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Enhydra lutris. By James A. Estes

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Enhydra Fleming, 1822

Enhydra Fleming, 1822:187. Type species *Mustela lutris* Linnaeus, 1758.

Pusa Oken, 1816:985. Type species *Pusa orientalis* Oken. Oken's names not available, by ruling of International Commission on Zoological Nomenclature.

Latax Gloger, 1827:511. Type species *Mustela lutris* Linnaeus. Replacement name for *Enhydra.*

Enydris Fischer, 1829:288, an emendation of *Enhydra* Fleming.

CONTEXT AND CONTENT. Order Carnivora, Family Mustelidae, Subfamily Lutrinae. G. B. Corbet (1978), following Pocock (1921) allocated *Enhydra* to a separate subfamily—the Enhydrinae. The genus *Enhydra* contains one extant species, *Enhydra lutris,* as treated below.

Enhydra lutris (Linnaeus, 1758)
Sea Otter

Mustela lutris Linnaeus, 1758:45. Type locality Kamchatka, USSR.

Lutra gracilis Bechstein, 1800:408. Type locality "Stattenland" (=southernmost of the Kuril Islands).

Pusa orientalis Oken, 1816:986. Oken's names are not available.

Lutra stelleri Lesson, 1827:156. Type locality Kamchatka, USSR.

CONTEXT AND CONTENT. Context noted above. Three subspecies are currently recognized. Roest (1973) suggested that *E. l. lutris* and *E. l. nereis* be synonymized, but Davis and Lidicker (1975) disagreed.

E. l. lutris (Linnaeus, 1758:45), see above.

E. l. nereis (Merriam, 1904:159). Type locality San Miguel Island, Santa Barbara Islands, California.

E. l. gracilis (Bechstein, 1800:408), see above.

DIAGNOSIS. The following diagnosis applies to both genus and species. The sea otter is the largest species in the Mustelidae; adult males attain weights of 45 kg (100 lbs) and total lengths of 148 cm (58 inches). Adult females attain weights of 32.5 kg (72 lbs) and total lengths of 140 cm (55 inches) (Kenyon, 1969). Adult dental formula is i 3/2, c 1/1, p 3/3, m 1/2, total 32. *Enhydra lutris* is the only species of fissiped carnivore with two pairs of lower incisors. All other species in the Lutrinae have three incisors on each lower jaw and 34 (*Amblyonyx cinerea*) or 36 (all remaining species) teeth. Molars are broad and flat with no cutting surfaces. The upper molars are large and quadrate with massive, rounded crowns, and medial tubercular portions expanded anteroposteriorly (Blair et al., 1957). Posteriorly oriented hind limbs are elongate and flipper-like (Murie, 1959); the tarsals and metatarsals are flattened. Digits on the hind limbs increase in length from the first to the fifth; forepaws are mitten-like and have retractile claws. The tail is less than one-third the body length, somewhat flattened dorsoventrally, and of similar thickness from base to tip. The fur is dense and glossy and contains 100,000 or more hairs/cm^2 (Kenyon, 1969). The teres ligament is absent (Taylor, 1914).

GENERAL CHARACTERS. The head is large and blunt; the neck short and thick (Bisaillon et al., 1976); and front limbs short (Fig. 1). Males average 34% heavier and 8% longer than females, and the head and neck of males are comparatively more robust. The only definitive characters by which the sexes may be distinguished in the field are the presence of a penial bulge in males and two abdominal mammae in females (Barabash-Nikiforov, 1947; Kenyon, 1969).

Pelage color varies from dark brown to reddish brown. Pelage consists of sparse guard hairs and a dense, soft underfur. Old individuals often become grizzled, with the head, neck, and shoulders taking on a paler color than the remainder of the body. The skin is loose and moves easily about the body (Lekh, 1907); a particularly loose flap of skin under each forelimb is used to hold and transport food. The body is entirely furred except for the rhinarium, inside the ear pinnae, the palmar surface of the forefoot, and small patches on the plantar surface of each digit of the hindlimbs. Fur covering the hindfeet is comparatively short and sparse.

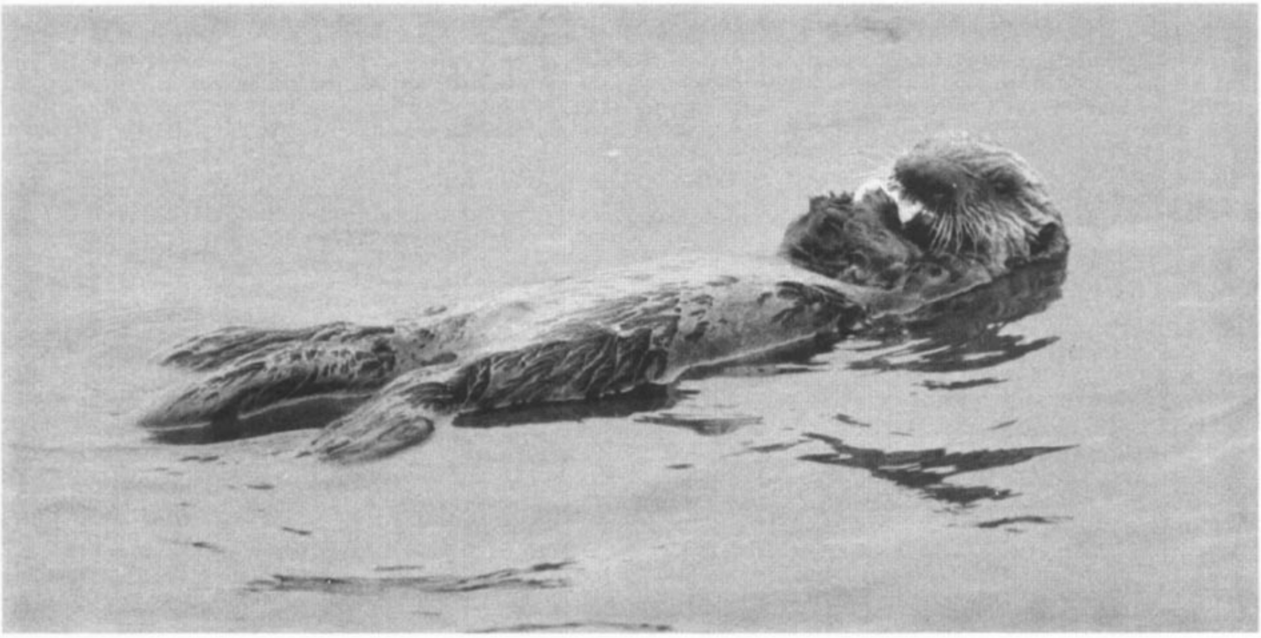

FIGURE 1. A sea otter consuming food. Only the surface of the fur is wetted. Photograph by James A. Mattison.

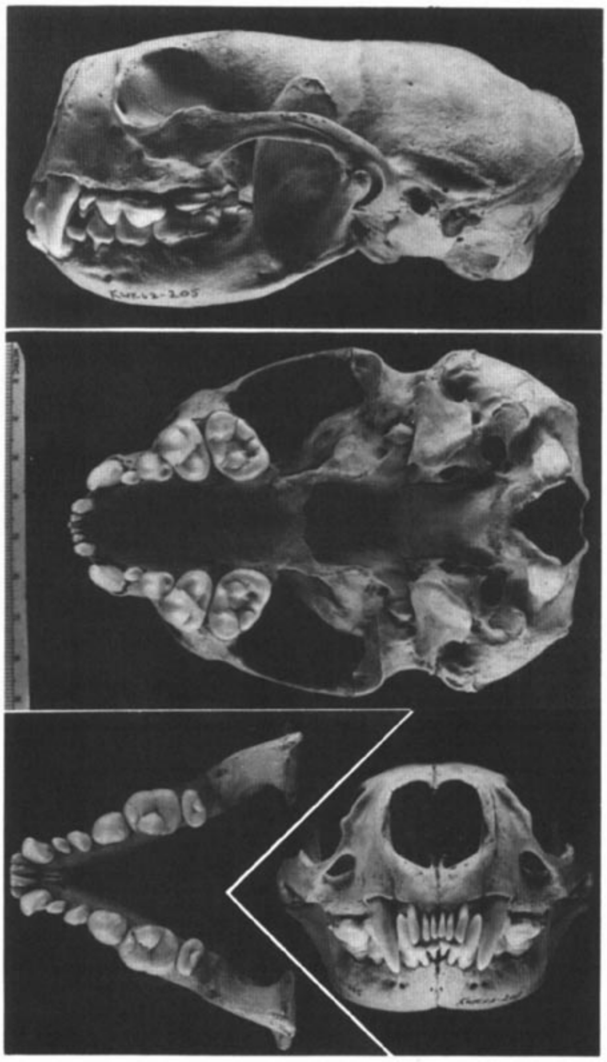

FIGURE 2. Skull of *Enhydra lutris* in lateral, ventral, and anterior views, and lower jaw in occlusal view. Photographs by Karl W. Kenyon.

In some individuals the left side of the cranium is slightly larger than the right, creating bilateral asymmetry of the skull in the form of a bend in the sagittal crest behind the interorbital constriction. There is a gap between the upper outer incisors and canines into which the lower canines fit when the jaw is closed (Fig. 2). Malocclusion is common (Kenyon, 1969). The skeleton often is purple due to polyhydroxynaphthoquinone ingested from sea urchin tests (Fox, 1953).

Ranges of external body measurements of adults from Scheffer (1951) and Kenyon (1969) are as follows: total length, males 126 to 145 cm, females 107 to 140 cm; weight, males 21.8 to 44.9 kg, females 14.5 to 32.7 kg. Kenyon (1969) reported that the average weights of adult males and females are, respectively, 28 and 16% greater in sparse than in crowded populations. Range of condylobasal length of skull is 125 to 144 mm in adult males and 115 to 136 mm in adult females (Roest, 1973). Barabash-Nikiforov (1947) and Ognev (1931) presented other skull and body measurements.

DISTRIBUTION. The original distribution was from 27°32′N on the Pacific coast of Baja California (Ogden, 1941), northward along the Pacific coast of North America to Prince William Sound, southwestward along the Alaska Peninsula and through the Aleutian, Pribilof, and Commander islands to Kamchatka, and south through the Kuril Islands to Sakhalin and Hokkaido (Fig. 3). The longest gap in the original distribution was 300 km between the Near and Commander islands (Lensink, 1960). Abundance was greatly reduced by human exploitation. Between 1751 and 1911 the distribution was reduced to 13 known remnant populations: two in the Kuril Islands and Kamchatka; one in the Commander Islands; five in the Aleutian Islands and along the Alaska Peninsula; and one each at Kodiak Island, Prince William Sound, the Queen Charlotte Islands, central California, and San Benito Islands. Several of these subsequently declined to extinction (Kenyon, 1969). A history of the populations and a thorough review of distributional records prior to 1968 are given by Kenyon (1969). Today much of the original range is occupied from the Kuril Islands, across the north Pacific to Prince William Sound; they are largely absent to the southeast of Prince William Sound. Translocations have reestablished sea otters at Chichagof and Baranof islands, southeast Alaska (Jameson et al., 1978), and Vancouver Island (Bigg and MacAskie, 1978); other translocated populations are probably declining (the coasts of Washington and Oregon) or extinct (Pribilof Islands and Near Islands, Aleutian archipelago).

Sizes of these populations are not precisely known. Presently, there probably are at least 100,000 sea otters from Prince William Sound, west through the Kuril Islands; 500 to 1000 in southeast Alaska (A. M. Johnson, pers. comm.); about 100 at Vancouver Island (Bigg and MacAskie, 1978); less than 50 in Washington and Oregon (R. J. Jameson, A. M. Johnson, and K. W. Kenyon, in litt.); and about 2000 in California (J. A. Ames, pers. comm.).

Sea ice limits the northern permanent range (Nikolaev, 1965; Schneider and Faro, 1975) which Gribkov (1963) and Kenyon (1969) believed is about 57°N. Individuals sighted in the northern Bering Sea (Lensink, 1960) and Arctic Ocean (Bee and Hall, 1956) may have drifted north on currents or retreating ice (Kenyon, 1969). The northernmost substantiated record is from Chaun Bay (70°N, 170°E) in the East Siberian Sea (Zimushko et al., 1968). Factors limiting permanent range to the south are unknown although on the Pacific coast the southern limit coincides with the 20 to 22°C isotherm, which also is about the southern limit of cool water upwelling and distribution of giant kelp (*Macrocystis*). Sea otters from central California occasionally wander south of Point Conception and into northern Baja California, Mexico (Leatherwood et al., 1978).

FOSSIL RECORD. Fossil remains of *Enhydra* are known from the eastern North Pacific: the earliest record is early Pleistocene (Leffler, 1964; Mitchell, 1966; Repenning, 1976). One extinct species, *Enhydra macrodonta* Kilmer (1972), is known from the late Pleistocene in California. Two lineages of *Enhydriodon* are suggested by Repenning (1976). One (from the Old World Miocene) gave rise to *Enhydriodon sivalensis*, which is known from the late Pliocene in India. The other branch (from the Old World Pliocene) apparently led to *Enhydriodon reevei* in the early Pleistocene of the North Atlantic, and to *Enhydra* in the North Pacific. *Enhydra* probably was confined subsequently to the North Pacific by the barriers of sea ice to the north and warm water to the south.

The different arrangements of gyri in the forelimb cortical projection area of the brain suggest that *Enhydriodon* evolved independently from aonychoid otters (Radinsky, 1968) for at least as long as their known fossil records. Repenning (1976) suggested that *Enhydriodon* and the aonychoid otters represent two separate derivations of crab-eating otters from earlier fish-eating forms.

FORM. Hairs are pale gray at their bases and are dark distally, varying from pale buff to nearly black. Guard hairs and underfur are slightly longer on the dorsum than on the venter (Barabash-Nikiforov, 1947). The absence of arrector pili permits the hairs to lie flat when wetted (Ling, 1970). A single guard hair associated with about 70 underfur hairs, a sweat gland, and two sebaceous glands that join on the anterior side of the guard hair comprise the pelage unit. Hair density and length decrease from mid-back to the hind foot (Tarasoff, 1972). Molting occurs throughout the year, although maximum follicular activity is during spring (Ognev, 1931; Kenyon, 1969). Fur density is lower in summer than winter (Barabash-Nikiforov, 1947). There are mystacial, superciliary, and nasal sensory vibrissae (Kenyon, 1969). There is little subcutaneous fat. Anal scent glands are absent (Tarasoff et al., 1972). The ear pinnae, when diving, fold back and close (Pocock, 1928).

High fat and low lactose content of milk, and a high fat/protein ratio, resemble these values in the milk of cetaceans and pinnipeds more than in the milk of terrestrial mustelids (Jenness and Williams, 1979).

Some myological and osteological characters are intermediate between those of *Lutra* and phocid seals (Tarasoff, 1972). The

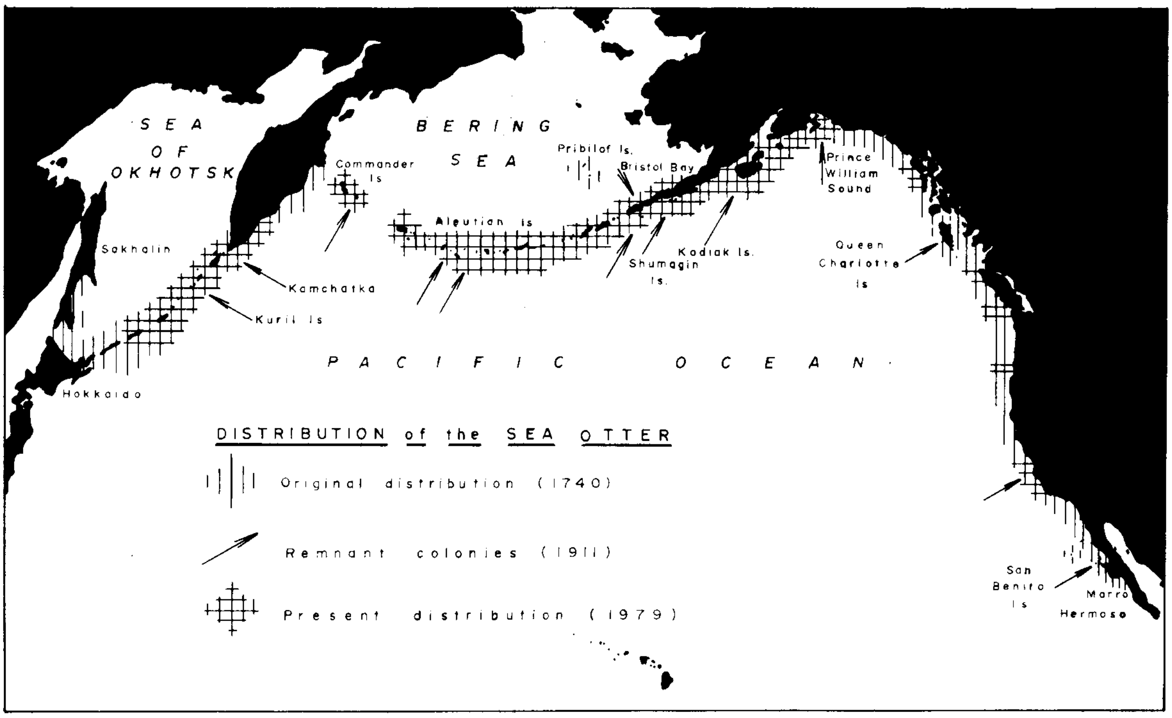

FIGURE 3. Original and present distribution of *Enhydra lutris.* Updated and redrawn from Kenyon (1969).

nasal aperture is large. The sagittal, lambdoidal, and occipital crests of adults are well developed (Scheffer, 1950). The auditory ossicles are similar to those of other diving mammals (Solntseva, 1975). Juvenile dentition consists of 44 teeth, of which 26 (i 3/2, c 1/1, p 3/3) are gingivally erupted at birth. Adult dentition is attained in less than one year. The postcanine teeth are bunodont (Murie, 1959; Kenyon, 1969) and are adapted for crushing (Ognev, 1931; Fisher, 1941). Lower incisors protrude and are spade-shaped to scoop food organisms from their shells (Hildebrand, 1954; Fig. 2). The size of the pulp cavity decreases with age from deposition of secondary dentine (Fisher, 1941). Malocclusion and dental attrition are common and may contribute substantially to mortality (Kenyon, 1969). Schneider (1973) estimated age in young animals on the basis of tooth eruption and skull changes, and in older animals by patterns of cementum deposition. The canines generally are broadest in males (Scheffer, 1951).

The vertebral column consists of seven cervical, 14 thoracic, six lumbar, three sacral, and 20 to 21 caudal vertebrae (Barabash-Nikiforov, 1947). Great flexibility in the spine has been achieved by reduction of vertebral processes, shortening and heightening of the centra, and enlargement of the intervertebral foramina (Taylor, 1914). The sternum and ribs are loosely articulated (Barabash-Nikiforov, 1947). A small scapula is related to the lack of dependence on forelimbs for support (Taylor, 1914). There is no clavicle, allowing extreme mobility of the pectoral girdle (Howard, 1975). The humerus is massive and twisted; the forelimb in general, and the wrist in particular, are highly mobile. Grasp function of individual forelimbs is poor; most forelimb functions are performed by apposing the forepaws (Murie, 1959; Howard, 1975). A long, narrow pelvis is loosely connected with the sacrum and extends posteriorly, parallel to the vertebral column. The pubic symphysis is weakly formed. The short hindlimbs extend posteriorly (Taylor, 1914). There is no pit in the head of the femur, corresponding to the absence of the ligamentum teres; this permits greater freedom of movement. Body skin encloses the femur and most of the shank (Tarasoff, 1972). Lengths of the rear digits and the interdigital web surface are relatively great (Zur Strasen, 1914). The fourth and fifth digits are closely bound to give rigidity to the hind flipper for propulsion (Pocock, 1928). The ventral surface of the calcaneus is shifted internally which makes it the most distinctive among Mustelidae (Stains, 1976).

Superficial and deep parts of the masseter muscles are unusually indistinct (Kenyon, 1969), although jaw muscles are well developed. The *arrector spinae* and *rectus abdominus* are well developed for the undulating movements of swimming (Barabash-Nikiforov, 1947). Howard (1973, 1975) described the structure and function of the limb musculature.

Extensive arterial and venous networks cover the dorsal and plantar surfaces of each flipper (Tarasoff, 1972). Blood characteristics of normal and pathological animals are described by Stullken and Kirkpatrick (1955).

The cerebrum is complexly fissured. Distinctive features of the cerbrum include an anterior arm of the ectosylvian gyrus depressed into the pseudosylvian sulcus and partially overlaid by the coronal and rear arm of the ectosylvian gyri, marked postcruciate sulcus, large ursine lozenge, well developed ansate fissures, long cruciate sulcus that curves caudally at its distal end, and a postrhinal sulcus with interrupted ventral surface such that the pyriform lobe and neopallium are superficially fused (England and Dillon, 1972). Cortical expansion of the lateral part of the posterior sigmoid gyrus is a common feature of *Amblyonyx*, *Aonyx*, *Paraonyx*, and *Enhydra*, and is associated with increased forepaw tactile sensitivity.

The thoracic cavity is large and the diaphragm is positioned obliquely (Barabash-Nikiforov, 1947). The right lung has four lobes, the left two (Tarasoff and Kooyman, 1973*a*). The trachea is incomplete dorsally; its rings are partially calcified, and its length and width are intermediate between *Lutra* and phocid seals (Tarasoff and Kooyman, 1973*b*). Cartilage-supported airways empty directly into alveolar sacs.

The stomach is large, the intestine is over 10 times body length, and the liver is five or six lobed. The gall bladder has a maximum length of 150 mm and a diameter of 20 mm, relatively thick walls, and many gland-like openings throughout the mucosa (Rausch, 1953). Various organ weights were given by Stullken and Kirkpatrick (1955), Kenyon (1969), and Morejohn et al. (1975).

The bicornuate uterus (Pearson, 1952) is compressed dorsoventrally (Sinha et al., 1966). The ovary is roughly a lenticulate, compressed oval with simple or complexly branched surface fissures. Sinha and Conaway (1968) described the ovarian microanatomy. A single Graafian follicle typically reaches the preovulatory stage while others atrophy. The corpus luteum of preimplantation pregnancy has a medium- to large-sized antrum, which is obliterated by the time the blastocyst implants. During delayed implantation, the luteal cells progressively hypertrophy and, by the time of implantation, they are polygonal and uniformly granular. The corpus luteum of pregnancy is 9 to 17 mm in diameter; luteal cells are small and spindle-shaped with basophilic vesicular nuclei (Sinha et al., 1966). The corpus luteum degenerates rapidly following parturition. A corpus albicans persists for at least two years (Sinha and Conaway, 1968). Changes in ovarian form, and in the gross anatomy and histology of the uterus during various stages of estrus and through pregnancy are described by Sinha et al. (1966). The chorioallantoic placenta is labyrinthine, zonary, and endotheliochorial; its development from implantation to birth is described by Sinha and Mossman (1966). The kidneys are large compared to other marine mammals (Kenyon, 1969) and consist of oval clusters divided into reniculi (Barabash-Nikiforov, 1947).

FUNCTION. The sea otter probably typifies early transitional forms in the evolution of semi-aquatic to more highly adapted marine species (Murie, 1959). Numerous characteristics of from, function, and behavior have convergently evolved with those of pinnipeds, cetaceans, and sirenians.

Standard metabolic rate is about 2.5 met, or 0.67 to 0.72 cm^3 O_2 $(g\ h)^{-1}$; elevated basal metabolic rate is an aquatic adaptation (Morrison et al., 1974). Maximum metabolic rate is about 10 met. Captives require between 190 and 250 kcal/kg/day (Kenyon, 1969; Costa, 1976), or about 20 to 25% of their body weight. Costa (1978) estimated free ranging energy consumption to be 270 kcal/kg/day. Assimilation efficiency is 80 to 85% (Costa, 1976; Fausett, 1976). Food passes through the gut in about 3 h (Stullken and Kirkpatrick, 1955). Starved sea otters lose 10% of their body weight per day (Kenyon, 1969) and rapidly develop gastroenteritis.

Sea otters can maintain body temperature by basal metabolism under normal environmental conditions in air or water (Morrison et al., 1974). The thermoneutral zone in air is at least −19 to 21°C. Minimum thermal conductance in air is less than 0.012 cm^3 O_2 $(g\ h\ ^{\circ}C)^{-1}$ and only doubles on immersion in water due to the fact that insulation from cold seawater is provided entirely by air trapped in the fur (Morrison et al., 1974). A well developed medulla in the guard hairs probably also contributes to insulation (Tarasoff, 1974). Infrared emissivity is nearly equivalent to that of a perfect black-body radiator (Hammel, 1956). Arterial and venous networks over the dorsal and plantar surfaces of the large flippers are important avenues of heat flux (Iverson and Krog, 1973). Morrison et al. (1974) estimated that two-thirds of the heat load passes through the flippers in water at 26°C and four-fifths in air at 28°C. The flippers are removed from the water during quiescent periods and the frequency of digital expansions is positively correlated with ambient temperature. The flipper is expanded during warm conditions to facilitate heat loss (Tarasoff, 1972). During cold conditions, thermal absorption by solar radiation is enhanced by dark color and the highly developed superficial venous circulation on the dorsal surface of the flipper (Tarasoff, 1974).

The sea otter is awkward on land. Terrestrial locomotion is achieved by walking with alternate movements of opposing forelimb and hindlimb; by moving the forelimbs and dragging the hindlimbs; or by bounding, in which the back is arched and the hindlimbs are drawn toward the forelimbs (Barabash-Nikiforov, 1947, Tarasoff et al., 1972). There are three modes of aquatic locomotion. Paddling with the hindlimbs and sculling with the tail are used only when supine on the surface. Dorsoventral undulations of the body are used for more rapid surface locomotion and when diving (Howell, 1930; Sokolov and Sokolov, 1970; Tarasoff et al., 1972). In this mode, the hindlimbs are extended posteriorly to increase the propulsive effect of body undulations (Sokolov and Sokolov, 1970). Aquatic locomotion in *Lutra* is achieved by movement of both forelimbs and hindlimbs whereas in *Enhydra* limb movement is restricted to the hindfoot (Tarasoff, 1972). Tarasoff (1972) suggested that reduction in hair density and length from the mid-back to hindfoot increases efficiency of locomotion by reducing water turbulence. Swimming velocity is about 1 to 1.5 km/h on the surface and up to 9 km/h underwater (Kenyon, 1969).

Underwater vision of sea otters is slightly poorer than that of *Zalophus* and *Phoca* and is probably no better than that of terrestrial mammals (Gentry and Peterson, 1967). Vision in air is poor although olfaction apparently is well developed. Tactile sensation in the forelimb and vision are used in food gathering (Kenyon, 1969).

The large lungs may function in buoyancy (associated with the absence of blubber, and also to support food, tools, and young while on the surface) and oxygen storage (Kooyman, 1973). Of the total oxygen storage capacity, 67% occurs in the lungs and 33% in the blood and muscle (Lenfant et al., 1970). Cartilagenous airways, by emptying directly into alveolar sacs, insure patency until compression collapse. This structure is found in other marine mammals but is absent in terrestrial mammals and *Lutra* (Kooyman, 1973). The blood has a higher buffering capacity than that of non-diving species (Lenfant et al., 1970). Resting heart rate is 132/min and respiration is irregular at about 12/min (Stullken and Kirkpatrick, 1955).

Sea otters drink seawater. Costa (1976) calculated a total water input of 0.266 liters/kg/day, of which 67.5% came from food, 9.2% from respiration, and 23.3% from consumption of seawater. Water is lost in the urine (71%) and feces (18%), and via respiration (11%) (Costa, 1978).

ONTOGENY AND REPRODUCTION. Breeding and pupping occur throughout the year (Fisher, 1940; Murie, 1940; Kenyon, 1969). In the Aleutian Islands, the number of estrous females and occurrence of breeding activity is greatest in October and November (Schneider, 1972); maximum birth rate occurs in late May or June. In California, maximum birth rate occurs from December to February (Sandegren et al., 1973); seasonal occurrence of estrous females and of breeding activity are unknown. Gestation has been estimated to last 7.5 to 9 months (Lensink, 1962; Schneider, 1972). Based on time between observed copulation and parturition in a captive sea otter, Brosseau et al. (1975) estimated the gestation period to be 6.5 to 7 months. Delayed implantation occurs (Sinha et al., 1966), but duration of the preimplantation period is not known. Most females ovulate or develop large follicles every year, and Schneider (1972) suggested that induced ovulation may occur. Kenyon (1969) and Schneider (1972) estimated that females give birth, on the average, once every two years, but females can give birth every year. The average interval between births is unknown. Implantation occurs with about equal frequency in each uterine horn. There is no tendency to alternate ovaries between successive pregnancies although in some individuals one ovary may be more active than the other (Schneider, 1972). Most implantations occur in the central third of the uterine horn (Kenyon, 1969; Schneider, 1972). Successful birth weights average 1.8 to 1.9 kg and range from 1.4 to 2.3 kg (Kenyon, 1969). Gestation may be shorter and birth weights less at high population levels. There are no differences between the sexes in fetal growth rates or birth weights (Schneider, 1972). Based on a sample of 313 fetuses, Schneider (1972) found the fetal sex ratio to be 44% males and 56% females. Kenyon (1969) estimated a birth rate of about 16 young per 100 independent animals per year. Mortality rate apparently is higher in males than in females during the first year of life.

About 4% of the ovulations and 2% of the pregnancies are multiple (Schneider, 1972). There is one report of twin births (Snow, 1910), although twins probably cannot be reared successfully and have not been reported from field observations. Resorption in utero may occur in about 5% of the pregnancies in high density populations. Mortality at or near parturition is less than 5% (Schneider, 1972). Females seldom copulate until after separation from their previous young (Kenyon, 1969; Schneider, 1972). Postpartum estrus may occur within a month after birth if the young does not survive (Brosseau et al., 1975). Caudal and cephalic fetal orientation are equally frequent (Kenyon, 1969; Schneider, 1972) although fetuses tend to assume cephalic orientation near term. Kenyon (1969) believed that females attain sexual maturity at about 4 years.

Spermatogenesis occurs in the population throughout the year (Lensink, 1962) although sperm probably are produced intermittently by individuals. Schneider (1978) suggested that males reach reproductive maturity at 5 or 6 years, and that they become active breeders several years later. There is no evidence of reproductive senility (Kenyon, 1969).

Birth probably occurs most often in water. The young are nearly helpless at birth and females provide a great deal of care and training until they are almost adult size. The period of dependency probably is 6 to 8 months (R. Hardy and F. Wendell, pers. comm.). Pups nurse about 8% of the time during daylight (Sandegren et al., 1973) and suckle until they reach almost adult size. Small pups suckle while lying on the female's chest; larger pups suckle while lying in the water perpendicular to the female. In the water, the young is supported on the female's chest where it is manipulated between her forepaws. On land, the female grasps the young in her mouth and drags it. Females share solid food with the young shortly after birth (Kenyon, 1969); large young aggressively take food from their mothers (Sandegren et al., 1973). The young begin to dive in the second month following birth; the duration of dives and foraging success increase as they develop. Motor patterns develop slowly and apparently there is considerable learning associated with swimming, grooming, and feeding during the period of dependency (Sandegren et al., 1973; Kenyon, 1969). Females with small young tend to be solitary and act aggressively toward other individuals. Sandegren et al. (1973) noted that this behavior was most common when inclement weather limited the locations suitable for care of the young. They suggested that competition among females with young occurred during winter in California when parturition rate was highest and kelp beds were sparse. Choppy sea conditions may distress the young, to which females respond by swimming downwind or seeking sheltered coves. Females with young in California are most active at dawn and dusk. When the young are very small, they seldom feed during daylight, but daylight foraging increases as the young grow larger (Sandegren et al., 1973). Females may adopt and nurse orphaned young (Kenyon, 1969).

ECOLOGY. Sea otters forage in rocky and soft-sediment communities, on or near the ocean floor. In central California, they seldom feed beyond a depth of 20 m, whereas in the Aleutian Islands they commonly forage at depths of 40 m or more. The maximum confirmed depth of dive was 97 m (Newby, 1975). Maximum depth of dive apparently varies geographically and among individuals, and probably is related more to the distribution, abundance, and quality of food than physiological constraints. Diet consists of invertebrates and, in some areas, fish.

Populations of certain invertebrates are limited by sea otter predation. Adult abalones and sea urchins in central California occur almost exclusively in substrate crevices which serve as refuges from sea otter predation (Lowry and Pearse, 1973). Sea otters greatly reduce the size and density of sea urchins in the Aleutian Islands (Estes and Palmisano, 1974). Subsequent to the overexploitation of sea otters by man, these invertebrate populations probably increased throughout much of the North Pacific Ocean and southern Bering Sea.

Where sea otters are absent in the Aleutian Islands, uncontrolled populations of sea urchins apparently are limited by competitive interactions; kelp beds are reduced or absent; and nearshore fishes are relatively uncommon. Where sea otters are abundant, sea urchins are small and scarce; there is a robust assemblage of macroalgae which are limited by competitive interactions (Dayton, 1975); and nearshore fishes are relatively abundant (Estes and Palmisano, 1974; Estes et al., 1978). Sea otters may enhance primary production and the abundance of higher trophic forms (Estes et al., 1978). Dense sublittoral kelp beds facilitate siltation of littoral zones in some sea otter-dominated communities by sheltering them from wave exposure. Silt accumulation smothers filter feeding mussels and barnacles, thus reducing their densities. Gastropod and asteroid predators on mussels and barnacles are consequently reduced. Hermit crabs apparently depend on gastropod shell resources and they also are reduced (Palmisano and Estes, 1977).

Diet varies according to location and time occupied by sea otters. Sea urchins, abalones and rock crabs are the sea otters' principal prey in newly reoccupied habitats of central California (Ebert, 1968; Vandevere, 1969). The number of abalones captured per dive subsequently declined in these areas (Ebert, 1968). Reduction of preferred prey (McLean, 1962; Wild, 1973) was followed by expansion of the diet to include such forms as mussels, turban snails, squid, octopus, chitons, tubeworms, large barnacles, scallops, and sea stars (Wild and Ames, 1974).

In recently repopulated areas of the Aleutian Islands, the diet consists largely of sea urchins, mollusks and crustaceans. Sluggish, epibenthic fishes are the most important prey in populations near equilibrium density. Prey switching apparently is related to reduced herbivorous invertebrates, enhanced kelp beds, and the consequent increase in abundance of nearshore fishes, many of which are dependent on kelp for protection or as a source of nutrition (Simenstad et al., 1977). Diet in the Commander Islands varies seasonally, with mollusks, crabs and fish most commonly eaten in summer and sea urchins most commonly eaten in winter (Barabash-Nikiforov, 1947). Bivalve mollusks are excavated by digging in sand or mud bottoms and are the most common prey in soft-sediment communities (Calkins, 1978). In some areas of central California, sea otters have reduced pismo clam populations (Miller et al., 1975; Stephenson, 1977).

Young sea otters are preyed on by bald eagles at Amchitka Island (Sherrod et al., 1975). Shark teeth have been found in wounded sea otters (Snow, 1910) and numerous beached carcasses in California (Orr, 1959; Morejohn et al., 1975; Ames and Morejohn, in litt.). Nikolaev (1965) observed an attack by a killer whale in the Kuril Islands, and Tikhomirov (1959) provided a possible instance of predation by Steller sea lions. Aside from man, no other predators are known. The distribution and composition of faunal remains in prehistoric kitchen middens suggested that aboriginal Aleuts reduced or eliminated sea otters from localized areas (Simenstad et al., 1978).

Voronov (1969) reported that a tsunami reduced sublittoral food resources at Urup Island in the Kuril archipelago causing sea otters to die and disperse to other islands.

The sea otter is definitive host for 14 known species of parasites (Dailey and Brownell, 1972; Hennessy and Morejohn, 1977). *Porrocaecum decipiens* (Nematoda) and *Microphallus pirum* (Trematoda) are thought to be highly pathogenic (Rausch, 1953). Hermit crabs (*Pagurus* spp.) and perhaps other decapod crustaceans are intermediate hosts to *M. pirum* (Rausch, 1953; Schiller, 1954). Rock greenling (*Hexagrammos superciliosus*) and red Irish lord (*Hemilepidotus hemilepidotus*) are intermediate hosts to small numbers of *P. decipiens* per fish (Schiller, 1954); hence the species is highly pathogenic only where fish are common in the sea otters' diet. Other helminth parasites recorded from sea otters in the North Pacific/Bering Sea are: *Orothosplanchus fraterculus*, *Phocitrema fusiforme*, *Pricetrema zalophi* (Trematoda); *Diplogonoporus tetrapterus*, *Pyramicocephalus phocarum* (Cestoda); and *Corynosoma strumosum*, *C. villosum*, *C. enhydri*, *C. macrosomum* and two unidentified species of *Corynosoma* (Acanthocephala) (Rausch and Locker, 1951; Morozov, 1957; Rausch, 1964; Dailey and Brownell, 1972). In central California, the acanthocephalan parasites, *Corynosoma enhydri*, *Polymorphus kenti*, *P. major*, and *P. altmani*, have been recorded in the sea otter. *Polymorphus* were rare in the specimens examined, but may be pathogenic when common (Hennessy and Morejohn, 1977). Sand crabs (*Emerita* and *Blepharipoda*) are common intermediate hosts to *Polymorphus*. About 3% of sea otters examined at Amchitka Island were lightly infested with nasal mites (*Halarachne miroungae*; Acarina) (Kenyon et al., 1965).

Forepaw infections may be caused by sea urchin spines (Kenyon, 1969). Enteritis is the most frequent symptom in dead animals (Kenyon, 1969; Morejohn et al., 1975); pneumonia-like conditions also have been reported (Morejohn et al., 1975).

Age composition of otter populations is unknown but probably varies according to the size and status. The rate of increase is about 10 to 12% per year in populations below equilibrium density.

Return of the Bering Expedition to Russia in 1742 with 900 sea otter pelts initiated exploitation of the sea otter in the Aleutian Islands and along the northwest coast of North America. Intense and uncontrolled exploitation occurred from 1742 to 1799, at which time Russia recognized the possibility of overexploitation and implemented conservation measures. After the sale of Alaska to the United States, intense overexploitation recurred until by the end of the nineteenth century the species was nearly extinct. In 1903 a high-quality skin was worth $1100 on the London market (Kenyon, 1971). Lensink (1960) estimated that more than 800,000 sea otters were taken by all nations during the period of Russian occupation of Alaska.

BEHAVIOR. Sea otters apparently are polygynous, although the exact nature of the mating system may vary. Mating occurs without pair bonding in some instances (Vandevere, 1970), but in others, a consortship lasts 3 to 4 days (Kenyon, 1969; Vandevere, 1970), during which time there are multiple copulations. Termination occurs when the female abandons the male. Copulation occurs in the water after the male clasps the female from behind and secures her nose or face between his jaws. There is considerable thrashing and rolling around the longitudinal axis of the pair during copulation, which may last 35 minutes with occasional periods of rest (Kenyon, 1969). The bloody nose of a female generally is indicative of mating activity (Brosseau et al., 1975), and the resultant nose scars, which vary in size, shape, and color, often are individually recognizable (Foott, 1970).

Kenyon (1972) believed that males searched for estrous females, and that distinct breeding territories were not established by males in the Aleutian Islands. Territorial behavior by males was observed by Vandevere (1970) and Loughlin (1977) in California, and by Calkins and Lent (1975) in Prince Willaim Sound. The mean area of territories of males observed by Loughlin (1977) was about 30 ha; these territories were located contiguously along the coast, adjacent to female resting areas. Several were maintained continuously for at least a year. Fighting is rare and is not the method usually employed in territorial defense. In Prince William Sound, males actively defended well-defined territories by patrolling their borders while vigorously kicking and splashing, which Calkins and Lent (1975) interpreted as visual and auditory displays. Territorial males often steal food from other individuals in their territory. In captivity, dominant males tolerate subordinate males only until they reach sexual maturity (Brosseau et al., 1975).

Sea otters segregate by sex and age (Schneider, 1978). In California, concentrations of animals at the ends of the range consist mostly of males (Vandevere, 1970; Wild and Ames, 1974; R. J. Jameson, pers. comm.). Permanent male and female areas occur in populations at equilibrium density in the Aleutian Islands. Male areas generally include only 400 to 800 m of shoreline and are densely populated; they include males of all ages except pups. Females rarely occur in male areas. Male areas tend to occur near exposed points where shallow water extends far offshore, and frequently they have the roughest sea conditions in the vicinity. They usually are 10 to 40 km apart and include only a small part of the available shoreline. Female areas are larger, less discrete, and less densely populated than male areas. They comprise most of the acceptable habitat between male areas and contain females of all ages. The number of adult males in female areas is correlated with the number of estrous females. Subadult males seldom occur in female areas. Schneider (1978) believed that competition for food, space, and breeding opportunities was the primary cause of sex and age segregation, and that variation in physiography, the distribution of food, and population status were the most likely causes of differences among areas in patterns of sex and age segregation. Loughlin (1977) estimated that the home range averaged 56 ha and was about twice as large for females as males.

Sea otters can spend their entire lives at sea (Ognev, 1931). They often rest in large groups, but otherwise they are solitary (Kenyon, 1972). They may rest on land or at sea. Resting on land is most common in areas where otter population density is high and they are not disturbed. At sea they prefer to rest in kelp beds and often wrap themselves in kelp to remain stationary (Kenyon, 1969). However, the largest congregations of resting animals have been seen where kelp beds are absent (up to 2000 animals in Bristol Bay; K. B. Schneider, pers. comm.). Sea otters rest in the water by lying supine on the surface with their paws held together on the chest and their flippers removed from the water (Fisher, 1939; Tarasoff, 1974). In some areas resting locations tend to remain constant over many years. Sea otters are non-migratory although both seasonal movements and long distance wandering of individuals may occur (Miller, 1974). Juveniles apparently wander more than adults (Kenyon, 1969). Translocated animals tend to disperse or return to the site of capture (Wild and Ames, 1974).

Foraging activity is greatest during morning and evening (Estes, 1977; Shimek and Monk, 1977). An average of 15 to 55% of the time during daylight hours is spent foraging; apparently this varies largely as a function of population status. Loughlin (1977) found that there was no difference between daylight and darkness in the length of foraging bouts, foraging areas, or the allocation of time to different activities. Larger animals were less active than smaller ones.

The tactile sense is important in locating food (Radinsky, 1968; Kenyon, 1969; Shimek, 1977). Prey generally are captured with the forepaws rather than between the jaws. Vision apparently is used to orient while on the surface and to capture elusive prey such as fish (Kenyon, 1969). Sea otters raise vertically in the water preceding a foraging dive, from which position they roll forward into the dive. They usually dive obliquely rather than straight down (Fisher, 1939). Average reported dive times vary from 52 to 90 seconds. The longest dive recorded by Loughlin (1977) was 4 min 25 s; Kenyon (1969) believed that the maximum duration of a dive was less than 6 min. In California, shorter dive times were required for snails and kelp crabs than for clams and abalones (Loughlin, 1977; Costa, 1978). Several dives in succession often are required to obtain a single abalone (Hall and Schaller, 1964). Some individuals feed successively on the same species for short numbers of dives (Hall and Schaller, 1964). Captured prey are transported in loose flaps of skin beneath the axilla (Barabash-Nikiforov, 1947; Kirkpatrick et al., 1955) and are consumed on the surface.

A rock tool or other object is often used to break the prey's shell or exoskeleton (Fisher, 1939; Murie, 1940; Hall and Schaller, 1964), or to dislodge prey underwater (Houk and Giebel, 1974). This permitted significant expansion of exploitable food resources to sea otters (Alcock, 1972). Ebert (1968) found that 80% of the abalone shells he examined had breakage planes suggesting that they were struck with tools by sea otters. Rock tools range in diameter from about 6 to 15 cm (Limbaugh, 1961). Variation in the incidence of tool use throughout the range is due largely to the nature of available food (Woodhouse et al., 1977). It is more common in California than in the Aleutian or Kuril islands (Murie, 1940; Barabash-Nikiforov, 1947; Novikov, 1956). Food items and other objects occasionally are pounded against the bare chest, particularly by pups. McCleneghan and Ames (1976) reported that one individual learned to tear open aluminum containers, and to extract octopuses that inhabited them. Sea urchins are opened primarily with the paws or teeth and the viscera and gonads are scooped out by the lower incisors and tongue (Hildebrand, 1954). Sea otters often roll laterally in the water while feeding, apparently to wash discarded scraps of food from their fur.

Sea otters meticulously and vigorously groom their fur to maintain its waterproof character (Kenyon, 1969). They commonly blow air into their fur, beat the water, and pleat the skin to renew entrapped air (Tarasoff, 1972). Loughlin (1977) described grooming as a stereotyped, five-step sequence with high fidelity in stage repetition and with strong correlation to hair density and exposure of different body areas to the water.

Fisher (1939), Kenyon (1969), and Sandegren et al. (1973) described the sea otters' vocalizations for which Kenyon identified eight distinct kinds.

GENETICS. There are 38 chromosomes (2n). Anbinder (1976) reported that the sea otter karyotype was similar to that of *Lutra conadensis*, *Martes zibellina*, and *M. americana*.

REMARKS. The economic value of sea otter fur played an important role in early exploration and development of the Pacific coast of North America. Discovery and decimation of sea otters greatly influenced world history and politics through trade and territorial acquisition by many of the major seafaring nations. Today sea otters are protected throughout their range although some animals are killed illegally or incidentally where contact with humans is frequent. I thank M. A. Bogan, R. L. Brownell, Jr., A. L. Gardner, E. R. Hall, E. T. Hooper, R. J. Jameson, C. Jones, K. W. Kenyon, and K. Ralls for advice or assistance in preparation of this account.

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