expanded this essay, entitled "On the Tendency of Varieties to Depart Indefinitely from the Original Type," and published it in conjunction with Darwin as a joint effort, titled "On the Tendency of Species to Form Varieties," in 1858. His *Contributions to the Theory of Natural Selection* (1870) and Darwin's *On the Origin of Species* (1859) are the two most significant early books on evolution.

Edward Osborne Wilson, Jr. (1929-). Born in Birmingham, Alabama, Wilson attended the University of Alabama before pursuing doctoral studies at Harvard University, where he received a Ph.D. in 1955. A professor of zoology at Harvard, Wilson has served as curator of entomology at the university's Museum of Comparative Zoology. He is also a trustee of the Marine Biological Laboratory at Woods Hole, Massachusetts. He received the Pulitzer Prize for general nonfiction in 1979 for *On Human Nature* (1978) and again for *The Ants* (with Bert Hölldobler, 1990). His *The Insect Societies* (1971) remains an important book in its field. He is one of the most significant figures in the controversial field of sociobiology, which examines the biological bases of behavior.

Roger Arliner Young (1889-1964). The first African American woman to earn a Ph.D. in zoology, which she received from the University of Pennsylvania in 1940. Young was also the first African American woman to publish extensively in her field. Born in Clifton Forge, Virginia, she conducted productive early research on the biological structures that control salt concentration in paramecia. She also published cogent research on the effect of direct and indirect radiation on sea urchin eggs. Burdened with a staggering teaching load and little support for her research, she finally was overcome by the pressures upon her and died in 1964.

—R. Baird Shuman

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Fouts, Roger, and Stephen Tukel Mills. *Next of Kin: My Conversations with Chimpanzees.* New York: Avon Books, 1997. Provides authentic, humorous, and moving documentation of the author's work with chimpanzees. This research leads to a greater understanding of intelligence, communication strategies, and use of language in both chimpanzees and humans.

Goodall, Jane. *The Chimpanzees of Gombe: Patterns of Behavior.* Cambridge, Mass.: Belknap Press of Harvard University Press, 1986. Documents the author's research on the complex social behavior, relationships, character, and perceptual world of chimpanzees. The engrossing and scientific text is enlivened by photographs revealing the animals' lives and activities.

_______. *In the Shadow of Man.* Boston: Houghton Mifflin, 1971. This classic describes Goodall's early years among the chimpanzees of Gombe, and is a record of her observations on chimpanzee life, emotions, habitats, and relationship to humans. Photographs by Hugo Van Lawick.

_______. *Through a Window: My Thirty Years with the Chimpanzees of Gombe.* Boston: Houghton Mifflin, 1990. Describes the author's life and scientific research, and analyzes the many facets and complexities of chimpanzee emotions and behavior.

Levine, Stuart P. *The Orangutan.* San Diego, Calif.: Lucent Books, 2000. This volume in the Endangered Animals and Habitats series describes past and present history and habitats of the orangutan, decreasing populations, and the impact of research, captivity, habitat loss, and human population growth. Provides names of organizations to contact, black-and-white photographs, and a glossary.

Other Mammals

Alexander, Shana. *The Astonishing Elephant.* New York: Random House, 2000. Gives a detailed account of the unique qualities of the elephant, including behavior patterns, communication, and emotional depths. Discusses genocide of elephants in American zoos and circuses, the march toward extinction of both the Asian and African elephant, and the struggle of scientists, biologists, and zoologists to understand and protect the animal. Also examines the role of elephants in religion, war, and entertainment.

Bass, Rick. *The New Wolves.* New York: Lyons Press, 1998. Chronicles the reintroduction of Mexican wolves, or lobos, to the American southwest. Presents concerns of environmentalists, ranchers, and others, and examines the conflict between modern life and nature. Describes, in a sensitive and dramatic manner, the dangers and wonders faced by wolves released on the mesa.

Bolgiano, Chris. *Mountain Lion.* Mechanicsburg, Pa.: Stackpole Books, 1995. Records seven years of extensive research on the place of mountain lions—cougars, panthers, and pumas—in North American history, folklore, and ecology. Describes controversial efforts, in laboratories and captivity, to save these endangered animals.

Caras, Roger. *Animals in Their Places.* San Francisco: Sierra Club Books, 1987. Presents absorbing accounts of wolves, elephants, bears, squirrels, panthers, condors, and many other animals in their natural surroundings. Indicates threats to this natural world, especially from humans.

Clyne, Densey. *The Best of Wildlife in the Suburbs.* South Melbourne, Australia: Oxford University Press, 1993. Detailed, amusing essays examine, on a month by month basis, the rich array of insects, birds, and animals in a suburban Australian garden. Behaviors, diets, and characteristics are described. Simple but charming drawings by Martyn Robinson enliven the text.

Fenton, M. Brock. *Bats.* New York: Facts on File, 1992. Investigates the world of different bats, their origins, anatomy, echolocation skills, food habits, social organization, family life, ecological value, health, and diversity. Describes attitudes toward bats, and their image in various cultures.

Gauthier-Pilters, Hilde, and Anne Innis Dagg. *The Camel: Its Evolution, Ecology, Behavior, and Relationship to Man.* Chicago: University of Chicago Press, 1981. Describes the life, traits, behaviors, and habitats of the camel, and discusses the interdependency of humans and camels in the desert.

Geist, Valerius. *Moose.* Stillwater, Minn.: Voyageur Press, 1999. Using striking color photographs by Michael H. Francis, this work explores all aspects of the life and world of the moose.

Hall, Tarquin. *To the Elephant Graveyard.* New York: Atlantic Monthly Press, 2000. Describes in a dramatic and vivid manner the search for a killer elephant in Northeast India. Reflects on the changing environment and its impact on human and elephant relationships.

Harrison, Kit, and George Harrison. *America's Favorite Backyard Wildlife.* New York: Simon & Schuster, 1985. Provides facts and details about wildlife that might be observed in American backyards, such as the box turtle, gray squirrel, opossum, woodchuck, sparrow, finch, and others. Accompanied by black-and-white photographs and a glossary.

Himsel, Carol A. *Rats.* Hauppage, N.Y.: Barron's Educational Series, 1991. Written as a manual for those raising rodent pets, the book has a chapter on understanding rats, as well as practical information on care, habitats and housing, nutrition, training, and health. Includes a glossary and interesting photographs and helpful drawings by Karin Skogstad, Fritz W. Kohler, and Michele Earle-Bridges.

Hoffman, Matthew, ed. *Dogs: The Ultimate Care Guide.* Emmaus, Pa.: Rodale Press, 1998. Covers numerous topics concerning dog characteristics, behaviors, and care. Includes information on dog breeds, health and longevity, training, feeding, emotions, communication, and grooming.

Kanze, Edward. *Kangaroo Dreaming: An Australian Wildlife Odyssey.* San Francisco: Sierra Club Books, 2000. Describes the experiences of two naturalists as they travel across Australia observing its unique wildlife: the kookaburra and other unusual birds, giant lizards, kangaroos, koalas, platypuses, crocodiles, wombats, and others. Provides interesting information on habitats and characteristic behaviors and gives humorous accounts of encounters with different animals.

Kirk, Mildred. *The Everlasting Cat.* New York: Galahad Books, 1977. Provides a history of the cat in literature, folklore, and religion, and discusses the relationship of people and cats through the ages.

Long, Kim. *Squirrels.* Boulder, Colo.: Johnson Books, 1995. Presents a comprehensive look at squirrel species, taxonomy, anatomy, diet, geographical range, behaviors, endangerment status, relationship to humans, and place in folklore. Includes useful illustrations, a list of wildlife and squirrel organizations, online resources, and products for squirrels.

McNamee, Thomas. *The Return of the Wolf to Yellowstone.* New York: Henry Holt, 1997. Chronicles the reintroduction of the gray wolf to Yellowstone National Park. Portrays conflicts and consequences surrounding this event. Politics, conservation, wolf biology and nature, and the relationship of wolves and humans are some of the topics studied.

Matthiessen, Peter. *Tigers in the Snow.* New York: North Point Press, 2000. A detailed and moving look at the Siberian tiger, its origins, history, place in mythology, and struggle for survival. Tells the story of the Siberian Tiger Project. Provides appealing and colorful photographs by Maurice Hornocker.

_______. *Wildlife in America.* New York: Viking, 1987. A classic history of the continent's rich wildlife, its exploitation and destruction by early European settlers and growing populations, and modern efforts to protect disappearing species. Provides photographs, maps, drawings, appendices, and information on wildlife legislation.

Mitchell, Hayley R. *The Wolf.* San Diego, Calif.: Lucent Books, 1998. This volume in the

Endangered Animals and Habitats series demystifies the image of the wolf by detailing its history, discussing its loss of habitat, and describing efforts to save it from extinction and provide new homes for the gray, red, Mexican, and Ethiopian wolf. Provides black-and-white photographs, a glossary, and the names of organizations to contact.

Mowat, Farley. *Never Cry Wolf.* New York: Bantam Books, 1983. Poignantly narrates the story of two summers and a winter spent on the frozen tundra studying wolves and caribou of the region. Debunks the image of the wolf as savage killer and enemy of humans, and pleads for understanding and preservation of this misunderstood animal.

Natural History New Zealand. *Wild Asia.* Gretna, La.: Pelican, 1999. Enriched by over 250 spellbinding photographs, the book is based on an award-winning international television series. Presents the deserts, rain forests, mountains, rivers, and woodlands of Asia, which are home to the teeming and varied wildlife of the massive continent.

Neary, John, and Time-Life Television Books. *Wild Herds.* Time-Life Films/Vineyard Books, 1977. Based on the television series *Wild Wild World of Animals*, the book provides information on what constitutes a herd, herds of the past and present, reasons for herding, and hooves and other anatomical features of herd animals. Among the wild herds are antelope, zebras, horses, camels, pigs, bison, buffalo, deer, sheep, goats, and horses. Presents attractive and informative photographs and drawings.

Penny, Malcolm. *Rhinos: Endangered Species.* New York: Facts on File, 1988. Explores reasons for the swift depletion of the rhinoceroses population, including beliefs and myths that support the hunting of these beleaguered animals. Investigates the evolution, breeding habits, social behaviors, and diets of Asian and African rhinoceroses, and discusses ways of saving them. Provides addresses of organizations.

Quinn, John R. *Wildlife Survivors: The Flora and Fauna of Tomorrow.* Blue Ridge Summit, Pa.: TAB Books, 1994. Examines major environmental changes and their impact on different animals. Considers, and documents through black-and-white photographs, the habits, characteristics, and habitats of reptiles, amphibians, insects, fish, birds, and mammals which are likely to survive. Reflects on why others will not. Provides a list of environmental organizations.

Reddish, Paul. *Spirits of the Jaguar: The Natural History and Ancient Civilizations of the Caribbean and Central America.* London: BBC Books, 1996. Serves as a companion to the BBC television series of the same name. Provides brilliant photographs and animated discussions of the region's natural history, peoples, and teeming wildlife.

Roth, Sara. *The Complete Pig: An Entertaining History of Pigs.* Stillwater, Minn.: Voyageur Press, 2000. Offers, through amusing photographs, drawings, and extensive research, a whimsical account of pigs in history, folklore, and literature.

Rundquist, Eric M. *Reptile and Amphibian Parasites.* Philadelphia: Chelsea House, 1999. Gives detailed information about the different parasites preying on reptiles and amphibians, the illnesses they can cause, and treatments that can be provided. Contains bright, glossy, and detailed photographs.

Schaller, George B. *The Last Panda.* Chicago: The University of Chicago Press, 1993. Describes the author's years in China studying the life of pandas in their natural habitat. Emphasizes the urgent need to fight to save pandas from extinction, and suggests strategies to do so.

Scherr, Lynn. *Tall Blondes: A Book About Giraffes.* Kansas City: Andrews McMeel, 1997.

Examines the physical traits, personalities, and current status of giraffes. Surveys their place in history, and their impact on culture and literature.

Souder, William. *A Plague of Frogs.* New York: Hyperion, 2000. Describes the race to identify and understand the reasons for mysterious deformities discovered in frogs in a Minnesota pond in 1995. Similar abnormalities have shown up elsewhere in the world. Considers frog physiology, environmental changes, and government and scientific efforts to solve the problem.

Steinhart, Peter. *The Company of Wolves.* New York: Alfred A. Knopf, 1995. Explores facts and myths about wolves and their relationship with humans, and presents points of view of biologists, ranchers, trappers, people who love or hate wolves, and people who study them.

Sterry, Paul. *Beavers and Other Rodents.* New York: Todtri, 1998. Gives a detailed account of the characteristics and behaviors of beavers and rodents both loved and hated by humans. Enriched by attractive and colorful photographs.

Stirling, Ian. *Polar Bears.* Ann Arbor: University of Michigan Press, 1988. Brilliant photographs by Dan Guravich depict the life and habitat of polar bears. Introduces readers to the study of these animals, their life cycle and behaviors, conflicts with humans, and conservationists' concerns for their survival.

Thomas, Elizabeth Marshall. *The Hidden Life of Dogs.* Boston: Houghton Mifflin, 1993. Identified by the author as "a book about dog consciousness," this work chronicles thirty years of observing and sharing life with various kinds of dogs, including dingoes and wolves. Throws light on the need of dogs to have a social life, create rituals and patterns of behavior, and display thoughts and feelings.

_______. *The Tribe of the Tiger: Cats and Their Culture.* New York: Simon & Schuster, 1994. Studies the behaviors, social lives, and individuality of both domestic and wild cats. Illustrated by Jared Taylor Williams.

Tuttle, Merlin. *America's Neighborhood Bats.* Austin: University of Texas Press, 1988. Dispels existing myths about bats, and explains their value to humans. Examines bat species, origins, behaviors, feeding habits, health, habitats, and colonies. Provides a glossary, photographs, and drawings.

Watson, Mary Gordon, Russell Lym, and Sue Montgomery. *Horse: The Complete Guide.* New York: Barnes & Noble Books, 1999. Examines in detail all the physiological, psychological, and behavioral aspects of horses. Reviews care of horses, equestrian sports, different breeds, and the impact of the horse on the human imagination.

Winston, Mark L. *Nature Wars: People vs. Pests.* Cambridge, Mass.: Harvard University Press, 1997. Explains how humans put their world at risk by indiscriminately attempting to control and destroy pests and organisms that are a necessary part of the chain of existence and balance of nature. Provides a brief history of pests and pesticides, and discusses the escalation of the battle between people and pests in modern times. Presents scientific and thought-provoking data, and pleads to manage rather than control, and reduce rather than eradicate.

Zimmer, Carl. *Parasite Rex: Inside the Bizarre World of Nature's Most Dangerous Creatures.* New York: The Free Press, 2000. Examines in minute detail the evolution, growth, and activities of parasites. Discusses parasite hosts, including humans, and argues that human beings are themselves parasites of other living things on earth.

—Nillofur Zobairi

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A quarterly journal of ornithology, published by the American Ornithologists' Union. Founded in 1883, the American Ornithologists' Union is the oldest and largest organization in the New World devoted to the scientific study of birds. Although the AOU primarily is a professional organization, its membership of about four thousand includes many amateurs dedicated to the advancement of ornithological science.

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The Chameleon Journals
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Fax: 303-735-1811
physzoo@spot.colorado.edu
Presents current research in environmental, adaptational, and comparative physiology and biochemistry. Subscription and author guidelines are available online.

Placenta
www.harcourt-international.com/journals/plac/default.cfm?
Publishes full-length papers and short communications of high scientific quality on all aspects of human and animal placenta.

Poultry Science Association
1111 N. Dunlap Avenue
Savoy, IL 61874
Ph.: 217-356-3182
Fax: 217-398-4119
www.psa.uiuc.edu/japr/japr.html
Official publication of the Poultry Science Association.

Recent Ornithological Literature Online (ROL)
www.nmnh.si.edu/BIRDNET/ROL
A serial compilation of citations and abstracts from the worldwide scientific literature that pertains to birds and the science of ornithology. The ROL deals chiefly with periodicals, but also announces new and renamed journals and provides abstracts of conference proceedings, reports, doctoral dissertations, and other serial publications. Scientists, who voluntarily scan journals for ornithological articles, generally according to their geographic region and special scientific interests, prepare the entries. Papers dealing exclusively with domestic birds and their husbandry are excluded, unless applicable to nondomestic species.

Small Farmer's Journal
P.O. Box 1627
Sisters, OR 97759-1627
Ph.: 800-876-2893 or 541-549-2064
Fax: 541-549-4403
E-mail: comments@smallfarmersjournal.com
www.smallfarmersjournal.com
International quarterly, strongly supporting independent family farms. Also offers information on the use of animal-power for farming.

Wildlife Journal
40 Monument Circle
Indianapolis, IN 46204
Ph.: 800-733-8273
www.wildlifejournal.com/Subscribe.htm
For those who appreciate and enjoy wildlife.

The Wilson Bulletin
www.ummz.lsa.umich.edu/birds/wos.html
Official publication of the Wilson Ornithological Society, a worldwide organization of professional ornithologists and serious amateurs interested in birds. The Wilson Society, founded in 1888, is a worldwide organization of nearly 2,500 people who share a curiosity about birds. Named in honor of Alexander Wilson, the Father of American Ornithology, the Society publishes

this quarterly journal of ornithology, and holds annual meetings.

Yellowstone Journal
Ph.: 800-656-8762 in the United States or (307) 332-3111
www.yellowstonepark.com
The online edition of the journal, published several times a year, provides current, in-depth coverage about wolves, grizzlies, other wild animals, recreation, geysers, fires, the environment, and more.

Zootecnica International
E-mail: zootecnica@zootecnica.it
www.zootecnica.it
Journal specializing in poultry science and breeding technology.

—Mary E. Carey

ORGANIZATIONS

AgBiotechNet
www.agbiotechnet.com
Web site offers an online service for agricultural biotechnology, providing information for plant and animal biotechnology including cloning, genomics, genetic engineering, in vitro culture, biosafety, intellectual property rights and all key issues in agricultural biotechnology through news, reviews, abstracts, reports, links, book chapters. Also includes news, book chapters, reports, abstracts, and conference materials on agricultural biotechnology, including genetic engineering of plants and animals.

All for Animals
www.allforanimals.com
Web site offers directory of animal rescue groups, animal rights groups, companies against animal testing, pet goods and services, nature and wildlife. This organization offers a free newsletter to assist readers in learning more about animal testing, cruelty-free companies, vegetarianism, cruelty-free investments, coexisting with wildlife, the links between animal abuse and domestic violence, and much more. Each issue of the newsletter features three sections: Cruelty-free Tip of the Month, Did You Know? and the Web site of the Month.

Alliance for the Wild Rockies (AWR)
P.O. Box 8737
Missoula, MT
Ph.: 406-721-5420
Fax: 405-721-9917
www.wildrockiesalliance.org/index.html
Web site describes works to protect rivers, wilderness ecosystems, biological corridors, and native wildlife in the northern Rockies. AWR formed to meet the challenge of saving the Northern Rockies Bioregion from habitat destruction. Multiple individuals, business owners, and organizations take a bioregional approach to protect and restore this region. A membership-based nonprofit organization, the board and advisors include some of the nation's top scientists and conservationists. The term "bioregion" refers to a physiographic region of wildlands that are biologically connected. The Wild Rockies Bioregion includes wildlands in parts of Idaho, Montana, Wyoming, Oregon, Washington, Alberta, and British Columbia.

American Association for Laboratory Animal Science (AALAS)
National Office:
AALAS
9190 Crestwyn Hills Drive
Memphis, TN 38125
www.aalas.org/opening.htm
Web site describes this organization as dedicated to the humane care and treatment of laboratory animals, and to quality research that leads to scientific gains benefiting both humankind and animals.

American Association of Anatomists (AAA)
9650 Rockville Pike
Bethesda, MD 20814-3998
Ph.: 301-571-8314
Fax: 301-571-0619
E-mail: exec@anatomy.org
www.anatomy.org/anatomy
Web site describes this scientific society representing biomedical researchers who are interested in structural biology.

American Association of Clinical Anatomists (AACA)
Lawrence M. Ross, M.D., Ph.D., Secretary AACA
Ph.: 713-500-6169

Fax: 713-500-0621
www.clinicalanatomy.org
Web site describes the AACA, an organization that advances the science and art of clinical anatomy. It encourages research and publication in the field and maintaining high standards in the teaching of anatomy. Clinical anatomy is defined as anatomy in all its aspects—gross, histologic, developmental, and neurologic, as applied to clinical practice, the application of anatomic principles to the solution of clinical problems and/or the application of clinical observations to expand anatomic knowledge.

American Biological Safety Association (ABSA)
1202 Allanson Road
Mundelein, IL 60060
Ph.: 847-949-1517
Fax: 847-566-4580
E-mail: absa@absa.org
www.absa.org
Web site offers information on all aspects of biosafety and biological safety, including documents, regulations, and guidelines for members and non-members of the ABSA.

American Society for the Prevention of Cruelty to Animals (ASPCA)
424 East 92d Street
New York, NY 10128
Ph.: 1-800-426-4435 (Animal Poison Control Center)
www.aspca.org/body_index.asp
Web site describes this organization dedicated to alleviating pain, fear, and suffering in animals. A free newsletter is available through this site. The ASPCA Animal Poison Control Center is the first and only nonprofit animal-dedicated poison control center in North America. The Center consults with animal owners, veterinarians, and others about animal poisonings and other toxicology-related issues. Licensed veterinarians and board-certified veterinary toxicologists answer center phones twenty-four hours a day.

American Veterinary Medical Association (AVMA)
Headquarters:
1931 North Meacham Road, Suite 100
Schaumburg, IL 60173
Ph.: 847-925-8070
Fax: 847-925-1329
E-mail: avmainfo@avma.org
Governmental Relations Division:
1101 Vermont Avenue NW
Washington, DC 20005
Ph.: 202-789-0007
Fax: 202-842-4360
E-mail: avmagrd@avma.org
www.avma.org/resources/default.asp
Web site includes information on publications, client service handbooks, disasters and emergency preparedness, pet ownership sourcebook, public health, and veterinary schools. The site also includes a Care for Pets Index featuring information about veterinarians and how to select them, managing the loss of a pet, buying a pet, animal safety, and general animal health.

American Zoo and Aquarium Association (AZA)
8403 Colesville Road
Suite 710
Silver Spring, MD 20910-3314
Ph.: 301-562-0777
Fax: 301-562-0888
www.aza.org
Web site describes this organization with a mission to promote the welfare of zoological parks and aquariums and their advancement as public educational institutions, as scientific centers, as natural science and wildlife exhibition and conservation agencies, and as cultural recreational establishments dedicated to the enrichment of human and natural resources.

Conservation International
1919 M Street NW, Suite 600
Washington, DC 20036
Fax: 202-912-1000
www.conservation.org
Web site provides information about biodiversity conservation in the world's endangered ecosystems, including a map of global biodiversity hotspots, profiles of hotspots, and many other resources. The site also provides access to video news releases. Fact sheets designed to make information and resources available to journalists in television, radio, and print media are also available.

4-H Clubs
FourHWeb Project:
www.4-h.org/fourhweb/index.htm
Site brings together all 4-H clubs and resources on the web in one location.
National 4-H Council:
www.fourhcouncil.edu
Site describes this nonprofit organization dedicated to building partnerships for community youth development that value and involve youth in solving issues critical to their lives, their families, and society.
National 4-H Headquarters:
www.4h-usa.org
Families, 4-H, and Nutrition:
CSREES/USDA
Stop 2225
1400 Independence Avenue SW
Washington, DC 20250-2225
Ph.: 202-720-2908
National 4-H Web:
www.4-h.org
Web site created and maintained by the National 4-H Youth Technology Corps. Offers both IRC and Java Chat.

Humane America Animal Foundation
P.O. Box 7
Redondo Beach, CA 90277
Ph.: 310-263-2930
Fax: 310-263-2937
E-mail: info@humaneamerica.org
www.humaneamerica.org/images/f_ha.gif
Web site includes information on Humane America's 1-800-Save-a-Pet.com program, designed to assist communities across the country in reducing their overpopulation of healthy companion animals to the point that euthanization is no longer necessary as a means of population control.

International Commission on Zoological Nomenclature (ICZN)
c/o The Natural History Museum
Cromwell Road
London, SW7 5BD, UK
Ph.: +44 (0)20 7942 5653
E-mail: iczn@nhm.ac.uk
www.iczn.org
Web site describes the official body responsible for providing and regulating the system for ensuring that every animal has a unique and universally accepted scientific name.

International Federation of Associations of Anatomists (IFAA)
E-mail: iwhitmore@argonet.co.uk
www.ifaa.lsumc.edu
Web site describes this international body for anatomical associations. The IFAA is composed of the following organizations: the Anatomical Society of Great Britain and Ireland, the American Association of Anatomists, the American Association of Clinical Anatomists, the Anatomische Gesellschaft, and the Spanish Society of Anatomy.

International Species Information System (ISIS)
E-mail: ivan@isis.org
www.worldzoo.org
Web site offers information about this organization that helps zoological institutes manage their living collections by providing software for records keeping and collection

management, and then pools this information. ISIS is an international nonprofit membership organization that serves nearly 550 zoological institutional members, from fifty-four countries, worldwide. There is a high level of global cooperation by mostly city-based facilities, presently including about half of the world's recognized zoos and aquariums. ISIS supports conservation and preservation of species by helping member facilities manage their living collections. Information is available on 286,000 living specimens of 7,500 species, along with an additional 1,413,000 of their ancestors. Most of these specimens were bred in member facilities. ISIS cooperates closely with many national and regional associations of zoos and aquaria, and hosts the Secretariat of the World Zoo Organization.

International Wildlife Rehabilitation Council
4437 Central Place, Suite B-4
Suisun, CA 94585
www.iwrc-online.org
Web site describes the work of this organization in protecting animals and their habitat through wildlife rehabilitation.

Internet Zoological Society
E-mail: e-mail@izoo.org
www.izoo.org
Web site describes this organization established to help support those organizations and individuals that deal directly with education about, and conservation and rehabilitation of, wild animals and ecosystems.

Jane Goodall Center for Excellence in Environmental Studies
WCSU Westside
Room 134A
181 White Street
Danbury, CT 06810
Ph.: 203-837-8726
E-mail: jgiinformation@janegoodall.org
www.janegoodall.org
Web site describes organization that studies issues relevant to the environment, both natural and human-centered. A collaboration between the Jane Goodall Institute and Western Connecticut State University.

Kids Go Wild
2300 Southern Boulevard
Bronx, NY 10460
Ph.: 718-220-5100
wcs.org/9822
Web site where children can learn about saving wild animals and the environment, conservation education, and events sponsored by the Wildlife Conservation Society.

Laboratory Animal Management Association (LAMA)
P.O. Box 877
Killingworth, CT 06419
E-mail: doc@animalvillage.com
www.lama-online.org
Web site describes LAMA, dedicated to enhancing the quality of management and care of laboratory animals throughout the world.

National Snaffle Bit Association Office (NSBA)
4815 S. Sheridan, Suite 109
Tulsa, OK 74145
Ph.: 918-270-1469
Fax: 918-270-1471
E-mail: nsbaoffice@aol.com
www.premierpub.com/futurity/nsba.htm
Web site describes the purpose of the NSBA, which is to define, promote, and improve the quality of the pleasure horse; to promote exhibits, events, and contests in expositions and shows; to promote the training of pleasure horses; to promote interest in pleasure horses among younger horsemen; and to use and encourage the use of the standard rules for holding and judging contests of the pleasure horse.

National Wildlife Federation
Ph.: 1-800-822-9919
www.nwf.org/includes/2ndlevel
Web site describes this large, member-supported conservation group. Includes educational resources such as Animal Tracks, Campus Ecology, National Wildlife Week, and ordering information for the following magazines: *National Wildlife*, *International Wildlife*, *Ranger Rick*, *Your Back Yard*, and *Wild Animal Baby*.

Species Survival Commission (SSC)
www.iucn.org/themes/ssc/siteindx.htm
Web site describes this volunteer commission of the IUCN, whose mission is to conserve biological diversity through studying and managing species and their habitats.

U.S. Fish and Wildlife Service (FWS)
www.fws.gov
Web site is the official site of the FWS, whose mission is to conserve, protect, and enhance the nation's fish and wildlife and their habitats for the continuing benefit of people. Information can be found on conserving wildlife and habitats including fish, birds, endangered species, and refuges. Information on how to work with others around issues of sports and recreation, landowners, partnerships, and grants is provided. An office directory by state and region is available through this site, as well as information about fishing and other wildlife permits.

Wildlife Conservation Society (WCS)
2300 Southern Boulevard
Bronx, NY 10460
Ph.: 718-220-5100
www.wcs.org
Web site offers information about the organization's conservation activities. Also described are other entities run by the WCS including the Bronx Zoo, the New York Aquarium, and works to save wildlife and wild lands throughout the world. The Bronx Zoo web site features pictures, maps, and details about the largest metropolitan wildlife conservation park in the United States. The New York's Aquarium for Wildlife Conservation's web site features information on fish and marine creatures, including beluga whales, sharks, walruses, and dolphins. Also included under the umbrella of the WCS is the Hornocker Wildlife Institute, which conducts long-term research on threatened species and sensitive ecological systems. The institute site also offers access to specialists in carnivore research.

The Wildlife Society
5410 Grosvenor Lane
Bethesda, MD 20814
Ph.: 301-897-9770
Fax: 301-530-2471
E-mail: tws@wildlife.org
www.wildlife.org/index.html
Web site provides information on research scientists, educators, communications specialists, conservation law enforcement officers, resource managers, administrators, and students from more than sixty countries.

Wildlife Web: Conservation
www.selu.com/bio/wildlife/text/conservation.html
Web site is a directory to conservation sites.

World Wide Fund for Nature (WWF)
www.panda.org/resources/publications
Web site includes access to publications and other resources, including the Living Planet series, featuring information on climate change, endangered seas, forests, species, toxins, and water. The multimedia series includes a photography collection, video library, and a "Just for Kids" section.

—Mary E. Carey

MAGILL'S ENCYCLOPEDIA OF SCIENCE

ANIMAL LIFE

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