

Ethology and Behavioral Ecology of Marine Mammals
Series Editor: Bernd Würsig



Randall W. Davis · Anthony M. Pagano *Editors*

Ethology and Behavioral Ecology of Sea Otters and Polar Bears

 Springer

Ethology and Behavioral Ecology of Marine Mammals

Series Editor

Bernd Würsig, Department of Marine Biology, Texas A&M University at Galveston, Galveston, TX, USA

The aim of this series is to provide the latest ethological information on the major groupings of marine mammals, in six separate books roughly organized in similar manner. These groupings are the 1) toothed whales and dolphins, 2) baleen whales, 3) eared seals and walrus, 4) true seals, 5) sea otter, marine otter and polar bear, and 6) manatees and dugong, the sirens. The scope shall present 1) general patterns of ethological ways of animals in their natural environments, with a strong bent towards modern behavioral ecology; and 2) examples of particularly well-studied species and species groups for which we have enough data. The scope shall be in the form of general and specific reviews for concepts and species, with an emphasis especially on data gathered in the past 15 years or so. The editors and authors are all established scientists in their fields, even though some of them are quite young.

More information about this series at <http://www.springer.com/series/15983>

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Editors

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Female sea otter with pup in Simpson Bay, Alaska. Image courtesy of R. Wolt



Female polar bear with cubs in the Canadian Arctic. Image courtesy of ©Amos Nachoum

*To the researchers who have dedicated their
lives to improving our understanding and
conservation of sea otters and polar bears*

Introduction to the Series

We—multiple topic editors and authors—are pleased to provide a series on the ethology and behavioral ecology of marine mammals. We define ethology as “the science of animal behavior,” and behavioral ecology as “the science of the evolutionary basis for animal behavior because of ecological pressures.” Those ecological pressures include us, the humans.

We determine, somewhat arbitrarily but with some background, that “marine mammals” habitually feed in the sea, but also include several mammals that went from saltwater oceans back into rivers, as seen in the chapter by Sutaria et al., in the first book on odontocetes. Polar bears represent a somewhat outlier “marine mammal,” as they are quite at home in the sea, but can also feed on terrestrial mammals, birds, berries, lichens, and mosses.

In six books, we include toothed whales (the odontocetes); baleen whales (the mysticetes); sea lions and fur seals (the otariids) as well as the walrus; true seals (the phocids); the special cases of the sea otter and polar bear; and manatees and the dugong (the sirens). Each of our chosen editors and their chapter authors have their own schedules, so the series will not arrive in the order given above, but within the 5 years of 2019 through 2023, all six marine mammal books on *Ethology and Behavioral Ecology of Marine Mammals* will see the light of day, and you, the readers, will be able to ascertain their worth and their promise, as to current knowledge and to accumulating data while our fields of science advance.

Since the first book on odontocetes came out in 2019, we added a seventh final book, on *The Human Factor*, with chapters on past assaults on marine mammals, continuing assaults on the marine and other environments, dawning of awareness of assaults, and perhaps ways that we humans can and must do better. Several of us simply felt that to detail modern science of marine mammal ethology and behavioral ecology was not enough—we need to be aware of the amazingly destructive Anthropocene epoch in which we live, and try to improve, for all of nature (and therefore also for us). While topics of human influence run throughout each of the first six books, a concentration on human actions and potential solutions is needed.

Not all mammals that occur in marine waters are represented, nor all that have gone back to freshwater. Thus, there is nary a mention of marine-feeding bats, marine-feeding river otters, those aspects of beluga whales that foray way up into major rivers, seals living in land-locked lakes at times thousands of kilometers from the ocean, and other species that occasionally make the marine environment or—as generally accepted marine mammals—adjacent freshwater systems their home. Such are the ways of a summary, and we apologize that we do not fully encompass all.

As series editor, I have been a science partner to all major taxonomic entities of this series, but to this only because I have been in the marine mammal field for about 50 years now, with over 65 graduate students who—in aggregate—have conducted research on all seven continents. In no manner do I pretend to have kept up with all aspects of diverse fields of modern enquiry. It is a special privilege (and delight) to have multiple up-to-date editors and their fine authors involved in this modern compilation and I am extremely grateful (and humbled) for this. Still learning, and ever so.

Each chapter is reviewed by the book editors, peer reviewed by other scientists as chosen by the editors, and perused and commented on by me. If you learned something new and imparted that to your colleagues, students, or your own mentors, then the series and sections of it shall have been worthwhile.

Tortolita Desert, Arizona, USA
May 2021

Bernd Würsig

Preface

Sea otters and polar bears: Here we have two mammals separated by different life histories and geographic ranges, but united by a common ancestry and a reliance on the marine environment for food. Sea otters are mostly aquatic, while polar bears prefer the sea ice or nearshore habitats, but neither is as well adapted to an aquatic life as are Cetacea (whales and dolphins), Sirenia (dugongs and manatees), or even Pinnipedia (seals, sea lions, and walrus). When at sea, both species spend most of their time swimming at the surface or making short, shallow dives when foraging or pursuing their prey. Compared with other marine mammals, sea otters and polar bears have a recent evolutionary history (~5 Mya and ~0.4 Mya, respectively), and so could be considered transitional between terrestrial carnivorans (family Carnivora) and more derived marine mammal species. Thus, they possess adaptations for life in both terrestrial and aquatic realms. In this book, we have assembled a group of authors who have expertise on sea otter and polar bear behavior and ecology. This information is timely because the effects of climate change in the arctic and subarctic will alter these ecosystems dramatically in the next 100 years. Biologists in the twenty-second century will observe markedly different behaviors in sea otters and polar bears. Here, we provide a snapshot of their behaviors at this time, during a period of rapid change to the earth's climate. We are grateful for the contributions of each author and our colleagues who reviewed individual chapters and are acknowledged therein, especially James Bodkin, who reviewed the sea otter chapters. Our thanks to Springer International for publishing this book series, with special recognition to our editors Éva Loerinczi and Bibhuti Sharma. Our series editor, Bernd Würsig, guided the preparation of this book and provided valuable comments. Finally, our thanks to Georgina Davis, who served as Assistant Editor and contributed to figure preparation. A book such as this is only possible with the contributions of many talented people, and we express our gratitude to all of them.

Galveston, TX, USA
Santa Cruz, CA, USA
May 2021

Randall W. Davis
Anthony M. Pagano

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Chapter 1

Introduction



Randall W. Davis and Anthony M. Pagano

Abstract Sea otters and polar bears are marine mammals in the taxonomic order of Carnivora. Behaviorally, most carnivore species are solitary and asocial except during reproduction or while rearing offspring, although there are notable exceptions. Sea otters are solitary foragers and exhibit little social cooperation but may form aggregations at sea called rafts. The primary social interaction among sea otters occurs during reproduction. Except during mating, the principal interaction among sea otters occurs between females and offspring during the 6-month dependency period. Polar bears are solitary hunters of seals and are neither gregarious nor social. Males and females briefly associate during courtship and mating, but the principal interaction of polar bears outside of mating occurs between a female and her offspring during the 2–3 year dependency period. This book examines the behavior and behavioral ecology of sea otters and polar bears and is divided into two sections. Chapters 2–10 focus on sea otters and Chaps. 11–17 on polar bears.

Keywords Behavior · Carnivora · Polar bear · Sea otter · Asocial

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1.1 The Behavior of Sea Otters and Polar Bears in the Marine Environment

Sea otters (*Enhydra lutris*) and polar bears (*Ursus maritimus*) are marine mammals in the taxonomic order of Carnivora (hereafter referred to as carnivorans), which includes Pinnipedia (seals, sea lions, fur seals, walrus). All marine mammals show varying degrees of morphologic, physiologic, and behavioral adaptive convergence for an aquatic life, yet retain the basic characteristics of all eutherian mammals: endothermic homeothermy, hair, live birth, and lactation. Cetacea (whales and dolphins), Sirenia (dugongs and manatees), and Pinnipedia have a long evolutionary history (~50 Mya for Cetacea and Sirenia; ~27 Mya for Pinnipedia) and are fully or primarily aquatic. Sea otters and polar bears have a shorter evolutionary history (~5 Mya and ~0.4 Mya, respectively) in the marine environment and are morphologically and physiologically less adapted for an aquatic life (Davis 2019). Sea otters are amphibious but seldom come ashore, and polar bears primarily occur on sea ice or along the shore. When at sea, both species spend most of their time swimming at the surface or making short, shallow dives when foraging or pursuing prey. Indeed, polar bears rarely pursue seals in water, but they are powerful swimmers and will stalk seals from the water. The ancestors of marine mammals were terrestrial (polar bears remain primarily pagophilic or terrestrial), and each taxonomic group has a unique evolutionary history. The one commonality is that they obtain food in an aquatic environment even though they are found in diverse habitats (both aquatic and terrestrial) and have different locomotory modes and foraging strategies.

Mammals exhibit a variety of behaviors, some of which are solitary (nonsocial) and others that occur between two or more individuals (social), usually conspecifics, when they form aggregations, engage in reproductive and parental behavior, cooperate to find food, or engage in disputes over territory and access to mates. The degree of sociality varies widely among mammalian species, and sometimes it is difficult to distinguish between gregariousness and social behavior, including mutual defense. Among mammals, obligatory behaviors include foraging and body maintenance (e.g., sleeping and grooming), which may be nonsocial or social. Obligatory social behavior includes reproduction (i.e., courtship and mating) and parental investment (i.e., lactation and care of offspring), which is provided primarily by the female. Among marine mammals, cooperative social behavior for foraging and mutual defense is evident in many species of Cetacea, such as bottlenose dolphins and sperm whales, which in some cases constitutes cultural learning (Würsig and Würsig 1980; Whitehead 2003; Pitman and Durban 2011; Wells and Scott 2018; Whitehead 2018). Among Pinnipedia, gregariousness during reproduction is common, but there is limited evidence of mutual defense against a threat (on land or at sea) other than vigilance. If a seal or sea lion is attacked by a predator, conspecifics generally flee and do not engage in mutual defense, although walruses defend pups from polar bears when on land or ice. There is little evidence of cooperative foraging among Pinnipedia, although sea lions and fur seals may surround bait balls (i.e., tightly packed swarms of small fish).

Behaviorally, most carnivore species are solitary and asocial except during reproduction or while rearing offspring, although there are notable exceptions in the families of Canidae (e.g., wolves [*Canis lupus*]), Felidae (e.g., lions [*Panthera leo*]), Hyaenidae (e.g., spotted hyenas [*Crocuta crocuta*]), and Herpestidae (e.g., meerkats [*Suricata suricatta*]). Social behavior for non-breeding purposes includes group foraging, predator defense, and alloparenting. However, such behaviors are relatively uncommon among carnivorans, as only 10–15% of all species aggregate outside the breeding season.

Among the carnivore families, Mustelidae exhibit a medium-high level of cooperation among the 13 extant species. However, limited cooperation occurs in sea otters, which are solitary foragers but may form aggregations called rafts when resting at the surface. Rafting sea otters are usually spatially segregated into male or female groups, which may be a form of group vigilance against predators. Despite their close spatial proximity in rafts, individuals do not frequently interact, although yearlings may engage in play behavior and wrestling. Although sea otters are gregarious, they are primarily asocial or, in the case of territorial males, antagonistic (i.e., antisocial) towards other males. The primary social interaction among sea otters occurs during reproduction, where dominant males actively search for estrous females or establish territories within female areas. A sexually receptive female may form a consortship with a male for mating, but it usually ends after a few days. Male sea otters play no role in rearing offspring. Except during mating, the principal interaction among sea otters occurs between a female and offspring during the 6-month dependency period.

In larger carnivores (e.g., wolves and lions) that feed (largely) on ungulates, sociality and cooperation are favored because of the need to capture large prey and defend carcasses. However, polar bears—the largest carnivoran—are solitary hunters of seals and are neither gregarious nor social. Males and females briefly associate during courtship and mating. During this time, males will aggressively compete for females. At other times, males generally avoid each other except for aggregations that form while summering on land, and females with cubs avoid males, which are known for infanticide. As with sea otters, the interaction of polar bears outside of mating occurs between a female and her offspring during the 2–3 year dependency period. This interaction is critically important when altricial cubs are born in the winter den.

This book examines the behavior and behavioral ecology of sea otters and polar bears and is divided into two sections. Chapters 2–10 focus on sea otters and Chaps. 11–17 on polar bears.

1.2 Chapter Sequence

To understand the ethology of sea otters, it is helpful to place them into an evolutionary context and discuss their phylogenetic relationship with other mammals, specifically members of the otter clade of Lutrinae, which has 13 extant

species. In Chap. 2, Timm-Davis and Marshall discuss the evolution of Mustelidae from arctoid carnivorans and the subsequent divergence of the subfamily Lutrinae ~8 Mya. This chapter also reviews hypotheses regarding the divergence of ancestral sea otters (*Enhydra*) ~5 Mya and their spread from Eurasia to North America and into the North Pacific Ocean 3–1 Mya. The Lutrinae have been semiaquatic for millions of years, so the behavioral ecology of sea otters shares many similarities with other otter species.

Morphology and physiology enable but also constrain an animal's behavior and physical performance, and sensory systems affect how an animal perceives its environment. In Chap. 3, Zellmer, Timm-Davis, and Davis examine morphologic, physiologic, and sensory adaptations in sea otters. Although sea otters spend most of their lives at sea, including the birthing of pups on the surface of the water, they are morphologically more similar to amphibious Pinnipedia than to Cetacea and Sirenia (Davis 2019). Because of their elevated resting metabolic rate and reliance on fur for thermal insulation, sea otter behavior is strongly influenced by foraging and body maintenance behaviors, such as grooming and resting. Social and reproductive behaviors represent a small proportion of daily activity.

Sea otters are marine specialists but diet generalists, which feed primarily on benthic invertebrates. In Chap. 4, Davis and Bodkin discuss the foraging behavior of sea otters. Because of their elevated metabolic rate, sea otters consume 25% of their body mass daily, so foraging is a prominent behavior. They locate and capture epibenthic and infaunal invertebrates with their forepaws by relying on vision and tactile sensitivity during short-duration dives (<4 min) in shallow waters (routine dives <30 m and maximum dive depth ~100 m). As a result, they have a significant top-down effect on benthic mega-invertebrates, which affects littoral community structure. Although sea otters use their teeth and powerful jaws to access the flesh of mega-invertebrates with a shell, exoskeleton, or test, they may use stones as hammers or anvils to open hard prey at the surface or underwater. The prevalence of tool use by sea otters varies geographically and may be passed culturally from females to offspring. Because of their broad diet, sea otters exhibit innovative problem solving when feeding. Extractive foraging tasks (e.g. puzzle-tasks) when handling hard-shelled prey indicate cognitive processes associated with problem solving.

Otters form a semiaquatic clade, which stands out among carnivorans. Of 13 extant otter species, only three are known to cooperate, although most species exhibit some form of sociality. In Chap. 5, Barocas and Ben-David review variations in the social structure of marine otters, including sea otters. Comparisons emphasize the North American river otter because it is one of the most well-studied species. The majority of carnivorans are solitary, so many species seldom aggregate outside the breeding season. Although many otter species exhibit social behaviors and live in groups, forms of cooperation have been unequivocally documented in only two species, neither of which are sea otters. Compared with North American river otters, the low frequency of social interactions may be a consequence of the more aquatic lifestyle of sea otters, as reduced time on land provides fewer opportunities for social activity. Sea otter rafts are often segregated by sex and composed of randomly assembled individuals, which aggregate after solitary foraging. Although sea otters

are sometimes gregarious, reproductively active males are antisocial towards other males when defending a territory. Between males and females, there is no indication of social cooperation, although rafts may be a form of group vigilance against predators. Hence, there is no indication of special social cognitive ability (i.e., social intelligence) in the social domain.

In Chap. 6, Pearson and Davis discuss the reproductive behavior of male sea otters. The reproductive system is resource defense polygyny in which males defend territories containing resources that attract females. As a result, the predominant trait of social-sexual behavior is segregation by age and sex. Males attempt to mate with females that enter their territories, but they cannot control their movements. An estrous female that is sexually receptive to the male may form a consortship, which typically lasts about three days and involves multiple copulations. Copulatory behavior induces reflex ovulation in females. Key components of male sea otter reproductive behavior include sexual segregation, resource defense polygyny, aquatic mating, and no participation in rearing offspring.

Although sea otters are semiaquatic, females give birth to young on the surface of the water. In Chap. 7, Cortez and Davis examine the reproductive behavior of female sea otters and their pups. As with most other mammalian species, the male does not participate in rearing offspring. As a result, female sea otters must care for pups during a 6-month dependency period. Pups are altricial and dependent on the female for care (nursing and grooming) and protection, and maternal behavior changes in synchrony with the pup's physical and behavioral development. Neonates sleep and nurse most of the day, but new behaviors, such as transiting (i.e., surface swimming), self-grooming, foraging, and interacting, develop over the first three months of life. In response, the female exhibits reduced vigilance and enhanced foraging to support the growing pup's nutritional needs with both milk and prey. At some point, the energetic demand may exceed the female's foraging ability and cause a decrease in body condition, which can lead to early weaning or pup abandonment in severe cases. After females wean or abandon their pups, mating occurs within a few days to weeks, and the cycle repeats.

In Chap. 8, Coletti discusses the effect of sea otter behavior on littoral (nearshore) community structure. Because of their elevated basal metabolic rate (2.9-fold higher than a terrestrial mammal of similar size) and food consumption, sea otters have a significant top-down effect on large invertebrates in the littoral zone, which results in a trophic cascade affecting littoral community structure. The near extirpation and subsequent recovery of sea otters throughout much of their historic range provide an opportunity to examine the influence of a large marine carnivoran on littoral habitats. The author also discusses the long-term goal of sea otter conservation and restoration to full pre-exploitation population levels throughout their historical range, which would inevitably result in the demise of commercial invertebrate (primarily clam, crab, and urchin) fisheries and a financial effect on economic markets (Davis et al. 2019).

Predators directly affect their prey as a source of mortality, and prey respond by employing antipredator strategies. In Chap. 9, Monson discusses antipredator strategies of sea otters. Although they are a keystone predator within the nearshore community, higher trophic level avian, terrestrial, and pelagic predators (e.g., bald

eagles, brown bears, wolves, white sharks, and killer whales) prey on sea otters. Three antipredator strategies used by sea otters are *avoidance* (seeking a location inaccessible to predators), *vigilance* (group or sentinel detection of danger), and *crypsis* (the ability to avoid observation or detection). Although these behaviors may reduce predation, they cannot eliminate it. The behavioral response to killer whales is so strong in some areas that it may limit sea otter dispersal, with implications for the connectivity and genetic health of the small, isolated populations. Avoiding high-risk habitats is a central theme of the ecology of fear in which fear-mediated behavior in response to a powerful and lethal predator can shape a species' behavior and distribution (Brown et al. 1999).

The maritime fur trade of the eighteenth and nineteenth centuries in the North Pacific Ocean nearly extirpated sea otters. In Chap. 10, Loshbaugh discusses the effects of the fur trade as a cautionary example of unsustainable resource exploitation and a socioeconomic driver of Western expansion into the Pacific region. This event changed the lives and cultural history of maritime Native people, who were often enslaved to hunt sea otters for Russian fur traders from the mid-1700s until the United States purchased Alaska in 1867. The trade's profound effects on the population biology of sea otters, indigenous cultures, and the littoral community of the Pacific Rim are still apparent today.

In Chap. 11, we transition from sea otters to polar bears as Cahill examines their taxonomy and evolution. Polar bears are similar to other members of the family Ursidae, for which there are eight extant species. Since their divergence from brown bears ~400 Kya, polar bears have evolved from terrestrial omnivores into marine carnivores in the Arctic sea ice environment. The evolutionary relationship of polar bears and brown bears has been the subject of substantial debate, with various studies leading to different interpretations. Genetic and genomic data have given us a better understanding of polar bear evolution, which differs from earlier taxonomic studies.

Polar bears possess morphologic and physiologic characteristics that reflect both a terrestrial lineage as members of the Ursidae and adaptations to the Arctic marine environment. In Chap. 12, Whiteman discusses polar bear morphologic and physiologic adaptations as an apex predator hunting seals on the Arctic sea ice. Nevertheless, they are powerful swimmers and can make short, shallow dives when pursuing prey. The features that distinguish polar bears since they diverged from brown bears reflect their adaptation to the sea ice habitat and to a hypercarnivorous diet of marine mammal prey. Physiology is critical in how polar bears respond to changes in their environment. Our current knowledge illustrates polar bear dependence on the sea ice environment and the prey it provides, a connection that links the alteration and loss of this habitat to the future of the species.

In Chap. 13, Pagano discusses polar bear foraging behavior, which occurs primarily on the sea ice over the shallow waters of the continental shelf. Polar bears are solitary ambush hunters, which catch seals when they surface to breathe in ice holes or when hauled out on ice to rest and molt or while pupping in subnivean lairs. However, foraging success varies seasonally, and the accumulation of body fat is vital for these bears to survive through the autumn and winter when seals are less

accessible or when adult female bears enter dens and fast. When sea ice retreats in summer, some bears exhibit a temporary switch to omnivory, feeding on a variety of terrestrial food. Reduced access to seals in the Arctic sea ice because of global climate change threatens the long-term survival of polar bears.

Polar bears share many reproductive characteristics with other bears, but they have significant adaptations, which enable them to reproduce and thrive in the ever-changing sea ice environment of the Arctic. In Chap. 14, Smith examines polar bear reproductive and denning behavior. The polar bear mating system is polygynous, with males competing for mating opportunities in the spring over large and dynamic ranges. During the winter, denning is restricted to pregnant females, which may remain in dens for up to seven months, during which time they give birth and nurse altricial cubs, emerging from the den in spring. Cubs are dependent on the female for milk and seal carcasses, and weaning may not occur until they are 2–3 years of age. The prolonged pre-weaning period and high rate of cub mortality result in a low reproductive rate compared with other terrestrial mammals.

Polar bear maternal behavior and neonatal development are difficult to study because maternal dens are secluded and generally inaccessible. In Chap. 15, Owen discusses what we know about polar bear maternal care, neonatal development, and occasional social interaction. Altricial polar bear cubs have limited sensory capacity, sparse fur, and are completely dependent on the female for nourishment, warmth, and protection. Energy for the female's metabolic requirements and milk production comes from body fat during the 12-week denning period, during which females may lose ~44% of their body mass. When cubs emerge from the den after 12 weeks, they have a litter mass that is similar to the gestational mass of other mammals for the same period. They nurse for up to two years, although they also eat seals captured by the female and will practice hunting independently as yearlings. Social interactions outside of reproduction are largely associated with concentrated resources, such as food or available habitat, and there is a range of characteristic social interactions in these settings, from adult social play to aggression, tolerance, and avoidance.

In Chap. 16, Aars discusses polar bear behavior in response to climate change. The Arctic is warming faster than other parts of the earth, and this is reflected in declining seasonal sea ice, the primary habitat of polar bears. The rapidly changing climate means that any response in polar bear behavior is unlikely to be driven by microevolution, but rather it will depend on behavioral plasticity. Fortunately, studies indicate high behavioral plasticity in polar bears despite their marked specialization as a marine predator. Recently, the most significant change in their feeding behavior has resulted in spending more time on land as seasonal sea ice recedes. Because polar bears do not occur in areas without sea ice for a significant part of the year, a diet of seals may not be fully replaceable with alternative terrestrial food, which poses a serious conservation concern.

As humans increasingly move into the Arctic, competition with polar bears will intensify, resulting in potential interaction and conflict, which poses a threat to human safety and economic well-being. In Chap. 17, Atwood and Wilder explore the nexus of polar bear and human behavior and environmental change in driving the nature and intensity of human-polar bear interaction and conflict. The authors

propose a conceptual framework, which conservationists and managers can use to mitigate future human-polar bear conflict in a rapidly changing Arctic.

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Part I
Ethology and Behavioral Ecology of Sea
Otters

Chapter 2

Taxonomy and Evolution of Sea Otters



Lori L. Timm-Davis and Christopher D. Marshall

Abstract Sea otters (*Enhydra lutris*) are members of the Mustelidae family, a monophyletic basal group of arctoid carnivores. They are the only member of the otter clade (subfamily Lutrinae; 13 extant species) that is fully aquatic (i.e., foraging, giving birth, raising offspring) in the marine environment, although they may occasionally rest on land. Lutrinae diverged from other mustelid lineages ~8 Mya in Eurasia. The earliest lineage to diverge from Eurasian otters ~5 Mya were the ancestors of sea otters (*Enhydra*). From the late Miocene to early Pliocene, a sister group of modern sea otters, *Enhydritherium*, was present in Eurasia. One hypothesis is that this group dispersed around the northern rim of the North Atlantic Ocean into the Gulf of Mexico. From there, *E. terraenovae* disseminated into the Pacific Ocean through the Central American Seaway. There it presumably gave rise to *Enhydra* (3–1 Mya), which is found only in the North Pacific Ocean. An alternative hypothesis is that *Enhydra* evolved in the North Atlantic and entered the North Pacific through the Arctic Ocean and Bering Straits. Today there exists one species of sea otter with three subspecies based on geographical and morphological differences.

Keywords Arctoidea · Caniformia · Carnivore · Enhydriodon · Enhydritherium · Lutrinae · Mustelidae · Sea otter · Subspecies

2.1 Taxonomy

Sea otters (Order Carnivora, Suborder Caniformia, Mustelidae, *Enhydra lutris*) are the smallest marine mammal and related to other otters (13 species) within the subfamily Lutrinae (Fig. 2.1). Sea otters once inhabited the North Pacific Rim,

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Fig. 2.1 Taxonomy of sea otters

Kingdom	Animalia
Subkingdom	Bilateria
Infrakingdom	Deuterostomia
Phylum	Chordata
Subphylum	Vertebrata
Infraphylum	Gnathostomata
Superclass	Tetrapoda
Class	Mammalia
Subclass	Theria
Infraclass	Eutheria
Order	Carnivora
Suborder	Caniformia
Infraorder	Arctoidea
Family	Mustelidae
Subfamily	Lutrinae
Genus	<i>Enhydra</i>
Species	<i>lutris</i>

ranging from northern Japan through Russia, Alaska, Canada, and along the coast of the contiguous United States to central Baja California in Mexico (Davis et al. 2019). Prior to their near extirpation during the Maritime Fur Trade in the eighteenth and nineteenth centuries, the population was estimated to be ~300,000 (see Chap. 10; Kenyon 1969; Johnson 1982). When the fur trade ended in 1911, an estimated 2000 remained (Kenyon 1969; Ralls and Siniff 1990; Larson et al. 2002). Sea otters, which now number ~150,000, have reoccupied much of their former range (albeit with significant gaps) from northern Japan to southern California.

There are three subspecies of sea otters based on geographic distribution and genetic analysis (Cronin et al. 1996; Scribner et al. 1997). Russian sea otters (*E. lutris lutris*; Linnaeus 1758) are distributed from northern Hokkaido (Japan) through the Kuril Islands and the Kamchatka Peninsula to the Commander Islands (Komandorski Islands, Russia). The current sea otter population in the Commander Islands is at or near equilibrium density (Doroff et al. 2011). Population distribution along the Kamchatka Peninsula is limited by sea ice in the northern region. Populations along the northern Kuril Islands have declined since 2003, but those in the central Kuril Islands may be at equilibrium density. The sea otter population in northern Hokkaido is small but growing from reproduction and immigration from the southern Kuril Islands (Hattori et al. 2005).

Northern (also known as Alaskan) sea otters (*E. lutris kenyoni*; Wilson et al. 1991) range from the Aleutian Islands to Prince William Sound and along the Pacific coast of Canada and Washington State. Three stocks are recognized within Alaska: southeast (Dixon Entrance to Cape Yakataga), south central (Prince William Sound, Kenai Peninsula, and Kachemak Bay), and southwestern (Alaska Peninsula, Aleutian Islands, Kodiak Islands, and Cook Inlet) (Doroff and Burdin 2011). Sea otter populations are stable in the Kodiak archipelago and in lower Cook Inlet. However, in Southwest Alaska and the Aleutian Islands, the Northern sea otter population are listed as threatened after a rapid population decline in the 1980s,

likely caused by killer whale (*Orcinus orca*) predation (Estes et al. 1998, 2005; Burn et al. 2003; Doroff et al. 2003; Williams et al. 2004; Reisewitz et al. 2006).

Southern (also known as California) sea otters (*E. lutris nereis*; Merriam 1904) have a small range along the central California coast between Point Conception near Santa Barbara and Año Nuevo Island in San Mateo County (Hanni et al. 2003; Doroff and Burdin 2011). Some sea otters are moving north of Año Nuevo Island, and a few have moved farther south towards Baja California, indicating that reoccupation of former habitat continues. After commercial hunting of sea otters was banned in 1911, the Southern sea otter population increased at a rate of 5% per year until the 1970s, when the population plateaued (Ralls and Siniff 1990). Complex factors influence sea otter population growth in California. Recent evidence indicates that the population is constrained by the linear nature of the coastline, which slows emigration from the center because it can occur only in two dimensions (at the northern and southern ends of the range) instead of multi-directional in more complex habitats (Tinker 2015). This constraint is reinforced by white shark predation, which further limits population expansion to the north and south (see Chap. 9; Tinker 2015). Other factors (such as disease) also have been identified as causes of mortality (Conrad et al. 2005; Johnson et al. 2009). As a result, California sea otters have been listed as a threatened species under the U.S. Endangered Species Act (Ralls and Siniff 1990; Doroff and Burdin 2011).

2.2 Early Evolution of Mammals

To understand the ethology of sea otters, it is helpful to place them into an evolutionary context and discuss their phylogenetic relationship with other mammals, specifically members of the otter clade. The monophyletic group of Mammalia evolved from the clade of Synapsida (Dilkes and Reisz 1996; Oftedal 2002). The fossil record for Synapsida shows the evolutionary rise of Therapsida, Cynodontia, and Mammalia (Fig. 2.2; Rubidge and Sidor 2001; Luo 2007). Synapsida is the amniotic clade that contains the stem and more derived groups of Pelycosauria and Therapsida. Pelycosauria is a paraphyletic group that appeared approximately 300 Mya in North America and Europe and is considered to be the more basal group (Fig. 2.2a; Reisz 1972; Kemp 2006). Therapsida originated around 275 Mya, replacing Pelycosauria as the dominant terrestrial synapsid (Fig. 2.2b). Those that survived the Permian-Triassic extinction displayed morphological trends that formed the foundation of modern mammalian traits. For example, the skull showed a reduced temporal shield and enlargement of the single temporal fenestration (Barghusen 1973; Rubidge and Sidor 2001; Kemp 2006). This enlargement was a precursor for a sagittal crest and zygomatic arches, which became new attachment points for the temporalis and masseter muscles.

Cynodontia (derived Therapsida) first appeared in the fossil record in the late Permian (Sidor 2001), with a masseteric fossa on the mandible and laterally flared zygomatic arches (Fig. 2.2c). These anatomical changes placed the coronoid process

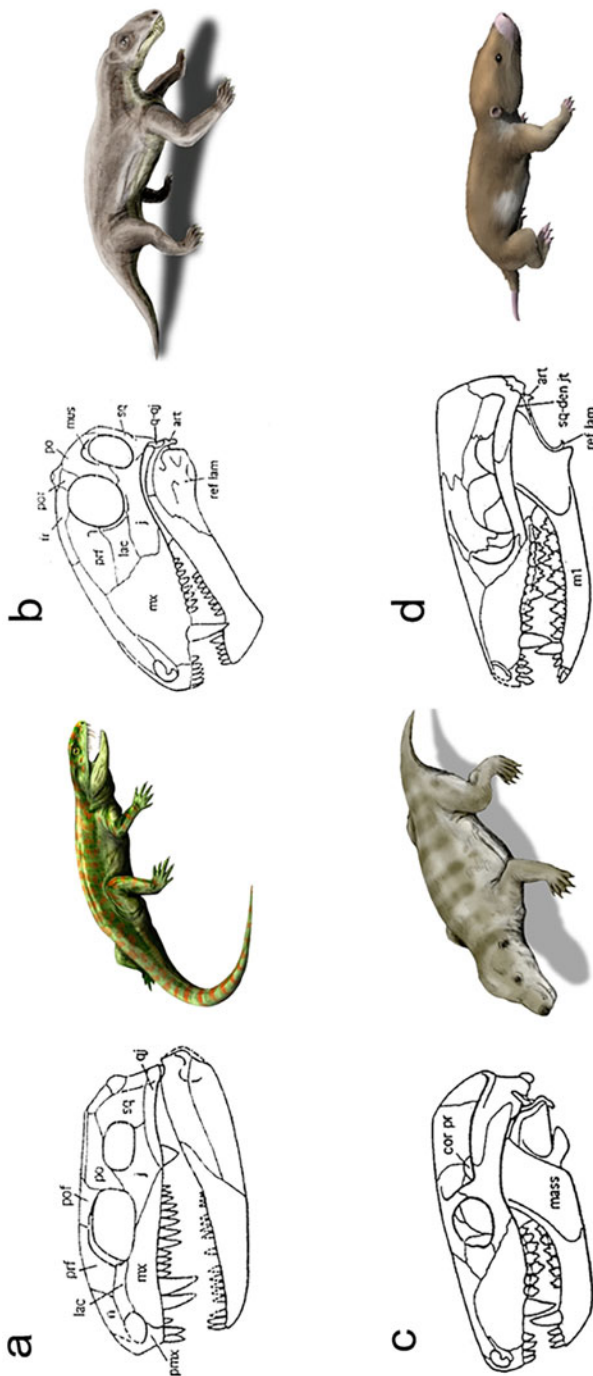


Fig. 2.2 Skulls and artist renditions of basal synapsids to early mammals. (a) *Eothyris parkeri*, a basal synapsid of the early Permian. (b) *Biarmosuchus tener*, a therapsid of the late Permian. (c) *Thrinaxodon liorhinus*, a cynodont of the late Permian. (d) *Morganucodon watsoni*, a mammaliaform of the early Jurassic. Skull images modified by Oftedal (2002). Artist renditions courtesy of Nobu Tamura

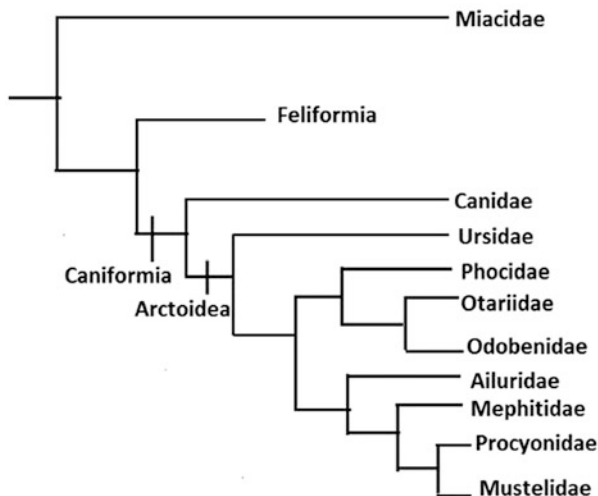
in the middle of the temporal fenestra for the attachment of masseter and temporalis muscles (Barghusen 1968; DeMar and Barghusen 1972; Rubidge and Sidor 2001). The development of these new adductor muscles was essential for mastication, which is a distinctive mammalian feature (Barghusen 1968). The masseter muscles control transverse jaw movements, precise occlusion for mastication, and increased bite force while reducing stress on the temporomandibular (i.e., jaw) joint. There also was a reduction in the angular bone and differentiation of teeth (e.g., heterodont dentition) (Rubidge and Sidor 2001; Sidor 2001). As the maxillary and palatine bones expanded, Cynodontia developed a secondary upper palate, which separated the respiratory and digestive systems, a feature crucial for nursing (Rubidge and Sidor 2001). Morganucodon, which appeared in the fossil record in the late Triassic or early Jurassic (250–200 Mya), is considered to be one of the earliest known mammals (Fig. 2.2d; Luo 2007; Ungar 2010). Fossil evidence suggests that they exhibited unilateral occlusion of the teeth, a trait seen in extant mammals (Ungar 2010).

Eutherian mammals evolved during the Cretaceous (~144 Mya; Cifelli and Davis 2003; Luo 2007). Their molars, which evolved from tribosphenic (three main cusps arranged in a triangle) cheek teeth of more ancestral mammals, enabled a diverse feeding ecology. Dental diversity and the ability to masticate food allowed them to radiate into open niches and exploit new habitats during the Cenozoic. Among this radiation were Miacidae (Clade Carnivoramorpha), which were civet-like carnivores that lived 62–34 Mya (Hiimeae and Crompton 1985; Luo et al. 2001). Miacidae coexisted with other mammals belonging to the Orders Creodonta (which include the families Oxyaenidae and Hyaenodontidae) and Condylarthra (family Mesonychidae) (Radinsky 1982). However, by the end of the Eocene, members of the two latter orders went extinct, allowing Miacidae to undergo rapid evolutionary radiation, giving rise to modern Carnivora.

2.3 Emergence of the Carnivora

Carnivora diverged from Miacidae in the Middle Eocene (~ 44 Mya) and became one of the most ecologically diverse mammalian orders, spanning a wide range of feeding adaptations (Radinsky 1981; Van Valkenburgh 1999, 2007; Wesley-Hunt 2005). The Order Carnivora is composed of two suborders: Caniformia (dog-like carnivorans) and Feliformia (cat-like carnivorans) (Van Valkenburgh 1999; Delisle and Strobeck 2005; Vaughan et al. 2011). These lineages rapidly radiated in the late Eocene and early Oligocene (37–28 Mya) (Van Valkenburgh 1999). Caniformia is comprised of Canidae (dogs and foxes) and Arctoidea (bear-like carnivores) (Delisle and Strobeck 2005). Arctoidea is comprised of eight extant families: Ursidae (bears), Mustelidae (weasels), Procyonidae (raccoons), Mephitidae (skunks), Ailuridae (red panda), Phocidae (seals), Otariidae (sea lions and fur seals), and Odobenidae (walrus) (Fig. 2.3; Bininda-Emonds et al. 1999; Flynn et al. 2005; Christiansen and Wroe 2007; Eizirik and Murphy 2008).

Fig. 2.3 Phylogenetic relationship of Mustelidae within Arctoidea (Eizirik and Murphy 2008)

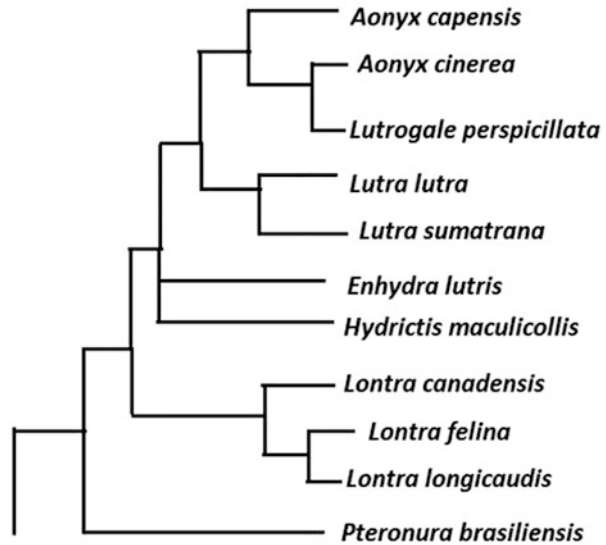


2.4 Mustelidae and the Otter Clade

Mustelidae is a monophyletic group that appeared in the fossil record ~35 Mya and is considered the basal group of the arctoid carnivores (Riley 1985; Marmi et al. 2004; Yonezawa et al. 2007). Phylogenetic analysis resolved the Mustelidae (Superorder Laurasiatheria) into seven primary divisions, including the otter clade (Subfamily Lutrinae) and a sister clade comprising mink and true weasels (Subfamily Mustelinae) (Koepfli et al. 2008). Stem mustelids (including the now extinct subfamily of Leptarctines) first arose during the Oligocene in Eurasia and spread to North America by the middle Miocene (Zhanxiang and Schmidt-Kittler 1982). Fossils of the carnivorous arctoid ancestors of sea otters can be traced to the Eocene (~45 Mya), but while Pinnipedia is now considered to be a sister group of the Ursidae, sea otters are clearly in the family Mustelidae.

The genus *Mionictus* is the oldest otter fossil and dates from the early Miocene of Europe and North America (~20 Mya) (Willemsen 1992; Koepfli and Wayne 1998). Within North America, descendants of *Mionictis* are found up to the Pliocene (5–3 Mya) (Willemsen 1992). The subfamily Lutrinae is comprised of three monophyletic clades that include seven genera and 13 species (Fig. 2.4; Carss 1995; Koepfli and Wayne 1998; Koepfli et al. 2008; Vianna et al. 2010; Moretti et al. 2017). Lutrinae occur in Europe, Asia, Africa, North America, and South America. All extant species forage primarily or exclusively in aquatic environments (Corbet and Hill 1980). The basal clade in Lutrinae includes the Old World river otters from Eurasia and Africa (*Aonyx*, *Lutrogale*, *Lutra*, *Hydrictis*) and sea otters (*Enhydra*). The second clade includes the New World otters (*Lontra*). A single genus *Lutra* previously included river otters in both *Lutra* and *Lontra* genera (Pohle 1919; Harris 1968). However, genetic and morphological differences between Africa/Eurasia river otters and North and South American river otters placed New World river otters in their own genus,

Fig. 2.4 Phylogenetic relationship of otters (Koepfli et al. 2008)



Lontra (van Zyll de Jong 1972, 1987; Wozencraft 1993; Koepfli and Wayne 1998; Koepfli et al. 2008). Giant river otters (*Pteronura brasiliensis*) are the sole members of the third and most derived clade of Lutrinae and do not appear to be closely related to New World otters (Koepfli and Wayne 1998).

Otters may have spread across Europe from a single refugium, although its location is unknown (Ferrando et al. 2004). During the Pleistocene, models of postglacial recolonization of Europe by otters are based on one or more southern or eastern refugia (Hewitt 1999). The importance of the Iberian Peninsula as the glacial refugium has been suggested (Bilton et al. 1998; Hewitt 1999). However, an increase in mutations suggests European otters may have originated in the Balkans or western Asia (Desmesure et al. 1996; Bilton et al. 1998; Ferrando et al. 2004).

2.5 Sea Otters

Lutrinae, a sister group of the Leptarctines, diverged from other mustelid lineages in the middle-to-late Miocene (~8 Mya) in Eurasia, and the ancestors of sea otters (*Enhydra*) diverged from other Eurasian otters in the early Pliocene (~5 Mya). As a result, sea otters may have been the earliest lineage to diverge within the Old World otters (Koepfli and Wayne 1998). Based on morphological and molecular evidence, *Lutra* is the closest extant relative of sea otters (Berta and Morgan 1985; Masuda and Yoshida 1994).

Two sister groups of modern sea otters appeared in the late Miocene to early Pliocene. One was *Enhydriodon*, which lived in Africa. The other was *Enhydritherium*, which occurred in Eurasia and North America based on fossils

from Spain and Florida (United States), respectively (Repenning 1976; Berta and Morgan 1985). There are two hypotheses regarding the dissemination of *Enhydritherium* from Eurasia into North America. One proposes that this group dispersed from Europe around the northern rim of the Atlantic Ocean and into the Gulf of Mexico, where the first fossils of *Enhydritherium terraenovae* appeared in Florida. *E. terraenovae* then made its way into the Pacific Ocean through the Central American Seaway, where presumably it gave rise to *Enhydra* (which is found only in the North Pacific Ocean) about 3–1 Mya. This avenue of dispersal remains uncertain, as it would have occurred around the time that the Central American Seaway closed in the late Pliocene (2.76–2.54 Mya).

In size, *E. terraenovae* was similar to *Enhydra* (~22 kg; Lambert 1997). However, the paleoenvironment of the fossil sites in Florida and California indicates that its habitat was not limited to the marine habitat of *Enhydra* but included both nearshore marine and inland freshwater habitats. The limbs of *E. terraenovae* are more similar to those of river otters (*Lutra* and *Lontra*) than to *Enhydra*, suggesting the forelimbs were used in aquatic (mode uncertain) and terrestrial locomotion (Lambert 1997). The thickened but heavily worn cusps on the carnassial teeth of *E. terraenovae* indicate a diet of extremely hard prey (e.g., mollusks) similar to the diet of *Enhydra*, although soft foods such as fish may have also been consumed when in freshwater. *E. terraenovae* had attributes of both river otters and modern sea otters by the late Miocene to early Pliocene (5–4 Mya), and so it appears to be transitional and more of a habitat generalist than a marine specialist.

The alternative evolutionary hypothesis proposes that *Enhydra* evolved in the North Atlantic (perhaps from *Enhydritherium*) and then spread into the North Pacific via the Arctic Ocean and Bering Straits (Boessenecker 2018). Evidence in the form of two fossil molars—found in strata dating from the early Pleistocene (2.2–1.7 Mya) in England—of *Enhydra reevei* supports this hypothesis (Willemsen 1992). The low, blunt, and inflated cusps of these fossil teeth resemble more those of *Enhydra* than *Enhydritherium*, whose post-canine teeth have sharper ridges. Additional support for this hypothesis arose with the discovery of a mandible of *Enhydra* sp. of similar age from the coast of the Chukchi Sea in northern Alaska (Repenning 1983). Unfortunately, the fossil record in the North Pacific is poor, so there is no evidence of *Enhydra* (e.g., *Enhydra macrodonta*) earlier than the middle Pleistocene (<0.7 Mya; Mitchell 1966; Kilmer 1972; Boessenecker 2018 revised the age of the Oregon femur in Leffler [1964] to 0.5–0.7 Mya, pers. com.). Therefore, the dispersal of sea otters into the North Pacific Ocean during the intervening 1–1.4 million years remains uncertain. What is clear is that *Enhydritherium* became extinct in the Atlantic, while *Enhydra* became extinct in the Arctic, although the timing is uncertain. Additional fossil evidence could improve our understanding of the evolutionary origins of sea otters (Davis 2019).

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