rostrum anterior portion or beak region of the skull that is elongated in most cetaceans

sexual dimorphism morphological differences between males and females of a species

ultrasonic high-frequency sounds, beyond the upper range of human hearing

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SPHENISCIFORMES

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What is a Penguin?

Penguins, with their upright stance and dinner-jacket plumage, constitute a distinct and unmistakable order of birds (Sphenisciformes). Granted there are a few embellishments here and there – the odd crest, a black line or two on the chest – but otherwise, penguins conform to a very conservative body plan. The design of penguins is largely constrained by their commitment to an aquatic lifestyle. Penguins have essentially returned to the sea from which their ancestors, and those of all tetrapods, came. In that sense, they share more in common with seals and sea turtles than they do with other birds. Their spindle-shaped bodies and virtually everything about them have evolved in response to the demands of living in water (**Table 1**).

The loss of flight associated with their aquatic makeover is the penguins' most telling modification. While isolated examples of flightlessness can be found in virtually all other groups of waterbirds, penguins are the only group in which all members cannot fly. Among birds generally, they share that distinction only with the ratites (the kiwis, ostriches, emus, and their ilk), where flight has been sacrificed for large size and running speed.

Despite earlier claims to the contrary, it is clear that penguins have evolved from flying birds. The evidence from morphological and molecular studies suggests that penguins are closely related to loons (Gaviiformes), petrels, and albatrosses (Procellariiformes), and at least some families of the Pelicaniformes, most notably frigate-birds. Despite this, the exact nature of the relationship between penguins and these groups remains unresolved: at the moment it would seem to be a dead heat between loons and petrels as to which group is the sister taxon of penguins (**Figure 1**). (On the surface, loons may seem strange candidates to be so closely allied to penguins – penguins are found in the Southern Hemisphere, loons in the Northern Hemisphere; penguins are wing-propelled divers, loons are foot-propelled divers. However, it seems that loons, or their ancestors, were wing-propelled divers in their past.)

If the relationship of penguins to other birds seems confusing and controversial, the relationships among penguins themselves are no less so. Penguins are confined to the Southern Hemisphere and the distribution of fossilized penguin bones discovered to date mirrors their present-day distribution. Fossils have been found in New Zealand, Australia, South America, South Africa, and islands off the Antarctic Peninsula. The oldest confirmed fossil penguins have been described from late Eocene deposits in New Zealand and Australia, dating back some 40 million years. However, fossils from Waipara, New Zealand, unearthed from late Paleocene/early Eocene deposits that are about 50–60 million years

Table 1 Some adaptations of penguins for an aquatic lifestyle

Attribute	*How modified*	*Purpose*
Wings	Shorter, more rigid. Flipper acts as paddle/propeller. Feathers much reduced to decrease resistance	Increase diving capacity. By eliminating flight, the birds no longer need to keep body light.
Body shape	Spindle shape. Very low coefficient of drag	Reduce drag and increase efficiency of swimming. Water is more dense and offers more resistance than does air.
Bones	Nonpneumatic	Unlike flying birds, which have spaces in their bones to make them light (pneumatic), penguins have solid bones to increase strength and density.
Feathers	Short, rigid and interlocking	Feathers trap air beneath them, creating a feather survival suit that provides most of the insulation necessary for a warm-blooded animal to exist in water.
Fat	Subdermal layer of fat	Whereas flying birds cannot afford to carry too much fat, the subdermal layer of fat in penguins contributes a little to their insulation and also enables them to endure long periods of fasting on land necessary for incubation and molting.
Coloration	Dark back, light belly	To aid concealment in the open ocean, like many pelagic predators, penguins have a dark back, so that they merge with the bottom when viewed from above, and a light belly, so that they merge with the surface when viewed from below.
Legs	Placed farther back. Very short tarsometatarsus. Upright stance on land	To reduce drag in water. Feet act as rudder.
Eyesight	Variable	The eye is able to be altered to accommodate refractive differences when moving between water and land.
Circulation	Countercurrent blood system	Allows penguins to reduce heat loss in the water or very cold environments, while aiding heat dissipation when hot.

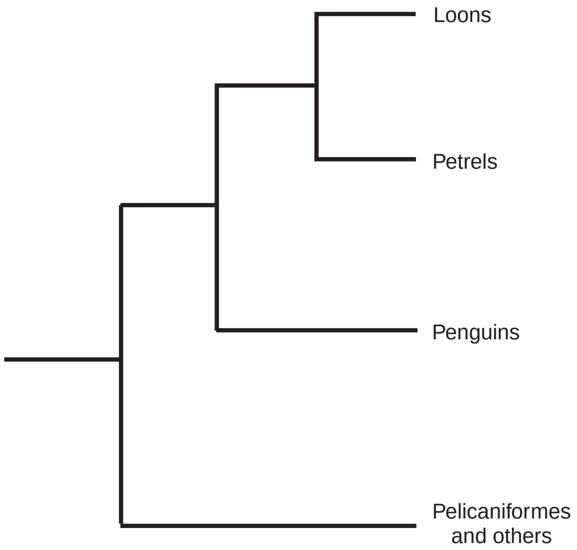

Figure 1 Nearest living relatives of penguins (adapted from Davis and Renner (in prep.)).

old, represent possibly the earliest penguin remains. These have still to be described fully, but they show a mixture of attributes from flying birds and those of penguins (the bones are heavy and nonpneumatic; the wing bones are flattened in a way that is consistent with being a wing-propelled diver). The Waipara fossils may very well be near the base of the penguin radiation, when the transition was being made from flyer to swimmer. In any case, by 40 million years ago, penguins were already very specialized, in much the same way as modern penguins, for underwater swimming.

Diving versus Flying

There is a trade-off between diving performance and flying. Even so, it would be wrong to conclude that flying birds, as a matter of course, cannot dive well; that somehow the riches that the sea has to offer are denied to them much beyond the surface. The truth is that some flying birds – for example, the diving-petrels and, especially, the alcids (auks, auklets, and murres) – can literally fly underwater as well as above. Although they are not closely related to penguins, auks are often considered to be the Northern Hemisphere's ecological equivalent of penguins, and in proportion to their size, auks can dive as deeply as many penguins. Nevertheless, the requirements for efficient flight – light bodies and flexible wings with a large surface area/small wing loadings – are not the same as those needed for diving efficiency – large, heavy bodies and stiff, powerful wings. Wingloadings are a measure of the body mass of the animal relative to the surface area of the wing. They give an indication of the lift that can be provided by the wing. If the linear measurements of a bird were simply scaled up, because body mass is a function of volume, the loading on the wing would become greater. This means that, to generate the same lift, larger birds must have wings with a disproportionately larger surface area.

Birds with relatively light bodies expend energy simply counteracting the buoyancy of their bodies in water. The time a bird can stay underwater and the depth to which it can travel are physiologically related to the size of the bird, providing another advantage to large birds. But as body mass increases, the surface area of wings needs to increase to a much greater extent just to maintain the same lift. There appears to be a cut-off point at about 1 kg beyond which it is not possible to both dive and fly efficiently. Indeed, auks that exceeded this size threshold, such as the extinct great auk, were flightless like penguins.

Logically, then, it seems that the transition from flighted to flightless would have taken place in birds around the 1 kg threshold, which is roughly the size of today's little penguins (*Eudyptula minor*) and consistent with the size of the smallest fossil penguins. However, once penguins were freed of the need to balance the requirements of flight with the requirements for underwater diving, they radiated rapidly and were able to attain much greater sizes. Many fossil penguins were larger than living penguins, with the tallest being up to 1.7 m and well over 100 kg.

Living Penguins

The species living today represent but a small remnant of the penguin diversity from times past. Exactly how modern penguins relate to the fossil penguins is not at all clear, as most of the extant (living) genera show up in the fossil record only relatively recently (within the last 3 million years or so). While there is argument about the precise number of species living today (most authorities list between 16 and 18 species), there is agreement that the extant penguins fall into six distinct genera (**Table 2**).

Sphensicus

In contrast to the popular misconception that penguins are creatures of the snow and ice, representatives of the *Spheniscus* penguins breed in tropical to temperate waters, with one species, the Galapagos penguin (*S. mendiculus*), breeding right on the equator.

There are four species: the African (*S. demersus*), Humboldt (*S. humboldti*) and Magellanic penguins (*S. magellanicus*), in addition to the Galapagos penguin. They were the first penguins to be discovered by Europeans. After Vasco de Gama's ships sailed around the Cape of Good Hope in 1497, they encountered African penguins in Mossel Bay, South Africa. However, the account of this discovery was not published until 1838 and the first announcement to the world at large concerning penguins was to come from another famous voyage, that of Magellan's circumnavigation of the globe (1519–1522). A passenger, Pigafetta, described in his diary a great number of flightless 'geese' seen on two islands near Punta Tombo, Argentina, home to a large concentration of Magellanic penguins.

The *Spheniscus* penguins are characterized by black lines on their chests and distinct black and white bands on their faces (as a consequence, they are sometimes referred to as the 'ringed' or 'banded' penguins) (**Figure 2**). Their faces are also distinguished by having patches of bare pink skin, which help to radiate heat. Warm-blooded animals like penguins and seals must be well insulated if they are to maintain a constant body temperature when in the water, because the sea acts as a huge heat sink; but this creates problems of overheating for penguins when ashore, especially in the hot climates that the *Spheniscus* penguins inhabit. For this reason, all these species nest in burrows or, where available, in caves, in clefts in rocks, or under vegetation.

Penguins, with their limited foraging range due to their being flightless, require a consistent and good food supply near to their breeding areas. Tropical waters are typically not very productive and are unable to support the dense swarms of fish or krill on which penguins depend. This has probably acted as a barrier, restricting penguins to the Southern Hemisphere. The *Spheniscus* penguins are able to breed as far north as they do because of wind-driven upwelling of nutrient-rich water and because the cold-water Benguela and Humboldt Currents, which run up the sides of southern Africa and South America, bring nutrient-rich waters from farther south. *Spheniscus* penguins feed mainly on small pelagic schooling fish such as sprats and anchovies. The top mandible is hooked at its far end, which helps the penguin to catch and hold fish.

With the exception of the Magellanic penguin, which is at the southern extreme of their range, the *Spheniscus* penguins are inshore foragers making

Table 2 Species of living penguins[a]

Species	*Scientific name*	*Principal location*	*Latitude* (°S)	*Body mass* (kg)	*Foraging type*	*Migratory*	*Nest type*	*Diet*
Galapagos	*Spheniscus mendiculus*	Galapagos	0	2.1 (M), 1.7 (F)	**□**	**□**	**□**	**□**
Humboldt	*Spheniscus humboldti*	Peru, Chile	5–42	4.9 (M), 4.5 (F)	**□**	**□**	**□**	**□**
African	*Spheniscus demersus*	South Africa	24–35	3.3 (M), 3.0 (F)	**□**	**□**	**□**	**□**
Magellanic	*Spheniscus magellanicus*	Argentina, Chile, Falklands Is.	29–54	4.9 (M), 4.6 (F)	■	■	**□**	**□**
Little	*Eudyptula minor*	Australia, New Zealand	32–47	1.2 (M), 1.0 (F)	□	□	**□**	□
Yellow-eyed	*Megadyptes antipodes*	New Zealand, Auckland Is.	46–53	5.5 (M), 5.1 (F)	**□**	**□**	□	□
Fiordland	*Eudyptes pachyrhynchus*	New Zealand	44–47	4.1 (M), 3.7 (F)	■	■	□	□
Snares	*Eudyptes robustus*	Snares Islands	48	3.3 (M), 2.8 (F)	■	■	■	□
Erect-crested	*Eudyptes sclateri*	Antipodes Is., Bounty Is.	47–49	6.4 (M), 5.4 (F)	■	■	■	□
Rockhopper	*Eudyptes chrysocome*	Subantarctic	37–53	2.5 (M), 2.3 (F)	■	■	■	□
Macaroni/ Royal	*Eudyptes chrysolophus*	Subantarctic	46–65	5.2 (M), 5.3 (F)	■	■	■	□
Gentoo	*Pygoscelis papua*	Subantarctic, Antarctic	46–65	5.6 (M), 5.1 (F)	**□**	□	■	■
Chinstrap	*Pygoscelis antarctica*	Antarctic	54–69	5.0 (M), 4.8 (F)	■	■	■	■
Adelie	*Pygoscelis adeliae*	Antarctic	54–77	5.4 (M), 4.8 (F)	■	■	■	■
King	*Aptenodytes patagonicus*	Subantarctic	45–55	16.0 (M), 14.3 (F)	■	■	■	**□**
Emperor	*Aptenodytes forsteri*	Antarctic	66–78	36.7 (M), 28.4 (F)	■	■	■	□
				Key				
				□	inshore	resident	burrow	fish
				□	either	either	forest	fish, cephalopods, crustaceans
				■	offshore	migratory	open	crustaceans

[a]M, Male; F, Female.

foraging trips of relatively short duration (1–2 days) throughout the breeding period. They lay two similar-sized eggs. Breeding can occur in all months of the year (African and Galapagos), at two peak times (Humboldt), or just once (Magellanic): a pattern that roughly corresponds with the more pronounced seasonality the farther south they breed.

Eudyptula

Little penguins (*Eudyptula minor*) are the smallest living penguins and are found only in Australia (often called fairy penguins) and New Zealand (often called little blue or blue penguins). While most authorities recognize only the single species, whether this really is a monotypic genus is a matter of debate. Six subspecies have been described and it has been suggested in some quarters that at least one of these, the white-flippered penguin (*E. m. albosignata*), is deserving of separate species status in its own right. However, the latter freely hybridize with other subspecies and analyses of isozymes and DNA do not support such a conclusion at this stage. More extensive genetic studies of this genus are warranted.

Apart from their small size, little penguins are characterized by being nocturnal (coming ashore after dark) and nesting in burrows, although they will breed in caves or under suitable vegetation in some locations. Morphologically they are quite similar to *Spheniscus* penguins and also feed on small schooling fish. The plumage of all penguins conforms to the dark top and white undersides common to pelagic marine predators, but in little

Figure 2 Magellanic penguins. (Photograph: L.S. Davis).

Figure 3 Little penguin chick, almost ready to fledge, begging for a meal from its parent. (Photograph: M. Renner.)

penguins the plumage on the backs has more of a blue hue compared to the blackish coloration of other penguins (**Figure 3**).

Patterns of breeding are very variable throughout their range in both the duration of the breeding period and the number of clutches per year (either one or two). Little penguins lay clutches of two similarly-sized eggs.

Typically they are described as inshore foragers (with foraging trips lasting 1–2 days), but there is evidence of plasticity in their feeding strategies. In some locations or in years of poor food supply, they may feed considerably farther offshore, with a concomitant increase in the duration of their foraging trips (up to 7 days or more).

Figure 4 Yellow-eyed penguin on nest. (Photograph: J. Darby.)

Megadyptes

The representative of another monotypic genus, the yellow-eyed penguin (*Megadyptes antipodes*), is often touted as the world's rarest penguin. (The Galapagos penguin may well be rarer, and the Fiordland penguin is not much better off.) It breeds on the south-east coast of New Zealand and the sub-Antarctic Auckland Islands. The yellow-eyed is a medium-sized penguin, distinguished by having pale yellow eyes and a yellow band of plumage that runs around the back of its head from its eyes (**Figure 4**). But perhaps its most unique characteristic is a behavioral one: it nests under dense vegetation and typically nests are visually isolated from each other. Whether this visual isolation is an absolute requirement or simply a consequence of their need for dense cover to escape the sun's heat, there is little doubt that yellow-eyed penguins are among the least overtly social of the penguins. Although they nest in loose colonies, individual nests can be from a few meters to several hundred meters apart. Perhaps partly as a consequence of this, mate fidelity is higher than in the cheek-by-bill colonies of other species where opportunities for mate switching and extra-pair copulations are rife.

Another factor contributing to the apparent faithfulness of yellow-eyed penguins is that adults remain more-or-less resident at the breeding site throughout the year, even though breeding occurs only between September to February. They are inshore foragers, feeding mainly on fish and cephalopods, and typically foraging trips are from 1 to 2 days during both incubation and chick rearing. The clutch consists of two equal-sized eggs and there appears to be little in the way of evolved mechanisms for brood reduction: if both chicks hatch, they have an equally good chance of fledging.

Eudyptes

In contrast, the members of the genus *Eudytptes*, which is closely related to *Megadyptes* and may have been derived from ancestors that were very like the yellow-eyed penguin, are famous for their obligate brood reduction (i.e., they lay two eggs but only ever fledge one chick). Collectively, the six Eudyptid species are known as the crested penguins. They are distinguished by plumes of yellow or orange feathers, of varying length, that arise above their eyes like out-of-control eyebrows (**Figure 5**).

For the most part, they are penguins of the sub-Antarctic, although Fiordland penguins (*Eudyptes pachyrhychus*) breed on the south-west corner of New Zealand (though some would argue that conditions there are not too dissimilar from the sub-Antarctic, especially as the Fiordland penguin breeds during winter). Other crested penguins also have quite restricted distributions: the Snares penguin (*E. robustus*) breeds only on the Snares Islands south of New Zealand; the erect-crested penguin (*E. sclateri*) breeds on the Bounty and Antipodes Islands, also near New Zealand; and the royal penguin (*E. schlegeli*) breeds only on Macquarie Island. However, there is a considerable body of evidence and opinion that argues that the royal penguin is really only a pale-faced subspecies of the more ubiquitously distributed macaroni penguin (*E. chrysolophus*). The rockhopper penguin (*E. chrysocome*), the smallest of the crested species, has a circumpolar distribution, but there are three recognized subspecies and preliminary analysis of DNA would suggest that they are at least as distinct as royal penguins are from macaroni penguins.

All the crested penguins are migratory, spending two-thirds of the year at sea (their whereabouts during this period are largely unknown) and, with the exception of the Fiordland penguin, returning to their breeding grounds in spring. Despite laying a single clutch of two eggs, they only ever fledge one chick. Moreover, the eggs are of dramatically different sizes, with the egg laid second being substantially bigger than that laid first (this form of egg-size dimorphism is unique among birds). In those species with the most extreme egg-size dimorphism (erect-crested, royal/macaroni), the second egg can be double the size of the first egg (**Figure 6**). Furthermore, although the laying interval between the first and second eggs is the longest recorded for penguins (4–7 days), the chick from the large second-laid egg usually hatches first.

Figure 5 Erect-crested penguins. (Photograph: L.S. Davis.)

Figure 6 Extreme egg-size dimorphism in erect-crested penguin eggs. (Photoraph: L.S. Davis.)

The evolutionary reasons for this bizarre breeding pattern have long been matters of debate and, it is fair to say, have yet to be determined satisfactorily. Crested penguins are probably unable adequately to feed two chicks. They are all offshore foragers (feeding on a mixture of fish, cephalopods, and swarming crustaceans). The logistics of provisioning chicks from a distant food source probably make it too difficult to bring back enough food to fledge two chicks; but this idea has not been tested properly yet. While in some species it can be argued that the small first egg provides a measure of insurance for the parents in case the second egg is lost (or the chick from the second-laid egg dies), this cannot be a universal explanation. Studies of erect-crested and royal penguins have found that first-laid eggs are usually lost before or on the day the second egg is laid and it has even been suggested that the parents may actively eject the first eggs. While the evidence for egg ejection must be viewed as equivocal, first eggs cannot provide much of an insurance policy in these species. In any case, none of this explains why it is the first egg that is the smallest and that usually does not produce a chick.

For penguins breeding in higher latitudes, overheating when on land is less of a problem, permitting them to breed in colonies in the open. Some, like macaroni penguins, form vast colonies, while Fiordland penguins nest in small colonies in forest or caves.

Pygoscelis

The three members of this genus are the classic dinner-jacketed penguins of cartoons. They all breed in the Antarctic to varying degrees. The gentoo penguin (*P. papua*) consists of two subspecies, one of which breeds on the Antarctic Peninsula and associated islands (*P. p. ellsworthii*) and the other (*P. p. papua*) on several sub-Antarctic islands. Chinstrap penguins (*P. antarctica*) breed below the Antarctic Convergence, mainly on the Antarctic Peninsula, but also on a few sub-Antarctic islands. The Adélie penguin (*P. adeliae*), with very few exceptions (Bouvetoya Island), breeds only on the Antarctic continent and its offshore islands.

The three species are medium-sized penguins with white undersides and black backs. They differ most obviously in the markings on their faces. Adélie penguins have black faces and throats, and prominent white eye-rings. The proximal ends of the mandibles are covered by feathers, giving the impression that the bill is short (**Figure 7**). Gentoo penguins also have black faces and white eye-rings, but have white patches above the eyes and a bright orange-red bill. Chinstrap penguins have white faces with a black crown, and a black line running under the chin, from ear-to-ear, producing the effect from which they derive their name.

All three species breed in colonies in the open and nest just once per year during the austral summer. A clutch of two eggs is laid, with the first slightly larger than the second. The northern subspecies of gentoo penguins (*P. p. papua*) lay their eggs in nests made from vegetation. They are inshore foragers and remain resident at the breeding site throughout most of the year. They nest in colonies, but the location of these colonies can shift from season to season as the area becomes soiled. Despite this, mate fidelity is high. In contrast, the other Pygoscelid penguins are migratory, make their nests out of stones, and the nest sites are more permanent. Chinstrap and Adélies are offshore foragers, with foraging trips commonly lasting two or more weeks during incubation. All the Pygoscelid penguins feed on a type of swarming crustacean known as krill (*Euphausia* spp.).

Aptenodytes

This genus is comprised of the two largest of the living penguins: emperor (*A. forsteri*) and king (*A. patagonicus*). Apart from their large size, these species are distinguished by their bright yellow (emperor) or orange (king) auricular patches and the fact that they lay a single large egg. Both are offshore foragers, and it seems unlikely that they could possibly bring back enough food to successfully rear two of their very large chicks (**Figure 8**). Each of them has a truly remarkable pattern of breeding.

Emperor penguins are notable for breeding during the heart of the Antarctic winter. They breed on ice in dense colonies: there are no nests, the single egg (or small chick) is carried upon the parent's feet. The male incubates the egg entirely by himself, while the female goes off to feed for about 2 months. Together with the period they are at the colony during courtship, that means the males go without food for up to 3.5 months. Emperor penguins feed on fish, cephalopods, or crustaceans, with the relative importance of each varying according to the location or time. To help reduce heat loss during the Antarctic winter, the penguins stand in a tight huddle.

In some ways the breeding of king penguins is even more remarkable. It takes them over a year

Figure 7 Adélie penguin with chick. (Photograph: L.S. Davis.)

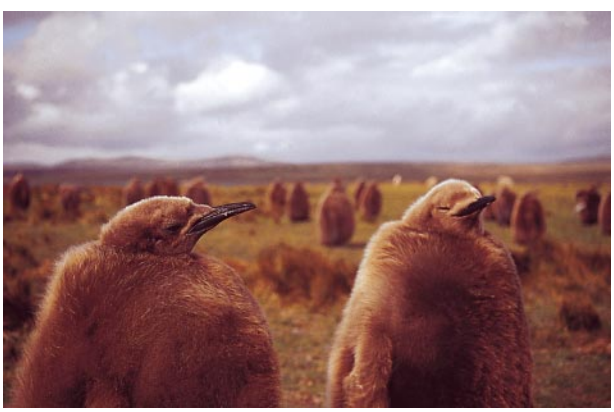

Figure 8 King penguin chicks on the Falkland Islands. (Photograph: L.S. Davis.)

(14–16 months) to provide enough food for their chicks to reach a sufficient size to fledge. As a consequence, king penguins can breed only twice every three years. During the winter months the parents must forage at great distances and the chicks are left to fast, sometimes for as long as 5 months! In anyone's book, that is a long time between dinners. The king penguin breeds on sub-Antarctic islands. It does not build a nest, carrying the large single egg on its feet like an emperor penguin, but it does defend a territory within the colony. Some colonies can be enormous, with 100 000 or more birds. Mate fidelity is low in both king and emperor species. During incubation, foraging trips can last 2 weeks or more. They feed largely on Myctophid fish.

Life in the Sea

Tests using life-size plastic models of penguin bodies have shown that they have lower coefficients of drag than those for any cars or planes that scientists and engineers have been able to manufacture. When swimming, penguins move their flippers to generate vortex-based lift forces, in essence creating a form of underwater jet propulsion. The usual underwater traveling speed of most penguins is around $2\,\mathrm{m\,s^{-1}}$. However, penguins are capable of high-speed movements known as 'porpoising', whereby they clear the water surface to breathe. Porpoising speeds can be $3\,\mathrm{m\,s^{-1}}$ or higher. The speed at which a penguin must be traveling to porpoise is related to its body size, and it is likely that for large penguins, like emperor and king penguins, porpoising requires just too much effort. All smaller penguins use porpoising to escape from predators. Porpoising is energetically expensive compared to underwater swimming and, consequently, inshore foraging penguins tend not to use porpoising simply for traveling to and from their foraging areas. For offshore foragers, however, the time savings gained from porpoising may outweigh the energetic costs, and it seems likely that porpoising may sometimes, at least, be used in these species as an expedient means of travel and not just an escape reaction.

Maximum dive depth and duration are correlated with body mass. Emperor penguins have been recorded diving to over 500 m and all but little penguins are readily capable of diving to depths of 100 m or more. Even so, most foraging takes place at much shallower depths: penguins are visual predators and so light levels in the water column will limit their effectiveness as hunters (albeit bioluminescent prey, such as squid, enable some penguins to hunt at very low light levels, either at night or at great depth). The prey of penguins tends to vary with latitude and phylogenetic grouping (**Table 2**).

A Life in Two Worlds

An important determinant of the breeding success of penguins is how they manage to balance the time at sea needed for foraging against the time required ashore for breeding and molting. Nesting duties are shared, and the male and female of a pair take alternating turns being in attendance at the nest or at sea foraging. The foraging penguin needs to find enough food to sustain itself, to cover the costs of getting the food and, once chicks hatch, to ensure the growth of its chicks. However, if it spends too long at sea either the partner on the nest might desert or, if the chicks have hatched, the chicks might starve to death.

For inshore foragers, which make short and frequent trips to sea, the risks of desertion and starvation are not as acute as for those that need to forage farther afield. All adult penguins are capable of enduring relatively long periods of fasting, yet there are finite limits to how long an incubating bird can live off its fat reserves (e.g., male Adelie penguins arriving at the colony at the start of the breeding season will endure just over a month without food). For many offshore foragers, foraging trips during the incubation period tend to be from 10 to 20 days (albeit female emperor penguins are away for about 2 months). The situation changes dramatically once the chicks hatch, as chicks of all species need to be fed frequently, requiring that foraging trips be relatively short during at least the early stages of chick rearing. For offshore foragers that take long foraging trips during incubation, this creates a dilemma: they must switch over to short foraging trips by the time the chicks hatch or risk losing them to starvation. There is a growing body of evidence that indicates that penguins have an internal mechanism that measures the duration of the incubation period, precipitating the early return of a foraging bird if its chicks are about to hatch. The remnants of the yolk sac provide a little insurance against a tardy parent by permitting penguin chicks to survive about 3–6 days without being fed from the time they first hatch. In the case of the emperor penguin – in which the male undertakes all the incubation – if the female has not returned by the time the chick hatches, the male is able to feed it an oesophageal 'milk' made from breaking down his own tissues even though he has not eaten himself for over 3 months.

In contrast to flying birds, which cannot afford to store much fat because of the weight, the ability of penguins to store enough fat to withstand long fasts is important not only when breeding but also when molting. Although a small amount of their insulation is provided by the subdermal layer of fat, most insulation comes from the feathers. But feathers wear and, to provide an effective barrier against heat-stealing waters, they must be renewed to maintain their integrity. This is an energetically expensive process, whereby a new suit of feathers is grown beneath the old one. During this process, which can take 2 or 3 weeks, the birds typically remain on land and are unable to eat.

Threats and Conservation

Desertions and starvations can be major causes of breeding failure for some species of penguins and the likelihood of these occurring will be exacerbated by anything that increases the time penguins must spend foraging. This makes penguins especially vulnerable to perturbations in the marine environment. Threats to penguins come from anything that reduces their food supply (causing a concomitant increase foraging times), such as commercial fisheries or pollution.

The major threat facing penguins may be from global warming. Warmer water associated with ENSO (El Niño Southern Oscillation) events can reduce the amount of upwelling of nutrients and seriously affect the availability of prey in various areas. ENSO events can be especially critical for nonmigratory species like Galapagos and yellow-eyed penguins, which rely on a persistent and steady food supply in a localized area. Breeding dates of little penguins throughout Australia and New Zealand are correlated with sea surface temperatures, with laying commencing later and fewer birds attempting to breed or being successful when water temperatures are warmer.

The commitment penguins made to the sea by becoming flightless has made them doubly vulnerable. Not only are they at risk from factors affecting their food supply, but their lack of agility on land makes them potentially easy targets for predators. It is for this reason that flightlessness in water birds has usually evolved on offshore islands or isolated places relatively free of predators. However, humans have managed to undo much of that by introducing exotic predators to many areas where penguins breed. Mustelids, rats, and feral cats have had serious impacts upon penguins when they have been introduced to places like New Zealand, South Africa, and the sub-Antarctic islands. During the nineteenth and early twentieth centuries, humans were often significant predators themselves, killing adult penguins for their oil and their skins and taking eggs for food. It has been estimated that in one area alone, over 13 million eggs were harvested from African penguins during a 30-year period. Humans also have an impact on penguins by reducing the availability of suitable habitat through harvesting guano (this is especially so of African and Humboldt Penguins in South Africa and South America, respectively) or deforestation. The latter dramatically reduced the numbers of yellow-eyed penguins breeding on mainland New Zealand: this trend has been reversed in recent years by extensive replantings.

Until fairly recently, the species inhabiting the Subantarctic and Antarctic have been able to rely on their isolation for protection. However, as humans reach ever more into these nether regions of the planet, they are no longer immune to the threats from overfishing, pollution, disturbance from tourists, introduced predators, and introduced diseases. On a positive note, however, the design of penguins has enabled them to survive, if not flourish, for over 40 million years. They have been through periods of vast climatic change in the earth's history. While they have had to conform to a design shaped by the requirements of living in water, paradoxically, this has given them a great deal of versatility with respect to the environments they can exploit on land. They are the only 100-degree birds: the only birds capable of breeding at temperatures from $-60°C$ (midwinter in the Antarctic) to $+40°C$ (midsummer in Peru). It is to be hoped that these qualities will serve them well for the next 40 million years.

See also

El Niño Southern Oscillation (ENSO). El Niño Southern Oscillation (ENSO) Models. Seabird Conservation. Seabird Foraging Ecology. Seabird Population Dynamics.

Further Reading

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