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.

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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 Bernd Würsig
May 2021

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	*Enhydra*
Species	*lutris*

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

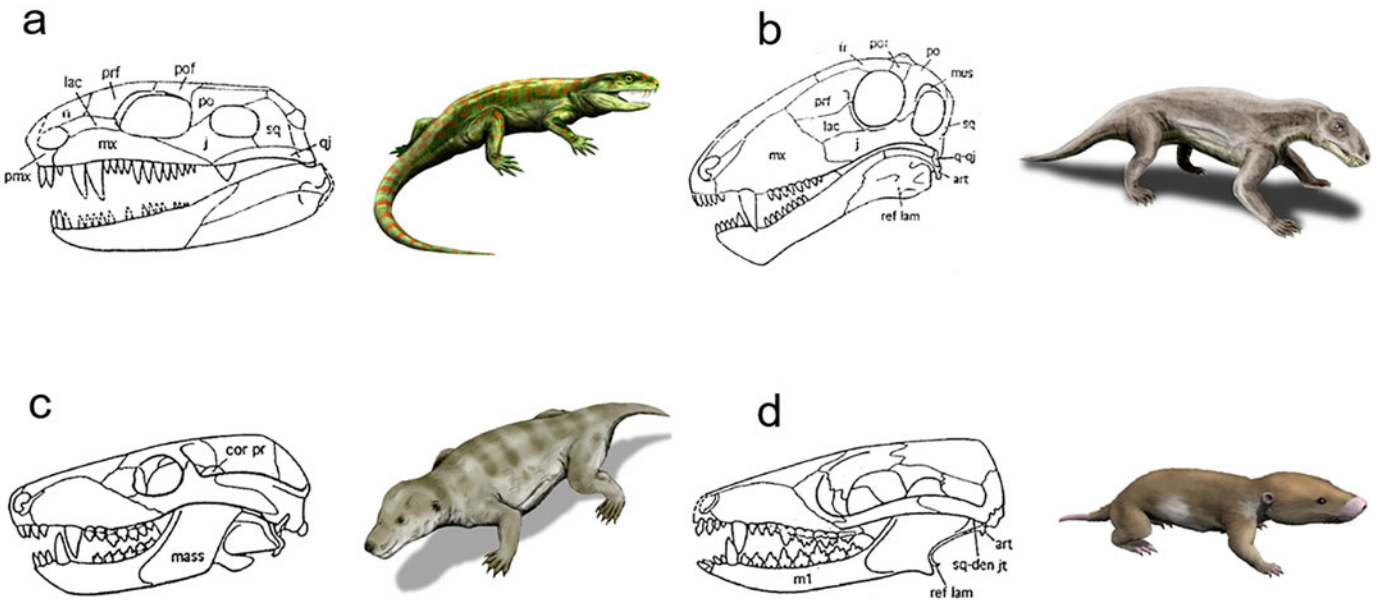

Fig. 2.2 Skulls and artists renditions of basal synapsids to early mammals. (**a**) *Eothyris parkeri*, a basal synapsid of the early Permian. (**b**) *Biarmosuchus tener*, a therapsid of the late Permian. (**c**) *Thrinaxodon liorhinus*, a cynodont of the early Triassic. (**d**) *Morganucodon watsoni*, 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 (Hiiemae 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).

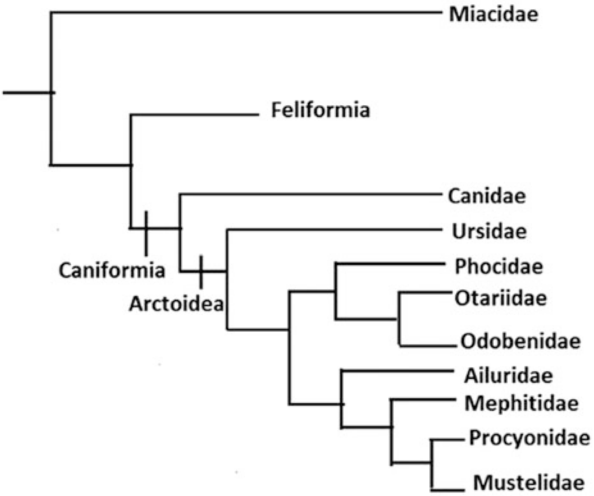

Fig. 2.3 Phylogenetic relationship of Mustelidae within Arctoidea (Eizirik and Murphy 2008)

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 (*Enhdyra*). 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,

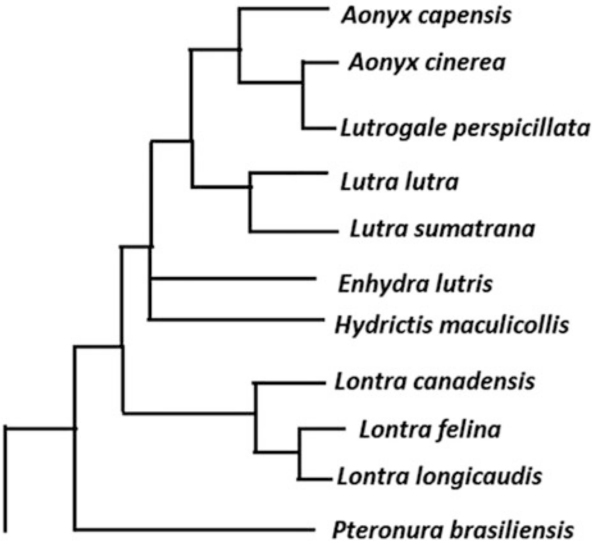

Fig. 2.4 Phylogenetic relationship of otters (Koepfli et al. 2008)

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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Chapter 3
Sea Otter Behavior: Morphologic, Physiologic, and Sensory Adaptations

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Abstract Morphology and physiology enable but also constrain an animal's behavior and physical performance, and sensory systems affect how an animal perceives its environment. Sea otters are grouped with other raptorial predators even though they capture and manipulate prey with their forepaws and consume it at the water's surface. They have a short, robust skull and mandibles that enhance bite force. Their postcanine teeth have rounded or conical cusps and large surfaces for cracking or crushing mollusk shells, crustacean exoskeletons, or the test of echinoderms, such as sea urchins. The axial skeleton of sea otters is modified for aquatic locomotion, with a flexible spine and foreshortened limbs to reduce hydrodynamic drag. Forelimbs are used to capture and manipulate prey and for using tools (e.g., rocks) to open hard-shelled prey, but not for locomotion. Sea otters use dorsoventral undulation with simultaneous pelvic paddling during routine submerged swimming, and their hindfeet are modified into flippers for more efficient thrust. Because of their large lung volume, sea otters are positively buoyant and rest (sleep) effortlessly or swim in supine position at the surface, using alternate stroking of the hind flippers, although they are clumsy and slow when walking on land. To offset the high thermal conductivity of water, sea otters have a mass-specific basal metabolic rate that is 2.9-fold higher than a terrestrial eutherian mammal. As a result, they consume about 25% of their body mass daily, which requires them to spend 14–50% of their activity budget foraging. Because sea otters rely almost exclusively on fur for thermal insulation, they groom (felt) their dense fur to trap an air layer next to the skin, and this essential behavior represents a significant part of the daily activity budget. Sea otters have dichromatic color vision, underwater acuity similar to other marine mammals, and the aerial acuity of many terrestrial mammals. Although sea otters detect underwater sounds, hearing is primarily adapted for air, and they do not vocalize underwater. Their forepaws have good tactile surface discrimination for

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identifying prey by touch, but the role of their vibrissae in foraging is uncertain. Sea otters discriminate odorants and have a vomeronasal gland, which may detect pheromones that convey social or sexual (endocrine) cues that influence behavior and reproductive physiology. Based on the presence of taste buds, sea otters may have a gustatory sense. Compared to cetaceans, the sensory systems of sea otters are more similar to amphibious pinnipeds and terrestrial carnivorans.

Keywords Audition · Behavior · Craniodental · Durophagy · Efficiency · Fur · Gustation · Insulation · Morphology · Olfaction · Performance · Physiology · Respiration · Sea otter · Sensory · Sleep · Tactile · Vision · Vomeronasal gland

Morphology and physiology enable but also constrain an animal's behavior and physical performance, and sensory systems affect how an animal perceives its environment (i.e., the world as it is experienced by a particular organism or its *Umwelt* as described by Jakob Johann Freiherr von Uexküll; Stella and Kleisner 2010). The proportion of time that an animal devotes to various behaviors ultimately depends on energy metabolism: that is, the balance between energy acquisition and the energy expended for essential physiologic processes (e.g., basal metabolic rate, thermoregulation, lactation) and behavioral activities (e.g., foraging, reproduction, and social interaction). Abiotic and biotic selection pressures modify behavior and enhance both performance and sensory modalities for a particular habitat, although they are often a compromise among competing demands that ultimately determine survival and fitness. In this chapter, we review the morphologic, physiologic, and sensory adaptations that influence sea otter behavior.

Previous studies have identified five distinct behavioral activities in sea otters: resting, foraging, transiting, grooming, and socializing/mating (Figs. 3.1 and 3.2; Kenyon 1969; Garshelis 1983 Thometz et al. 2014; Cortez et al. 2016a). For territorial males, patrolling (searching for sexually receptive females and excluding other males) is an additional behavior and, for females, an additional behavior is grooming the pup. Nursing occurs while the female is resting and is a behavior usually assigned to the pup. Some of these behaviors are associated with body maintenance (i.e., resting, grooming) and some with performance (i.e., foraging, transiting, socializing/mating patrolling) that enhance survival and fitness, but all are influenced by morphologic and physiologic adaptations. The percentage of time associated with these behaviors varies by age, sex, location, season, and whether a male can maintain a territory or a female can produce and rear a pup. Hence, the values in Figs. 3.1 and 3.2 are representative of a particular location and season and are intended to illustrate types of behaviors and relative amounts of time allocated. Dependent pups are altricial and develop many adult behaviors as they mature during the six-month dependency period (Fig. 3.2c, d). One important behavior that does not appear in most activity budgets is predator avoidance (see Chap. 9). Predation on sea otters by killer whales and sharks is difficult to observe (i.e., these are short-duration events) even though predation can have a profound effect on

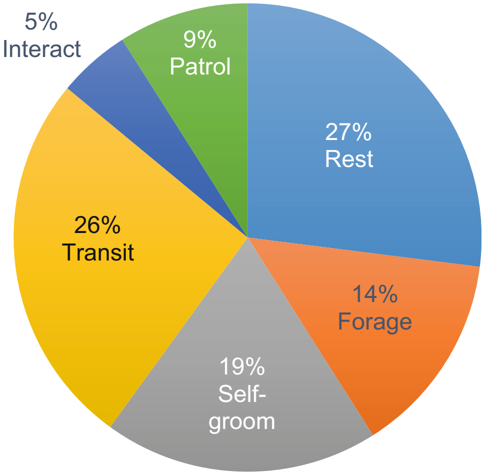

Fig. 3.1 Average 24-h activity budget for territorial male sea otters. Resting behavior includes sleeping on the water's surface. Foraging behavior includes the time submerged and while handling prey at the surface between dives. Self-groom refers to felting the fur to maintain an air layer. Transit refers to directed swimming at the surface, usually in the supine position (belly up with head facing backward) using alternate or simultaneous pelvic paddling. Patrol refers to swimming at the surface in the prone position (belly down with head facing forward). Interacting includes social and mating behavior. Data were collected in Simpson Bay, Alaska, from June-August. Data adapted from Finerty et al. (2009)

behavior and population density (Estes et al. 1998; Tinker et al. 2016). Predator avoidance may influence other behaviors, such as foraging and resting locations.

3.1 Morphology

3.1.1 Craniodental Morphology and Feeding

Sea otters are durophagous (from Latin *durus* [hard] + *−phagy* [feeding on]) and feed primarily on invertebrate prey with a shell (mollusks), exoskeleton (crustaceans), or test (sea urchins), although they feed opportunistically on other prey, such as sea cucumbers, octopuses, slow-moving benthic fishes, egg cases of rays, and herring roe on kelp. Hence, sea otters are marine specialists but diet generalists (see Chap. 5).

Sea otters have a short, robust skull with a blunt rostrum (Fig. 3.3a–d). The skull is characterized by (1) a wide, vaulted palate, (2) prominent sagittal, lambdoidal, and occipital crests, (3) a large coronoid process on each ramus of the mandibles for insertion of the temporalis muscles, and (4) long zygomas (zygomatic arches) that allow the masseter muscles to attach more anteriorly to increase force at the posterior jaw near the molars. These functional traits enhance bite force at large gape angles and provide greater control over mastication associated with durophagy (Wilson

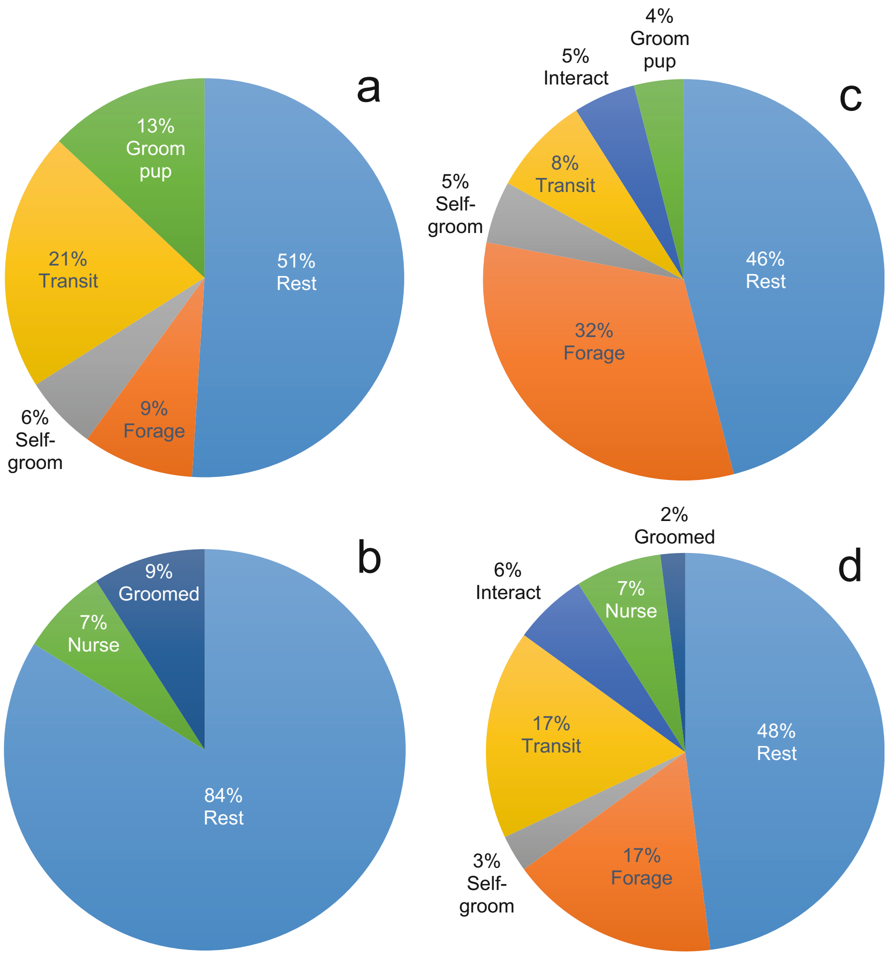

Fig. 3.2 Average 24-h activity budgets for female sea otters with pups of varying age: (**a**) female with (**b**) pup <4 weeks old; (**c**) female with (**d**) pup 8–12 weeks old. Resting behavior includes sleeping on the water's surface. Foraging behavior includes the time submerged and time handling prey at the surface between dives. Self-groom refers to felting the fur to maintain an air layer. Groomed refers to the pup being groomed by the female. Transiting is directed swimming at the surface, usually in the supine position (belly up with head facing backward) using alternate or simultaneous pelvic paddling. Nursing refers to the percentage of time spent suckling. Interact refers to socializing with other otters and, for the female, occasional mating behavior. Data for females with pups were collected simultaneously in Simpson Bay, Alaska, from June-August. Data adapted from (Cortez et al. 2016a, b)

et al. 1991; Timm-Davis et al. 2015, 2017; Law et al. 2017). The mandibular bluntness index (MBI) is 1.2 (Timm-Davis et al. 2015), indicating that the maximum width is greater than the length, which is unusual among terrestrial carnivorans. Despite having well-developed jaw musculature, the superficial and deep parts of the masseter are not well defined as they are in Lutra (Riley 1985).

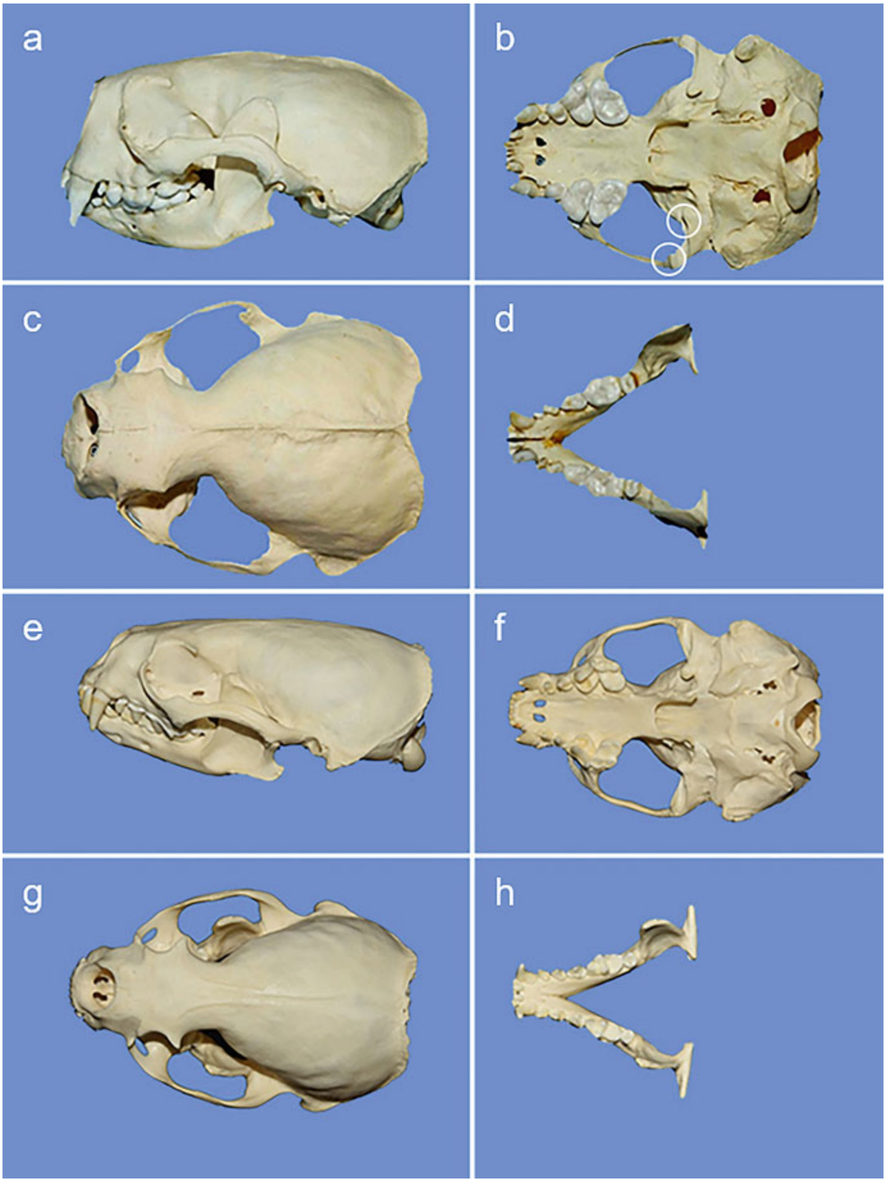

Fig. 3.3 Skull and jaw of a sea otter (**a**–**d**) and river otter (**e**–**h**). Circles in (**b**) identify the pre-articular and postglenoid processes, which partially surround the mandibular fossa and condyle, preventing transverse movement of the jaw

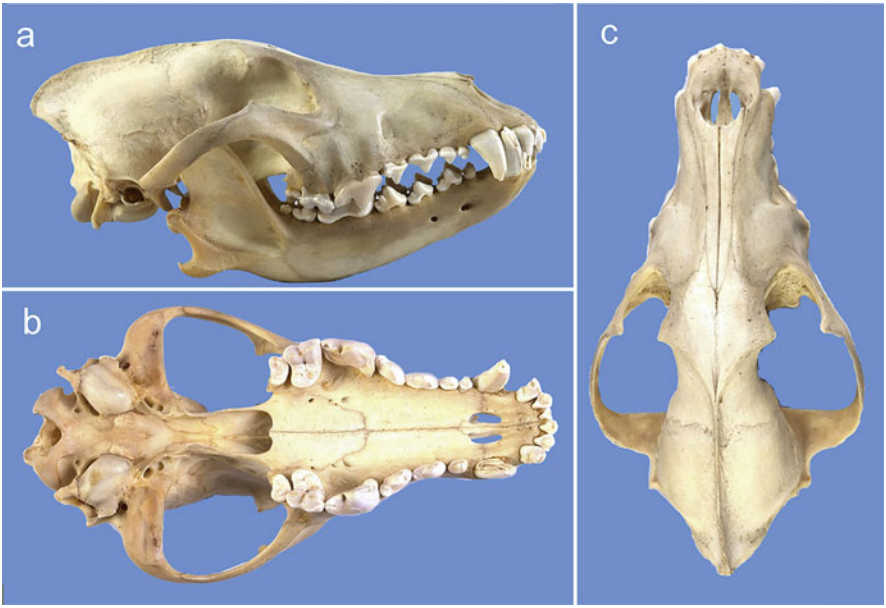

Fig. 3.4 Skull of a grey wolf

Foreshortening of the sea otter skull and jaw results in a reduced number of teeth (32 with the upper/lower dental formula: incisors 3/2, canines 1/1, premolars 3/3, molars 1/2; Fig. 3.3b, d) compared to the generalized heterodont dentition of early eutherian mammals (44 with the upper/lower dental formula: incisors 3/3; canines 1/1; premolars 4/4; molars 3/3), similar to that of the grey wolf (Fig. 3.4). While the incisor and canine teeth of sea otters are similar to other carnivorans, the postcanine teeth, especially the enlarged, upper third premolars and lower first molars, have rounded or conical cusps (bunodont dentition) and large occlusal surfaces for cracking or crushing hard-shelled, benthic invertebrates (Fig. 3.3b; Blair et al. 1968; Estes 1980; Lewis 2008; Timm 2013). Sea otters are the only extant otter species that possess a bunodont dentition for durophagy. To prevent transverse dislocation of the jaw when biting on hard prey, the pre-articular and postglenoid processes partially surround the mandibular fossa and condyle (Fig. 3.3b). In addition, the enamel of sea otter teeth is 2.5-fold stronger and more chip-resistant than that in humans (Ziscovici et al. 2014). The lower incisors protrude slightly and are spade-shaped for scooping flesh from the shells of bivalves. In comparison, North American river otters have a more elongate skull and additional teeth (36 with the upper/lower dental formula: incisors 3/3, canines 1/1, premolars 4/3, molars 1/2), which are adapted for grasping, piercing, tearing, and slicing soft prey, such as fish (Fig. 3.3e–f; Fisher 1941).

Sea otters are grouped with other raptorial predators even though they capture and manipulate prey with their forepaws (hand-oriented capture or prehension) (Werth

2000; Timm-Davis et al. 2015, 2017). This contrasts with the raptorial feeding behavior of mouth-oriented North American river otters, which feed on fish, small crustaceans, and amphibians. Unlike other carnivorous marine mammals, sea otters consume their prey at the surface rather than underwater. As a result, prey ingestion and mastication are similar to that in terrestrial carnivorans (Reilly and Lauder 1990; Hiiemae 2000; Markey and Marshall 2007; Timm-Davis et al. 2017). In contrast, Odontocetes (toothed whales) and Pinnipeds (seals, sea lions, fur seals, and walruses) capture and consume small prey underwater using raptorial biting and/or suction without mastication, or slash and tear off pieces from larger prey that are small enough to swallow without further processing in the oral cavity.

To extract the tissue of clams, mussels, and gastropods, sea otters position prey in the back of the mouth between the upper and lower premolars and molars, which requires a wide gape. In sea otters, routine gape angle ranges from 61–66° with a maximum angle of 82°, which is greater than the maximum gape angle (55–65°) for other carnivorans (Herring and Herring 1974; Christiansen and Adolfssen 2007; Timm-Davis et al. 2017). The jaws are closed, and the shell is cracked or crushed with a bite force of up to 554 Newtons (125 pounds) (Timm 2013). The shells of otter-predated clams and other hard-shelled bivalves are commonly found along beaches and typically have one broken valve and one intact valve joined at the hinge (Fig. 3.5b, d). When a hard-shelled clam is cracked, the broken piece distal from the hinge is discarded, and the otter then opens the clam and scoops out the flesh with its lower incisors and canines (Fig. 3.5e). Soft-shelled clams (e.g., Macomas) are easily crushed into multiple pieces and discarded, while the broken shell and flesh of small mussels are ingested entirely. The arms of decapod crabs are consumed with the exoskeleton, while the body is consumed after first removing the dorsal carapace with the canine teeth (Fig. 3.5f).

Because of their durophagous mode of feeding, the primary occlusal area provided by the enlarged upper third premolars and lower first molars shows the greatest wear, breakage, and infection, which may limit longevity (Fig. 3.6; Fisher 1941; Kenyon 1969). In addition, significant malocclusion of the postcanine teeth may occur in recently weaned pups feeding on hard prey but whose deciduous teeth have not been replaced. When sea otters can no longer feed efficiently, they die rapidly of starvation because of their elevated basal metabolic rate (see Sect. 3.2.4).

3.1.2 Axial and Appendicular Skeletal Morphology, Prey Capture, and Locomotion

3.1.2.1 Axial Specialization

The axial skeleton of the sea otter has been modified for aquatic locomotion to a greater extent than that of the amphibious North American river otter (Fig. 3.7a, b). The vertebral column exhibits adaptations for increased spinal flexibility, including (1) a larger intervertebral foramina, especially posteriorly, (2) smaller vertebral

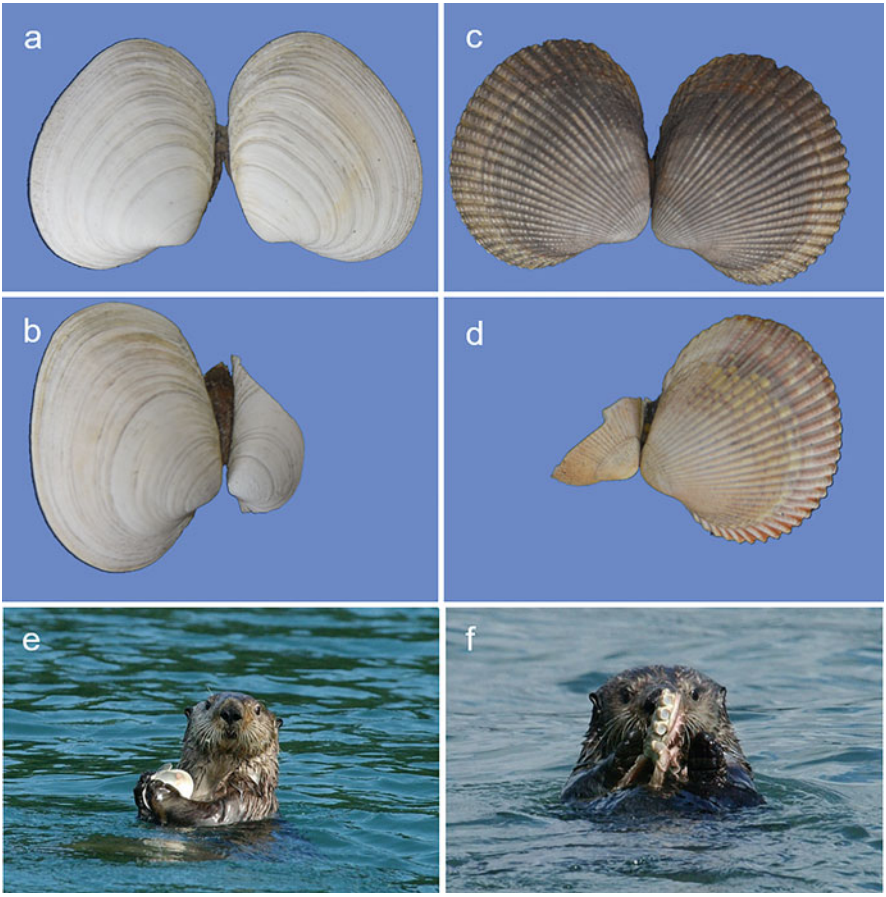

Fig. 3.5 Butter clams (*Saxidomus gigantea*) with (**a**) two intact hinged valves and (**b**) one broken valve resulting from sea otter predation. Nuttall's cockles (*Clinocardium nuttallii*) with (**c**) two intact hinged valves and (**d**) one broken valve resulting from sea otter predation. (**e**) Sea otter with a butter clam that has been cracked open and the flesh ingested. (**f**) Sea otter eating a decapod crab. Images (**e**, **f**) obtained under USFWS Marine Mammal Permits MA-043219 and MA-078744 to R. Davis

processes, (3) an increase in centra height (solid central part) and overall shortening of the vertebrae (Fig. 3.8a, b; Taylor 1914;). As a result, the vertebrae are less tightly coupled, which enhances spinal flexion during dorsoventral undulation with simultaneous pelvic paddling (see Sect. 3.1.2.3). The neck is short relative to the creating a more fusiform body shape, which reduces hydrodynamic drag. The thoracolumbar and caudal regions are modified for aquatic propulsion, including increases in mass of the epaxial musculature (*multifidus lumborum* and *longissimus thoracis*) and in the length of the neural spines and transverse processes of the lumbar and caudal vertebrae for muscle attachment (Taylor 1914; Gambarjan and Karapetjan 1961). The *rectus abdominus* muscle is well developed to assist in dorsoventral undulation

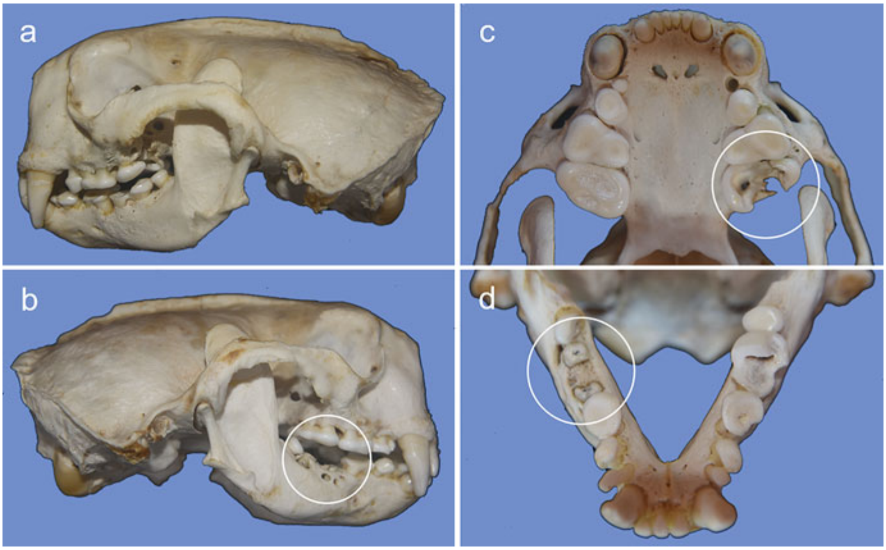

Fig. 3.6 The left (**a**) and right (**b**) side of the skull and the upper jaw (**c**) and lower jaw (**d**) of an adult sea otter skeleton that was found above the high tide line in Simpson Bay, Alaska. The teeth were heavily worn, and one upper and one lower molar (circles) were broken or missing. Bone necrosis was evident around the broken teeth

(Barabash-Nikiforov 1947). Compliant cartilaginous sternal ribs (costal cartilages) extend from the ends of the first ten boney vertebral ribs to the sternebrae, resulting in a compressible thorax that prevents barotrauma during diving (Fig. 3.8c; Barabash-Nikiforov 1947; Davis 2019). The tail is less muscular and flattened dorsoventrally compared to that of the North American river otter (Figs. 3.7a and 3.8a, b).

3.1.2.2 Appendicular Specialization

The hindfeet of sea otters are enlarged, webbed, and modified into flippers for more efficient thrust production in water, although they make terrestrial locomotion awkward (Figs. 3.7a and 3.8a, b). The hindfeet of North American river otters are smaller, webbed, and adapted for both terrestrial and aquatic locomotion (Figs. 3.7b). The forelimbs of sea otters are proportionally smaller than the hindlimbs, and both are foreshortened to reduce hydrodynamic drag. Sea otters use dorsoventral undulation with simultaneous pelvic paddling for locomotion, which involves only the hindlimbs. North American river otters use a similar mode of locomotion, but the forelimbs may assist in thrust production. The scapulae are small and postscapular fossae absent, indicating their reduced role for aquatic or terrestrial locomotion (Taylor 1914; Tarasoff et al. 1972). The clavicles are absent, providing extreme mobility of the pectoral girdle so that a sea otter can reach every

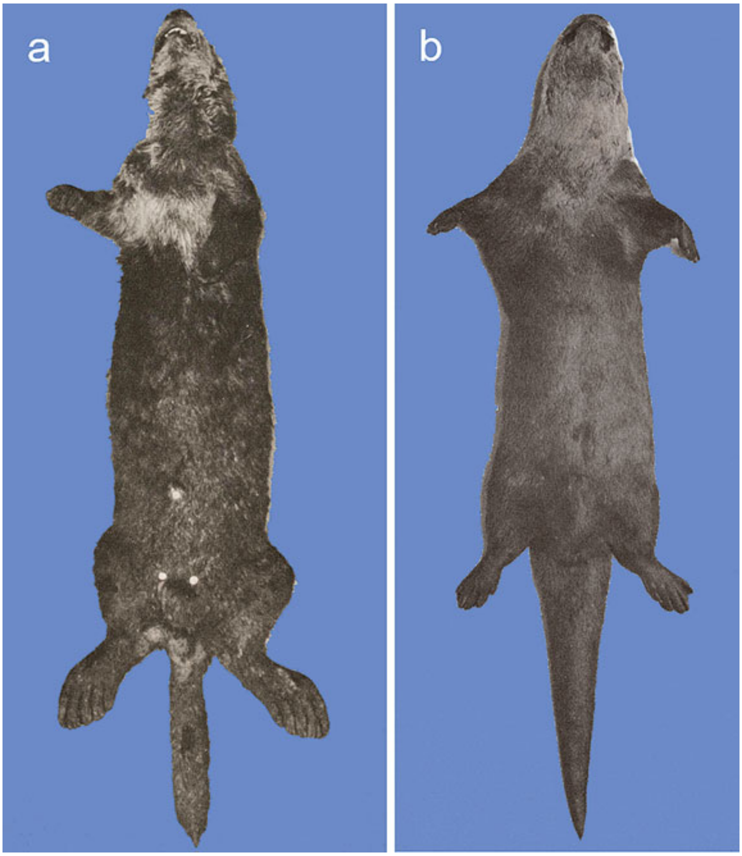

Fig. 3.7 External anatomy of an adult (**a**) sea otter and (**b**) North American river otter. Images adapted from Kenyon (1969)

part of its body when grooming, an essential behavior for thermoregulation (Howard 1975; Estes 1980). The palmated forepaws are small and mitten-like, with small metacarpals, short phalanges, and retractable claws (Figs. 3.8a and 3.9a, b, d; Kenyon 1969; Tarasoff et al. 1972; Estes 1980; Kilbourne 2017). Sea otters use their forepaws to capture and manipulate prey and to manipulate tools (e.g., rocks) used to open hard-shelled prey, but they do not use them for aquatic locomotion (Hall and Schaller 1964; Estes 1980; Bodkin et al. 2004; Fujii et al. 2015). The phalanges are encased within the paws (i.e., no division between the phalanges) and provide no independent movement or dexterity, so prey and rocks must be held between the paws (Fig. 3.5e, f; Pocock 1928; Howard 1975). These forelimb specializations for prey manipulation and grooming contrast with those of the ancestral *Enhydrotherium*, which were specialized for swimming (Lambert 1997; see Chap. 2).

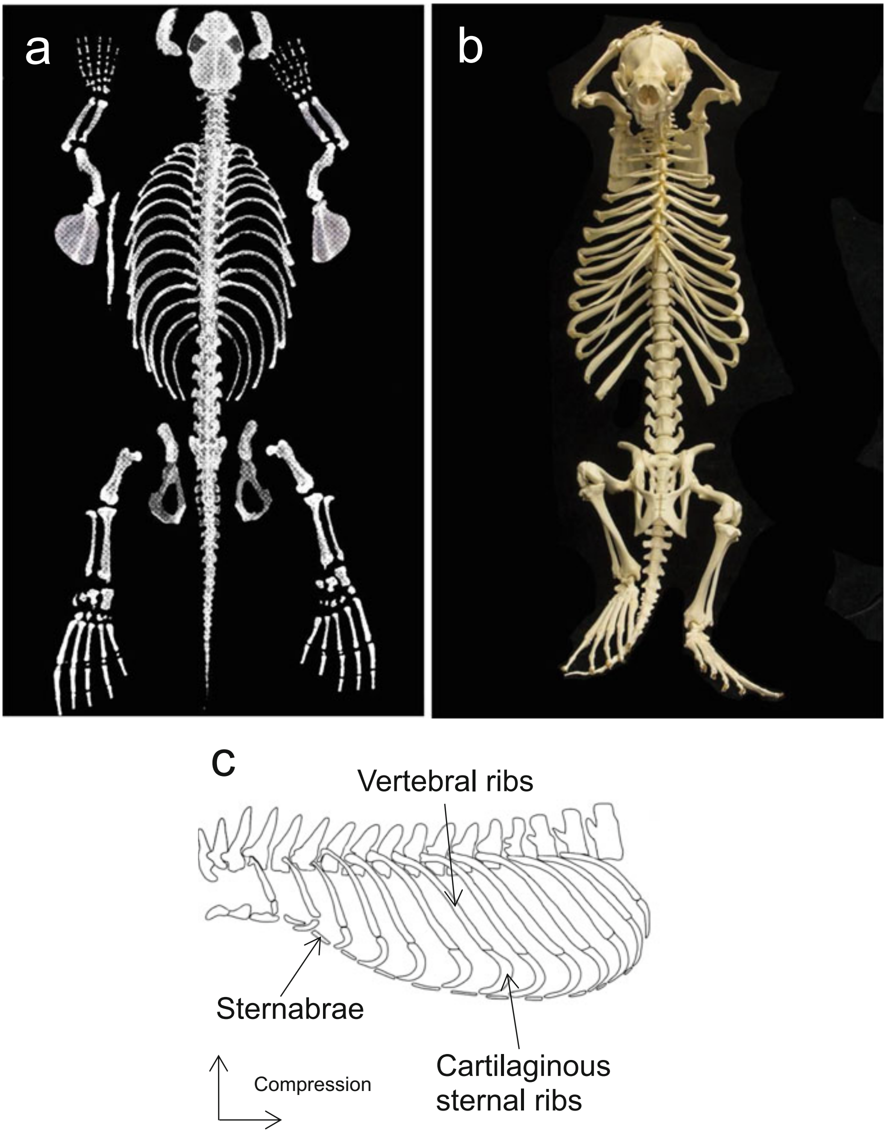

Fig. 3.8 (**a**) Dorsal view of the disarticulated sea otter skeleton, and (**b**) ventral view of the articulated skeleton. (**c**) Compliant cartilaginous sternal ribs (costal cartilages) extend from the ends of the first ten boney vertebral ribs to the sternebrae resulting in a compliant thorax with increased mobility. Image (**a**) modified from Kenyon (1969). Image (**b**) used with permission from Pinterest, and (**c**) adapted with permission from S. Rommel

The narrow and robust sea otter pelvis is elevated, making it parallel with the vertebral column and extended posteriorly (Fig. 3.8a, b). It is loosely connected to the sacral vertebrae and has a poorly fused pubic symphysis (Taylor 1914). Sea otter

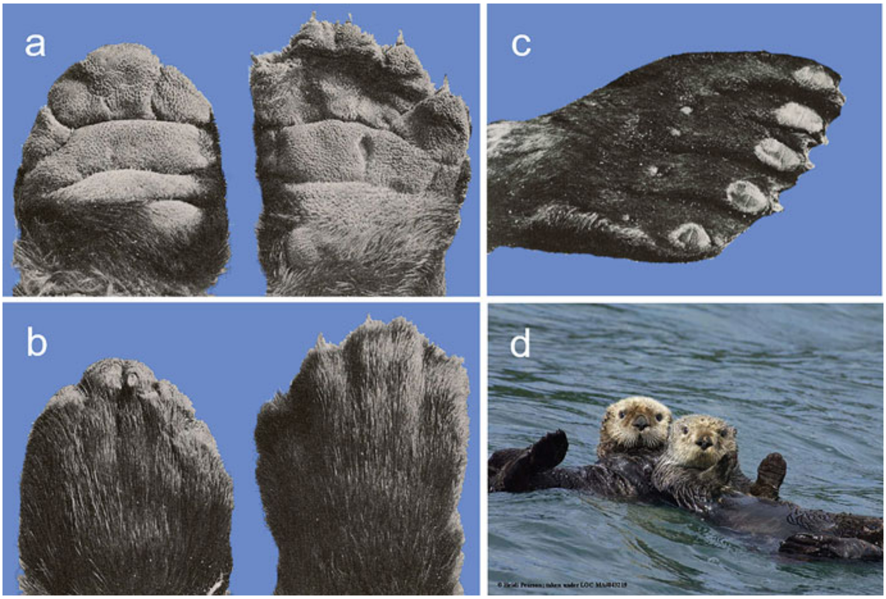

Fig. 3.9 (**a**) Ventral and (**b**) dorsal surface of sea otter forefeet (paws). (**c**) Ventral surface of a hindfoot (flipper). (**d**) Female and pup with fore and hindlimbs out of the water. Images **a**, **b**, **c** adapted from Kenyon (1969). Image (**d**) courtesy of H. Pearson obtained under USFWS Marine Mammal Permits MA-043219 and MA-078744 to R. Davis

femurs are disproportionately shorter than the tibias and fibulas, and most of the legs are encased within the body wall so that only the hindfeet project (Figs. 3.7a and 3.8a, b). The anterior surface of the robust femur is extended, causing the distal articular surface to face more posteriorly, resulting in a greater backward extension of the limb (Taylor 1989). The epicondyles of the femurs (bony protrusions located on the medial sides) are narrower and more rounded than those of the giant river otter (*Pteronura brasiliensis*), a species of similar size to the sea otter. This is likely due to the rarity of sea otters walking on land compared with the semiaquatic lifestyle of the giant river otter (Botton-Divet et al. 2016). The femur of sea otters, like that in Phocidae (seals), lacks the fovea capitis (a small, oval-shaped dimple on the ball-shaped end of the femur) and ligamentum teres (the ligament that inserts into the fovea capitis to prevent dislocation of the femoral head), which allows greater joint mobility at the acetabulofemoral (hip) joint (Estes 1980; Taylor 1989). This greater mobility is an adaptation among some hindlimb-specialized swimmers. The medial malleolus (the point of attachment of the major ligament on the inner side of the ankle) of the tibia is long and causes reduced mobility of the ankle. In addition, the fibulas are short and robust. These traits enhance aquatic locomotion but result in poor mobility on land.

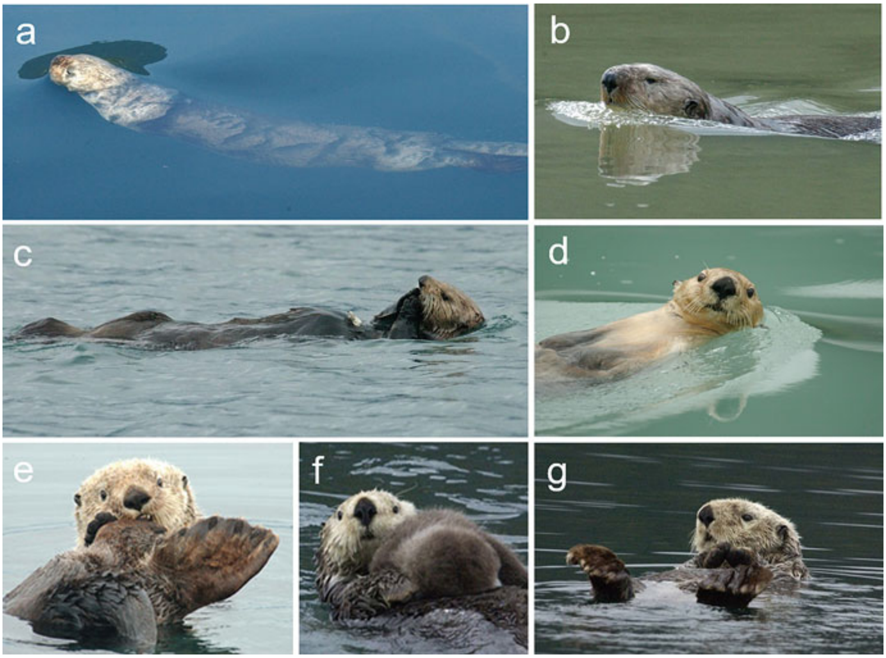

Fig. 3.10 Sea otter aquatic locomotion: (**a**) submerged swimming using dorsoventral undulation with simultaneous pelvic paddling, (**b**) male patrolling while surface swimming in the prone position using dorsoventral undulation with simultaneous pelvic paddling, (**c**) surface swimming in the supine position using alternate or simultaneous pelvic paddling, (**d**) surface wave generated during supine surface swimming, (**e**) enlarged hind flippers used for submerged and surface swimming, (**f**) newborn pup resting on the female's chest while surface swimming, (**g**) resting at the surface using positive buoyancy provided by the large lung volume. Images obtained under USFWS Marine Mammal Permits MA-043219 and MA-078744 to R. Davis

The hindfeet are modified into flippers by the elongation and spreading of the digits (Figs. 3.8a, b, and 3.9c; Taylor 1989). To achieve this, the metatarsals and phalanges have been elongated and flattened with webbing between the digits (Estes 1980; Taylor 1989). The fifth digit is the longest, decreasing in length to the first. The fifth and fourth digits are closely bound together beginning at the distal end of the proximal phalanx, thereby increasing the rigidity of the flipper during propulsion (Fig. 3.10e; Pocock 1928; Wilson et al. 1991). The fourth and third digital webbing starts at the proximal end of the proximal phalanx, with webbing for the other digits beginning in the distal metatarsal region (Tarasoff et al. 1972; Wilson et al. 1991). On the ventral surface, the distil end of each digit has a small pad and a non-retractable claw (Fig. 3.9c). There are no plantar and metatarsal pads, and most of the foot is covered with short hairs that do not trap an air layer (see Sect. 3.2.4). When the phalanges are spread, the foot doubles in width, thereby increasing propulsive surface area (Taylor 1989).

3.1.2.3 Aquatic Locomotion

Sea otters use dorsoventral undulation with simultaneous pelvic paddling during routine submerged swimming at speeds $<1.4 \text{ m s}^{-1}$ (Williams 1989; Figs. 3.10a). A wave (produced by flexion and extension of the back) travels rearward along the body and acts as a lever arm, allowing the hind flippers to move through a greater vertical displacement, which imparts more momentum to the water and greater thrust (Fish 2000). The wave created by undulation continues to produce thrust even during the recovery stroke of the hind flippers, but the mechanical efficiency is probably less than the lift-based propulsion in Cetacea, Sirenia, and Pinnipedia (Davis 2019). This mode of swimming is used during foraging dives and high-speed underwater travel, during which the otter may occasionally porpoise at the surface. The forelimbs make no contribution to any of the aquatic locomotory modes (Tarasoff et al. 1972).

With a lung volume substantially (3.3-fold) larger than in a terrestrial mammal of similar size, sea otters are positively buoyant (Kooyman 1973; see Sect. 3.2.1). This enables them to swim or rest effortlessly in the supine (belly up with head facing backward) position at the surface using simultaneous or alternating strokes of the hind flippers, usually at a speed of $<0.8 \text{ m s}^{-1}$ (Fig. 3.10c–g; Williams 1989). When resting on the surface with fore and hindlimbs out of water, subcarangiform tail flexion is used to change orientation or move slowly. Patrolling male sea otters swim at the surface in the prone position (belly down) using dorsoventral undulation with simultaneous pelvic paddling similar to submerged swimming (Fig. 3.10b). The head and scapular regions remain above water with the forepaws held against the chest, while the hindfeet stroke in unison. When transiting at the surface, sea otters may alternate between prone and supine swimming. Surface swimming is generally slower than when submerged because the otter's body acts like a displacement hull and generates a wake, which increases drag (Fig. 3.10d; Williams 1989).

3.1.2.4 Terrestrial Locomotion

Although agile swimmers, sea otters are clumsy and slow while walking on land because of their short forelimbs and large hind flippers (Kenyon 1969). Nevertheless, sea otters are capable of remarkable agility and speed when startled. They share a similar footfall pattern to river otters while walking or bounding but are more awkward and less efficient. Unlike river otters, they lack a running gait between their walking and bounding modes (Tarasoff et al. 1972). Walking cadence involves either alternate movement of opposing fore and hindlimbs or by moving the forelimbs and then dragging the hindlimbs, with limb position for both gaits identical to those of river otters (Tarasoff et al. 1972). The back is arched to keep the abdominal region off of the ground while the distal 1/3–1/2 of the tail drags behind. The hindfeet rest over the distal tarsal, metatarsal, and digital areas. While moving forward, the tarsometatarsal region makes first contact, followed by the "slap" of the digital region. At high speeds, sea otters transition to bounding, where the back is more highly arched and the hindlimbs are drawn towards the forelimbs (Tarasoff et al. 1972). Limb position is similar to that of river otters, with the tail often dragging on the ground as in the walking mode. While bounding, the feet move laterally in a rolling gait similar to that of the California sea lion (*Zalophus californianus*) (Peterson and Bartholomew 1967; Tarasoff et al. 1972).

3.2 Physiology

3.2.1 Respiration, Lung Volume, Buoyancy, and Oxygen Stores

As with terrestrial mammals, gas exchange in sea otters occurs in alveolar lungs with active ventilation at the surface. It may seem paradoxical that sea otters spend much of their lives submerged where they cannot breathe. Terrestrial mammals generally have unlimited access to air, so why would a group of mammals evolve to live in an aquatic environment where oxygen becomes a critical and limiting resource? There may be many answers to this question, but food seems one logical explanation.

The lung size of most marine and terrestrial mammals scales isometrically with body mass (BM; Fig. 3.11) (Tenney and Remmers 1963; Lenfant et al. 1970; Kooyman 1973; Gehr et al. 1981). However, sea otters have lungs (3.9% of body mass, BM), 3.3-fold larger than those in most marine and terrestrial mammals (Stahl 1967; Tarasoff and Kooyman 1973). This means that the calculated total lung volume (V_L) of a sea otter with a BM of 25 kg is 5354 ml (viz. V_L [ml] = (53.5 × $BM[kg]^{1.06}$) × 3.3; Stahl 1967). This value is less than that reported by Lenfant et al. (1970) but is consistent with the adjusted (3.3-fold greater) allometric prediction for mammals ranging in size from mice (25 g) to steers (500 kg). Because V_L and resting tidal volume (V_T; the volume of gas inhaled or exhaled during relaxed breathing) scale isometrically with BM, the calculated V_T is 722 ml (viz. $V_T[ml] = 7.69 \times BM[kg]^{1.04} \times 3.3$; Stahl 1967), which is 13% of V_L. In contrast, resting respiratory rate (RR) decreases allometrically with body mass ($kg^{-0.26}$) in terrestrial mammals. As a result, resting minute volume (MV; the volume of gas inhaled or exhaled per minute), which is the product of tidal volume and respiratory rate, scales allometrically with body mass ($kg^{1.04} \times kg^{-0.26} = kg^{1.04-0.26} = kg^{0.78}$), similar to the resting metabolic rate for eutherian mammals ($kg^{0.72}$) and carnivorans ($kg^{0.75}$) specifically (Davis 2019).

Unlike other marine mammals that breathe apneustically (periods of apnea after inhalation), sea otters have a eupneic breathing pattern similar to terrestrial mammals (a brief pause between breaths after exhalation), with a resting respiratory rate (RR) of 15 breathes min^{-1} (R. Davis unpub. obs.; T. Kendall pers. com). This is less than the predicted RR of 18 breathes min^{-1} for a 25 kg terrestrial mammal (viz. RR [breaths min^{-1}] = 252 × $BM[g]^{-0.26}$; Crosfill and Widdicombe 1961).

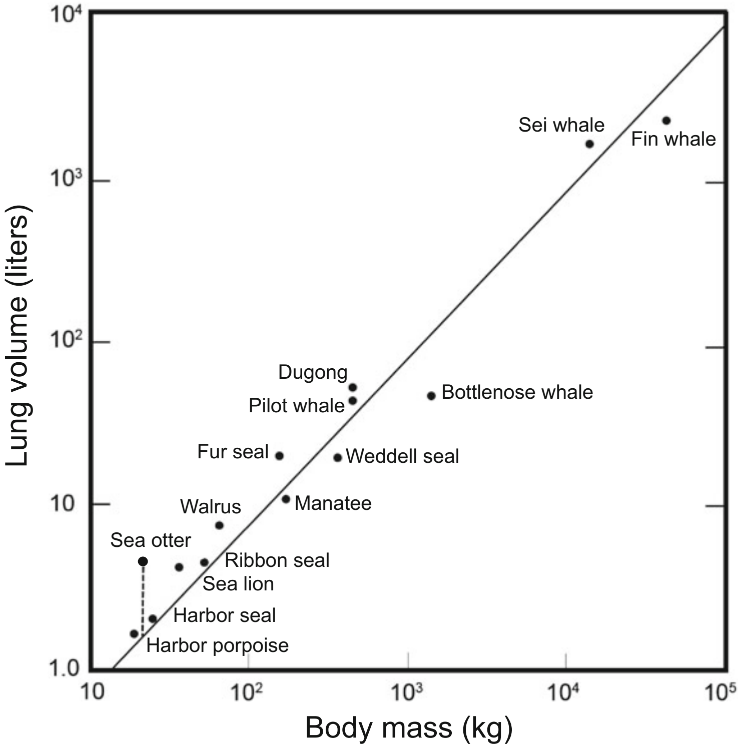

Fig. 3.11 Lung volume as a function of body mass for marine and terrestrial mammals. The regression line has a slope of 1.02 and is from the bat-to-whale data of Tenney and Remmers (1963). The sea otter has a lung volume that is threefold larger than a terrestrial mammal of similar mass. Adapted with permission from Kooyman (1973)

However, with an RR of 15 breathes min^{-1} and a large V_T of 722 ml, the MV is 2.7-fold larger than that of a terrestrial mammal of similar size. Ordinarily, this would result in hyperventilation. However, sea otters have a basal metabolic rate (BMR) that is 2.9-fold greater than the allometric prediction for terrestrial eutherian mammals (see Sect. 3.2.3). An elevated BMR requires an elevated MV of similar magnitude to maintain normal levels of alveolar and arterial PO_2 (100 mmHg or 13.3 kPa) and PCO_2 (40 mmHg or 5.3 kPa), which are independent of body mass. Because of their enlarged lungs and tidal volume, sea otters have an elevated MV that matches their elevated BMR.

A large lung volume along with air trapped in the fur (see Sect. 3.2.3) make sea otters positively buoyant on the surface, which enables them to rest and sleep effortlessly, even females with pups on their abdomen (Fig. 3.12). However, positive buoyancy means that they actively stroke with hind flippers when descending during a dive. The diving lung volume of sea otters has not been measured, but they hyperventilate and inhale prior to a foraging dive. Inhalation inflates the lungs, and otters float higher in the water, so they may dive on a full lung volume (R. Davis

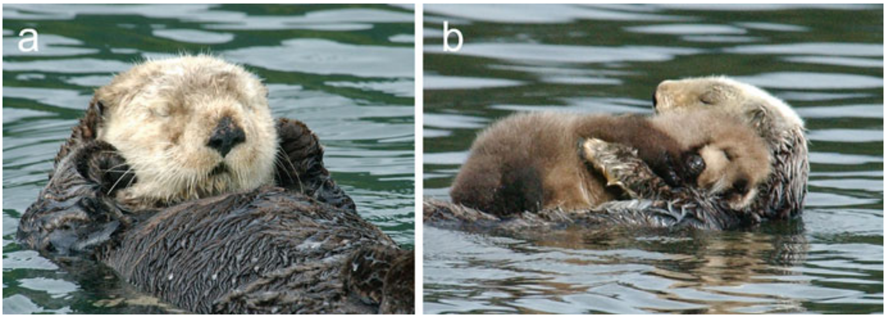

Fig. 3.12 (**a**) Sea otter sleeping on the surface and (**b**) female sea otter with and pup sleeping. Images obtained under USFWS Marine Mammal Permits MA-043219 and MA-078744 to R. Davis

unpub. obs.). To overcome positive buoyancy at the beginning of a foraging dive, a sea otter may leap out of the water with a powerful kick of the hind flippers, arch its back, and descend (Fig. 3.13).

The air layer trapped by a sea otter's fur provides thermal insulation, but it also adds to the animal's buoyancy. A 25 kg sea otter has a body surface area of 0.752 m^2 (viz. surface area$[m^2] = 0.087$ BM$[kg]^{0.67}$; Costa and Kooyman 1982) not including forepaws and hind flippers, which do not trap an air layer next to the skin. Their fur has a hair density of up to 1189 hairs mm^{-2}, but it is still 70% air by volume (Williams et al. 1988; Liwanag et al. 2012; see Sect. 3.2.3). Although the underhairs are ~1.9 cm long, the height of the air layer trapped in the fur is ~4 mm based on a whole-body thermal conductance of 6.68 W m^{-2} $°C^{-1}$ for adult sea otters resting in water at 13 °C, and a thermal conductivity for air of 0.025 W m^{-1} $°C^{-1}$ (viz. 0.025 W m^{-1} $°C^{-1}$ $\div$ 6.68 W m^{-2} $°C^{-1}$ $\times$ 1000 mm m^{-1}; Yeates et al. 2007; Davis 2019). This value is similar to the height of the air layer in the fur of fur seals (Liwanag et al. 2012). As a result, the volume of air trapped in the fur of a 25 kg sea otter is 2.1 L (viz. air volume[L] = (0.752 $m^2 \times 0.004$ m $\times 0.7 \times 1000$ L m^{-3}). With a V_L of 5.354 L (see calculation above), the total volume of air (fur and lungs) is 7.5 L, of which air in the fur represents 28%. Assuming sea otters dive with full lung volume, the positive buoyancy (N, Newtons) provided by air is:

$$7.5\ \mathrm{L} \times 1.024\ \mathrm{kg\ L^{-1}} \times 9.8\ \mathrm{m\ s^{-2}} = 75\ \mathrm{N}$$

where 1.024 kg L^{-1} is the density of seawater and 9.8 m s^{-2} is acceleration due to gravity. The buoyancy of lean tissue is −17 N (viz. −0.6689 N $kg^{-1} \times 25$ kg; Davis and Weihs 2007) and, because sea otters generally have little or no subcutaneous fat, their net buoyancy at the surface is 58 N (viz. 75 N – 17 N). As the otter descends during a dive, air in the lungs and fur compresses, and the otter becomes less buoyant until it reaches neutral buoyancy at a depth of ~35 m. This is deeper than for most foraging dives (<30 m) made by sea otters in Alaska and California (Bodkin et al. 2004; Tinker et al. 2007; Wolt et al. 2012). Hence, sea otters must actively stroke to remain submerged while capturing infaunal and epibenthic prey during routine dives

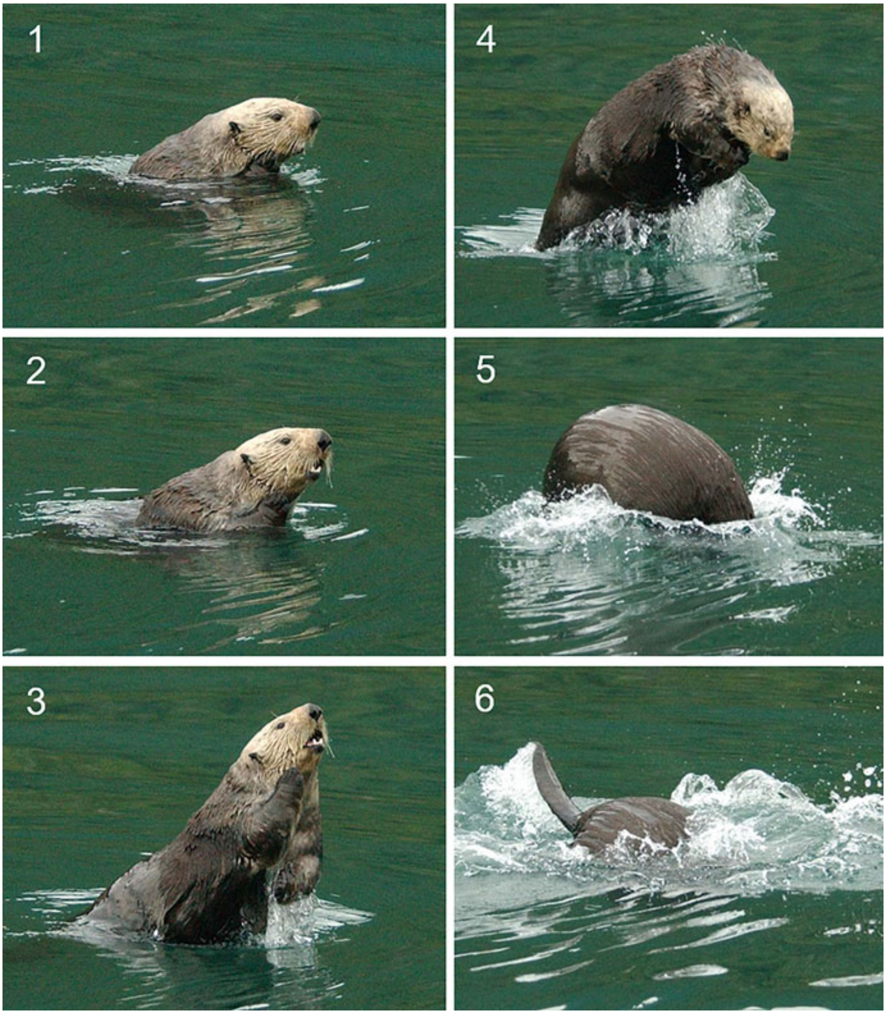

Fig. 3.13 The leap of an adult sea otter at the beginning of a foraging dive. This maneuver gives the sea otter momentum during the initial part of descent when it is the most buoyant. Images obtained under USFWS Marine Mammal Permits MA-043219 and MA-078744 to R. Davis

less than ~35 m deep. When they are ready to ascend, sea otters stop stroking and rise passively to the surface. At the maximum recorded dive depth of 100 m (Bodkin et al. 2004), which is rare, a 25 kg sea otter has a negative buoyancy of -10 N, so stroking would be required during initial ascent until it becomes positively buoyant above a depth of ~35 m. Hence, the mode of locomotion during a dive changes from active swimming during descent and benthic foraging to passive gliding during ascent above a depth of ~35 m.

3.2.2 Effects of Pressure

Aside from changes in buoyancy, air-filled lungs pose several challenges caused by increased pressure at depth when breath-hold diving. Aquatic, air-breathing vertebrates experience one additional atmosphere (101.3 kPa; kilopascal) of pressure for every 10 m of depth, which can have a profound influence on lung volume (Boyle's Law), the partial pressures of gases in a mixture (Dalton's Law), and the amount of dissolved gas in the blood (Henry's Law). As a result, deep-diving marine mammals have adaptations to avoid barotrauma, decompression sickness (DCS), and nitrogen narcosis (Davis 2019). However, compared to most other marine mammals, sea otters make relatively short and shallow dives (maximum duration of 4.5 min and depth of ~100 m), which limits benthic foraging to shallow coastal habitats. Routine dive depths (<30 m) and durations (2–3 min) are even more modest. As a result, pressure-related risks for sea otters are small, and there is no evidence for adaptations in lung morphology for deep diving, as observed in Cetacea and Pinnipedia (Davis 2019). In addition, the relatively shallow dives of sea otters pose no risk of high pressure nervous syndrome (HPNS), which is associated with neurological malfunctions (e.g., tremors, convulsions) at pressures of ~15–100 atmospheres (1.52–10.1 MPa; Megapascal) and equivalent to depths of ~150–1000 m (Kylstra et al. 1967).

3.2.3 Adaptations for Breath-Hold Diving

Sea otters spend 14–50% of each day foraging, depending on location, age, and reproductive status (e.g., males defending territories, lactating females with pups of varying age) (Figs. 3.1 and 3.2; Chaps. 6 and 7; Finerty et al. 2009; Wolt et al. 2012; Thometz et al. 2014). To capture infaunal and epibenthic prey, sea otters make routine breath-hold dives of <4 min, a behavior that provides energy for all essential physiologic processes and behaviors (Bodkin et al. 2004; Wolt et al. 2012). Unlike terrestrial mammals, which generally have unlimited access to air for gas exchange, sea otters and other marine mammals are adapted for interruptions in breathing yet are able to maintain an oxygen-based metabolism and physiologic homeostasis while underwater. The latter point is especially important; they not only avoid hypoxic tissue damage and death but also maintain behavioral (e.g., hunting behavior), physical (e.g., exercise), and physiologic functions (e.g., digestion and renal function) similar to terrestrial animals (Davis et al. 1983; Davis and Kanatous 1999; Davis et al. 2004; Davis 2014; Davis 2019).

The principal physiologic adaptation for breath-hold diving is the dive response, which is associated with apnea (cessation of breathing), bradycardia (reduced heart rate and cardiac output), and peripheral vasoconstriction, which maintains central arterial blood pressure. The dive response integrates the primitive cardiovascular response to protect animals from asphyxia with the equally primitive exercise (i.e.,

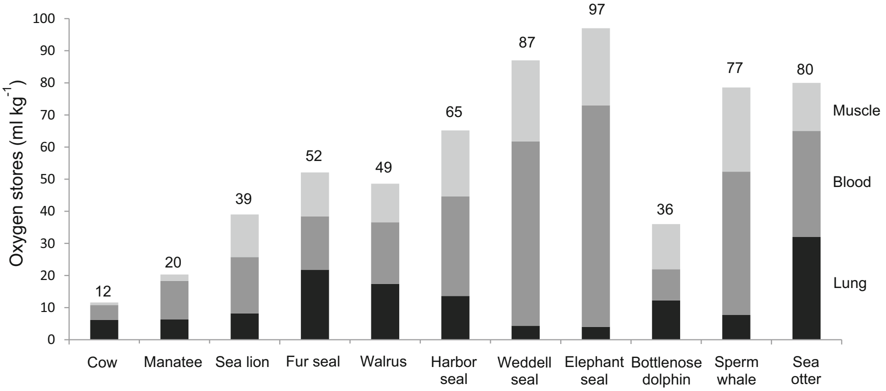

Fig. 3.14 Magnitude (ml O_2 kg^{-1}) and distribution (lungs, blood, and muscle) of body oxygen stores for a sedentary terrestrial mammal (cow, 450 kg), sea otter (25 kg), California sea lion (35 kg), northern fur seal (154 kg), harbor seal (24 kg), Weddell seal (450 kg), northern elephant seal, walrus (65 kg), Atlantic bottlenose dolphin (200 kg), sperm whale (10,000 kg), Florida manatee (350 kg). Data from Scholander and Irving (1941), Lenfant et al. (1970), Kooyman (1989), Kooyman and Ponganis (1998), Polasek and Davis (2001), and Thometz et al. (2015). Reprinted and adapted with permission from Davis (2019)

fight-or-flight) response to regulate blood flow in a manner that maintains aerobic metabolism at different levels of submerged exercise and maximizes the aerobic dive limit (ADL) (Davis 2019). Prior to a dive, sea otters hyperventilate to oxygenate blood hemoglobin and muscle myoglobin, which for many marine mammals are the primary oxygen stores. In sea otters, the large lungs also are a significant (40%) source of oxygen during a dive. Compared to a sedentary terrestrial mammal (e.g., cow), sea otters have a higher (42%) blood hemoglobin concentration (19 g Hb 100 ml^{-1}), a larger (2.4-fold) blood volume (173 ml kg^{-1}), and a higher (8.8-fold) muscle myoglobin concentration (3.5 g Mb 100 g^{-1} muscle). This results in an oxygen store of 80 ml O_2 kg^{-1} (Fig. 3.14). With an average diving metabolic rate of 21.5 ml O_2 min^{-1} kg^{-1}, a 25 kg sea otter has an ADL of ~3.7 min (viz. 80 ml O_2 kg^{-1} $\div$ 21.5 ml O_2 min^{-1} kg^{-1}; Cortez et al. 2016b). Hence, maximum aerobic dive duration and depth are constrained by available oxygen stores and the cost of locomotion. This limits the routine dive depth and available foraging habitat to near-coastal waters.

3.2.4 Metabolism and Thermoregulation

The thermal conductivity of water (0.025 W m^{-1} °C^{-1}) is 23-fold greater than that of air. This poses a potential thermoregulatory challenge for marine mammals, which are homeothermic (i.e., stable core body temperature of ~37 °C; Davis et al. 1988), especially for smaller species such as sea otters because of their large body surface area available for heat loss relative to the volume (volume = body mass body [kg] ÷ body density [0.99 kg l^{-1}]) of tissues that produce heat. Enhanced thermogenesis resulting in an elevated basal metabolic rate (BMR) is an adaptation to offset heat loss in water for all marine mammals except manatees (Davis 2019). Marine mammals have an average BMR that is 2.3-fold higher (range 1.6 [harbor seal] to 2.9 [sea otter]) than the allometric prediction for terrestrial eutherian mammals and 2.0-fold higher (range 1.4 [harbor seal] to 2.6 [sea otter]) than the allometric prediction for terrestrial carnivorans (Davis 2019). With the exception of the manatee, the average elevation of BMR in marine mammals is consistently higher than for any other group with two exceptions: among terrestrial eutherian mammals, the soricine shrews (e.g., Etruscan shrew, *Suncus etruscus*) and, among terrestrial carnivorans, the least weasel, *Mustela nivalis* (McNab 2008). An increase in BMR resulting from adaptive thermogenesis (i.e., regulated heat production through futile cycles) to balance heat loss in water seems plausible, and sea otters have the highest mass-specific BMR (0.234 kJ min^{-1} kg^{-1}) of any marine mammal (Costa and Kooyman 1982; Davis 2019). To support their high BMR, sea otters consume 25% of their body mass in food daily, which requires them to spend 14-50% of their daily activity budget foraging, depending on prey type and availability (Finerty et al. 2009; Wolt et al. 2012; Thometz et al. 2014). Female sea otters with pups may spend 30–50% of their day foraging, depending on the age and nutritional needs of the pup (Cortez et al. 2016b). Because of their high BMR, foraging behavior is a significant part of the sea otter daily activity budget (Figs. 3.1 and 3.2).

Most marine mammals rely on blubber for thermal insulation in water. Sea otters are the only marine mammal that relies exclusively on fur (Fig. 3.15a, b, c). To be an effective insulator in water, the fur must be waterproof and trap an air layer next to the skin. The flattened guard hairs (2.9 cm long) cover and shield the underhairs (1.9 cm long), creating a protective, water-resistant outer layer (Kooyman et al. 1977; Liwanag et al. 2012). Hair density (up to 1198 underhairs mm^{-1}) is the highest for any mammal, and the commercial market for this luxuriant fur nearly resulted in their extinction during the 18th and 19th century Maritime Fur Trade (Davis et al. 2019). The size and shape of cuticular scales on underhairs play an important role in trapping air in the fur of marine mammals (Fig. 3.15d). Elongated scales create differential friction along the length of the underhairs so that they easily slide past each other in one direction but not in the opposite. This differential friction enables sea otters to felt their fur (a process of condensing and pressing fibers together through repeated agitation so that they become tightly intertwined or interlocked) and trap an air layer next to the skin. In addition to felting, sea otters blow air into their fur through their nostrils while grooming. As sea otters groom their fur, the interstices between the underhairs become so small that water does not penetrate because of the high surface tension of water, creating an air layer that provides 70% of the thermal insulation (Kooyman et al. 1977; Williams et al. 1988). A 25 kg sea otter has a body surface area of 0.752 m^2 (*viz.* surface area[m^2] = 0.087 BM[kg]$^{0.67}$; Costa and Kooyman 1982), not including forepaws and hind flippers, which do not

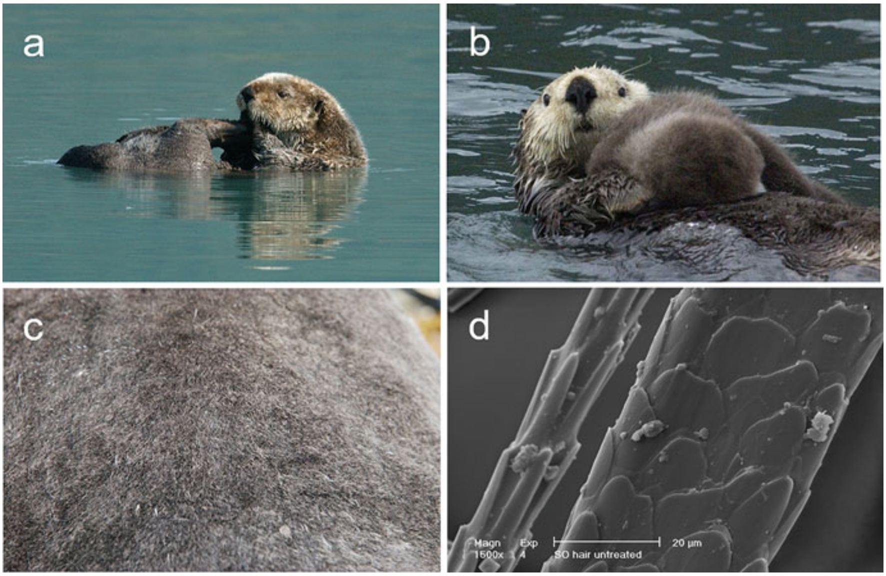

Fig. 3.15 (**a**) Sea otter grooming (felting) its fur, (**b**) female sea otter grooming the lanugo of its young pup, (**c**) the pelage of an adult sea otter, (**d**) electron micrograph showing the cuticular scales on the surface of a sea otter underhair (thin fiber) and guard hair (thick fiber). Images (**a**), (**b**), and (**c**) obtained under USFWS Marine Mammal Permits MA-043219 and MA-078744 to R. Davis. Image (**b**) courtesy of T.M. Williams

have an air layer next to the skin. Although the underhairs are 1.9 cm long, the thickness of the air layer trapped in the fur is 4.0 mm and the air volume is 2.1 L (Yeates et al. 2007; Davis 2019; see Sect. 3.2.3). During diving, air in the fur compresses, increasing whole body conduction. However, metabolic rate also increases 1.9-fold (from 4.5 to 8.7 W kg^{-1}; Yeates et al. 2007). At a depth of 9 m, the volume of air in the fur is reduced 48% to 1.1 L, and the thickness of the air layer is 2.1 mm. At this depth, diving metabolic heat production balances heat loss (i.e., 8.7 W kg^{-1}). At deeper depths, heat loss exceeds heat production, and the otter needs to rewarm at the surface between dives or make shallower dives to maintain a stable core body temperature of 37 °C.

Because sea otters rely on fur for thermal insulation, grooming behavior is a significant part of their daily activity budget (Figs. 3.1 and 3.2). Although many mammals groom their fur, adult sea otters spend about 5–19% of each day grooming their fur with their forepaws and, for females, grooming their young pups, which have a lanugo (dense natal fur) (Fig. 3.15a, b; Cortez et al. 2016a). Although grooming behavior may be instinctive, sea otter pups do not master this skill until they are 1–2 months of age, so the female must groom the pup to maintain an air layer in the fur.

3.2.5 Sleep

All mammals that have been studied exhibit periods of sleep based on behavioral and electrophysiologic criteria (Tobler 1988; Lyamin et al. 2008). Although the function of sleep remains poorly understood, it is believed to be an essential biological process. Wakefulness and sleep are usually considered mutually exclusive mental states: the former required for interacting with the abiotic and biotic environment and the latter serving a yet unknown function but one that often leaves the animal less responsive and vulnerable (Joiner 2016).

The electroencephalogram (EEG) is commonly used to characterize the transition from wakefulness to sleep at the cortical level as a change from bihemispheric, low-amplitude, and irregular fast waves to high-amplitude slow waves called slow-wave sleep (SWS). SWS is the deepest sleep with the least ability to be aroused and the lowest metabolic brain activity. Periodically, SWS changes to a low-amplitude and regular fast pattern called rapid-eye-movement (REM) sleep. This stage is characterized by high brain metabolic activity but paralysis of skeletal muscle (i.e., muscle atonia or inability to move in a coordinated manner). Behavioral sleep in terrestrial mammals is usually associated with closed eyes and varying degrees of body relaxation, immobility, and a reduced level of vigilance, but with a return to wakefulness given sufficient stimuli. Because respiration normally continues during sleep, an aquatic lifestyle poses a risk of drowning for marine mammals at sea.

There are no EEGs for sleeping sea otters, so we cannot distinguish between resting and sleeping using electrophysiologic criteria (Fig. 3.12a, b). In the summer, territorial male sea otters spend about 27% of their time resting or sleeping, which is less than predicated for terrestrial carnivorans (Fig. 3.1; Siegel 2005; Finerty et al. 2009). Female sea otters with newborn pups spend up to 50% of their time resting or sleeping, which gradually decreases as the pup matures, and the females spend more time foraging (Fig. 3.2a, c; Cortez et al. 2016a). This amount of time is similar to the prediction for terrestrial carnivorans (Siegel 2005). Newborn pups spend 83% of their day resting or sleeping (Fig. 3.2b), which is very different from some neonatal Odontoceti (e.g., bottlenose dolphins *Tursiops truncatus* and killer whales *Orcinus orca*) and their mothers, which remain active throughout the day for the first month postpartum (Lyamin et al. 2005). By the age of three months, the amount of time that sea otter pups spend resting or sleeping decreases to 48%, which is similar to that of the female (Fig. 3.2d; Cortez et al. 2016a). Sea otters often rest or sleep between foraging bouts, and the additional heat generated during digestion (Heat Increment of Feeding) may be important for thermoregulation during periods of reduced activity (Costa and Kooyman 1984).

Because sea otters have a large lung volume (see Sect. 3.2.1), they are buoyant and able to float effortlessly on the water's surface, sometimes with eyes closed as if asleep, forepaws resting on their chest, hind flippers out of the water, and with infrequent movement of the tail (Fig. 3.12a, b). Sea otters do not sleep underwater, but occasionally sleep on land, often curled up like a dog. In captive sea otters, behavioral sleep consistent with SWS (motionless on land or in water for more than 20 s) and REM sleep (single and serial jerks and twitches of the head, paws, and whole body) has been observed while they are on land and in water (Lyamin et al. 2000). Sea otters often rest on the water's surface with eyes closed, and their unresponsiveness is consistent with profound sleep and sometimes REM sleep (including occasional penile erection in males). Because of their buoyancy, muscle atonia during REM sleep is not a problem. It is not known whether sea otters exhibit unihemispheric slow-wave sleep (USWS), which has been recorded in bottlenose dolphins and fur seals. It is possible that sea otters exhibit patterns of SWS, USWS, and REM sleep similar to fur seals, but more research is needed (Davis 2019). From what little information we have, their sleep behavior is similar to terrestrial carnivorans, which is consistent with their shorter evolutionary history in the marine environment (see Chap. 2).

Sea otters are vulnerable to predation because they rest at the water's surface for long periods (up to 50% of each day; Fig. 3.2a). The effect of killer whales and white sharks (*Carcharodon carcharias*) on sea otter populations can be severe, so the options for sea otters to rest without predation may be limited (Estes et al. 1998; Tinker et al. 2016). As a result, group vigilance (rafting) on the water's surface or on land is essential (see Chap. 9). However, avoiding direct threats by sleeping in shallow lagoons and bays and avoiding detection (crypsis) in a kelp bed are also strategies to reduce vulnerability. In areas of Southcentral Alaska, sea otters ignore killer whales that come into the bays because they feed on salmon (R. Davis pers. obs.). As a result, adaptive behavior and learning may influence where sea otters rest and sleep. Refugia from wind and waves are also important for resting and sleeping.

3.3 Sensory Systems

Sensory receptors are specialized cells for transducing information from an animal's environment (exteroception) into nerve impulses (i.e., the movement of ionic currents in neurons) that are then transmitted to the central nervous system for processing and integration to detect external (environmental) variables and initiate responses that enhance survival (Willmer et al. 2005). Each type of receptor has its own sensory modality, such as vision, audition, olfaction, and gustation, although not all receptor types are present in every species, and some are more highly developed (i.e., provide greater acuity) than others. Hence, an animal's perceived world (its *Umwelt*) is only a subset of the actual physical world and presumably includes those sensory modalities most important for the survival and fitness of a species.

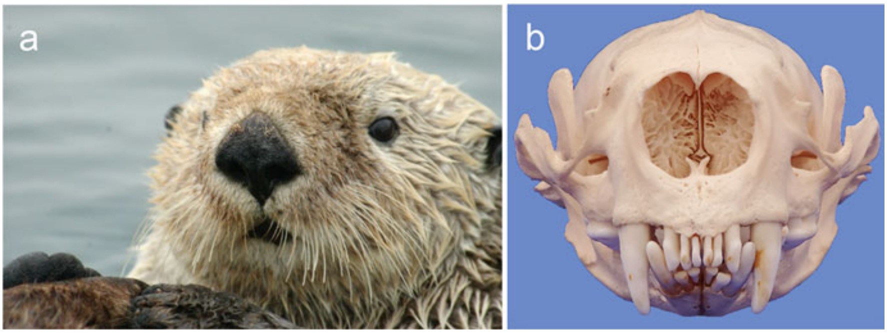

Fig. 3.16 (**a**) Head of an adult sea otter showing small eyes, large nose, and well-developed vibrissae. (**b**) Narial chamber of an adult sea otter. Image (**a**) obtained under USFWS Marine Mammal Permits MA-043219 and MA-078744 to R. Davis

3.3.1 Vision

The eyes of sea otters are small and resemble those of diurnal terrestrial mammals (Fig. 3.16a; Mass and Supin 2007). Instead of a spherical shape as occurs in Cetacea and Pinnipedia, the lens is lenticular except at the anterior surface, which has a protuberance with increased curvature. Unlike in other marine mammals, the iris is attached to the front of the lens, so when the iris contracts or dilates, it significantly influences the curvature of the lens and allows for emmetropic (focused) vision both in air and underwater. This gives sea otters an accommodative range of 60 diopters, which is three-fold greater than any other mammal and enables them to compensate for the loss of the refractive power of the cornea in water (Murphy et al. 1990). Based on retinal resolution, sea otter visual acuity in water is 7 arcmin, similar to the underwater acuity of other marine mammals and to the aerial acuity of many terrestrial mammals (Mass and Supin 2018). The retina has rods and cones with middle/long-wavelength and short-wavelength sensitive opsins, which indicate dichromatic color vision. The peak spectral sensitivity is predicted to be 501 nm, similar to terrestrial mammals (Levenson et al. 2006).

3.3.2 Audition and Sound Production

Although sea otters can detect underwater sounds, their hearing is primarily adapted for air and is similar to other carnivorans. Underwater, their hearing is less sensitive than that for Pinnipedia (Reichmuth et al. 2013). They have external pinnae, and their middle and inner ear morphology is probably similar to other mustelids (Fig. 3.16a). Sea otters have a U-shaped audiogram with a frequency range of 125 Hz to 32 kHz and peak sensitivities of ~1.6–22 kHz in air and 4–22.6 kHz underwater, similar to that of Pinnipedia (Fig. 3.17; Ghoul and Reichmuth 2012,

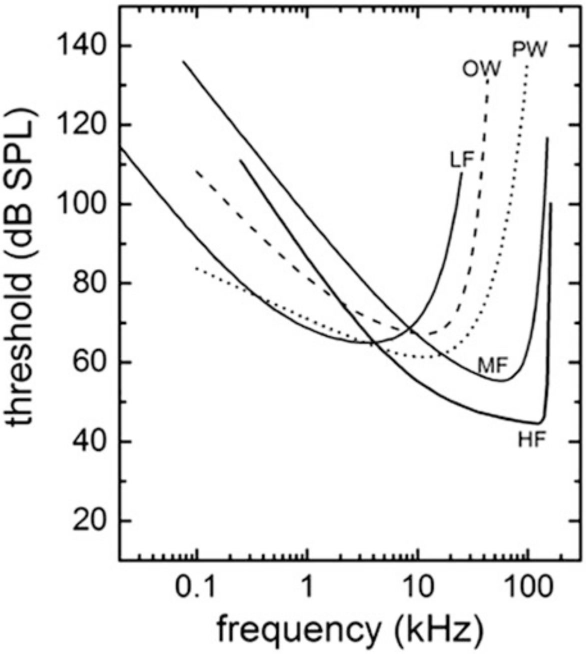

Fig. 3.17 Composite audiograms obtained through behavioral testing except for LF that was calculated. *HF* high-frequency cetaceans, *LF* low-frequency cetaceans, *MF* mid-frequency cetaceans, *OW* Otariidae, walrus, and sea otter in water, *PW* Phocidae in water. Thresholds are expressed in dB RMS re 1 μPa. Reprinted with permission from J.J Finneran and National Academies of Sciences, Engineering, and Medicine (2016)

2014, 2016). There is no evidence for underwater directional hearing, which has been demonstrated in some Phocidae (Wartzok et al. 1992). Sea otters produce a variety of aerial vocalizations (e.g., screams, baby cries, whistles, whines, hisses, snarls, coos, grunts, squeals, squeaks, and whimpers) for short-range communication (Kenyon 1969; McShane et al. 1995). Starting at birth, pups routinely produce a high-frequency cry when in distress or seeking attention from the female. Adults produce high-intensity screams that can be heard over long distances (up to 1 km), especially if they are distressed (e.g., when a female and pup are separated). Whether a pup and female recognize each other's vocalizations is unknown. Territorial males also are capable of producing high-intensity screams when interacting with females (R. Davis, unpub. obs.). There is no indication that sea otters produce vocalizations underwater.

3.3.3 *Sense of Touch and Vibrissae*

Sea otters capture and manipulate prey with their forepaws, often by searching for infaunal prey in muddy sediments where visibility is limited because of turbidity or epibenthic prey under low light conditions (Figs. 3.5e, f, and 3.9a, b, d). The threshold for tactile surface discrimination (i.e., alternating grooves) is ≤ 0.5 mm with a very rapid (<1 s) response time, and this ability is consistent with the enlarged somatosensory cortex representing the paws (Radinsky 1968; Strobel et al. 2018). This gives sea otters good tactile sensitivity to detect and distinguish prey, and they are 87% successful while making foraging dives (Shimek 1977; Wolt et al. 2012).

Sea otters have mystacial vibrissae that are mobile, while their supraorbital ones are not (Fig. 3.16a; Marshall et al. 2014). The follicle-sinus complex at the base of the vibrissae, along with the expansion of the somatosensory cortex, is convergent with those in Pinnipedia, indicating a similar vibrissal tactile sensitivity, but how sea otters use their vibrissae remains uncertain. They appear to rely on the tactile sensitivity of their forepaws or on vision to locate and capture sessile invertebrates (Strobel et al. 2018). This is different from the mouth-oriented raptorial or suction feeding of Pinnipedia that use their vibrissae to locate prey by direct contact or by sensing hydrodynamic trails produced by fish (Dehnhardt et al. 2001; Wieskotten et al. 2011). Sea otters do not whisk the seafloor when searching for epibenthic or infaunal prey, and they rarely pursue highly mobile fish. Hence, the role of vibrissae has yet to be determined.

3.3.4 Olfaction (Smell)

Sea otters have a large nose and narial chamber with extensive ethmoturbinate bones (Fig. 3.16a, b; Van Valkenburgh et al. 2011). An olfactory bulb is present but reduced in size relative to that of marten (*Martes* spp.: England and Dillon 1972). There is some experimental evidence that sea otters can discriminate odorants (Hammock 2005). Sea otters also have a vomeronasal gland, which may detect volatile and nonvolatile pheromones released by females, which convey social or

Fig. 3.18 Male sea otters nosing the anogenital region of a female before copulation. Image obtained under USFWS Marine Mammal Permits MA-043219 and MA-078744 to R. Davis

sexual (endocrine) cues that can influence behavior and reproductive physiology (Chamero et al. 2007; Liberles 2009). However, the proportion of functional receptor genes has not been determined. Sea otters sniff at feces on shore, and males nose the anogenital region of females before copulation (Fig. 3.18). Whether this involves receptors in the main olfactory epithelium or the vomeronasal organ is unknown.

3.3.5 Gustation (Taste)

Sea otters capture and manipulate sessile invertebrates with their forepaws (hand-oriented capture or prehension) and ingest prey at the surface (Fig. 3.5e, f). Other marine mammals are mouth-oriented predators (raptorial, suction, or a combination) that ingest smaller prey underwater but may tear larger prey into smaller pieces underwater or at the surface. In contrast, sea otters masticate their food and have a narrow, mobile tongue that is used to manipulate food in the oral cavity. The tongue is covered primarily with filiform papillae (non-sensory) of different shapes, which assist in the ingestion of food and in grooming the fur (Shimoda et al. 1996). Fungiform papillae with taste buds are scattered among the filiform papillae, and circumvallate papillae (large and specialized) with taste buds are present in a V-shaped row on the posterior region of the tongue. Taste buds also occur in the mucosa of the pharyngeal part of the tongue. Genetic data indicate that the receptor for sweet tastants is a pseudogene (non-functional) in Asian short-clawed otters (*Aonyx cinereus*; Jiang et al. 2012). There are no genetic data for receptor genes associated with umami, bitter, sour, or salty tastants in sea otters or other mustelids. Based on the presence of taste buds, sea otters may have a gustatory sense, which is reduced compared to other mammals.

*3.3.6 The Multimodal Sensory Perception (*Umwelt*) of Sea Otters*

Sea otters appear to have good aerial vision and hearing for detecting conspecifics and threats (Ghoul and Reichmuth 2012, 2014; Mass and Supin 2018). Aerial sound production is associated with social interactions. Underwater, sea otters have good vision (Mass and Supin 2018). However, their hearing is less sensitive than in other amphibious marine carnivores such as Pinnipedia, and there is no evidence for directional hearing (Reichmuth et al. 2013). Sea otters do not vocalize underwater. Tactile discrimination is good and used for capturing infaunal and epibenthic prey (Strobel et al. 2018), but the role of vibrissae has not been determined. There is some experimental evidence that sea otters can discriminate odorants (Hammock 2005). The well-developed vomeronasal gland may detect volatile and nonvolatile pheromones, which convey social or sexual (endocrine) cues and can influence behavior and reproductive physiology (Chamero et al. 2007; Liberles 2009). Based on the presence of taste buds, sea otters may have a gustatory sense that is reduced compared to other mammals. Compared to Cetacea, the sensory systems of sea otters are more similar to those of amphibious Pinnipedia and terrestrial carnivorans.

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Chapter 4
Sea Otter Foraging Behavior

Randall W. Davis and James L. Bodkin

Abstract Sea otters are marine specialists but diet generalists, which feed primarily on benthic mega-invertebrates (i.e., body dimension >1 cm). They locate and capture epibenthic and infaunal prey with their forepaws by relying on vision and tactile sensitivity during short-duration dives (generally <2 min) in shallow waters (routine dives <30 m and maximum dive depth ~100 m) of the littoral zone. Sea otters have an elevated resting metabolic rate and small or no energy reserves in the form of blubber, so they feed every 3–4 h. Foraging dives often occur in bouts (i.e., two or more consecutive dives), which may last several hours with 1–2 min between dives, depending on the type of prey. Sea otters consume small or soft prey entirely or use their teeth or stone tools to access the flesh of mega-invertebrates with a shell, test, or exoskeleton. The daily percentage of time that sea otters devote to foraging depends on age, sex, presence of a pup, time of year, and prey abundance, which varies geographically, seasonally, and episodically. In areas occupied by sea otters for many years, epifaunal prey generally decline first followed by infaunal species, and this may result in greater foraging effort and diet specialization associated with density-dependent competition for food. Although prey availability strongly influences sea otter carrying capacity, both intrinsic and extrinsic factors influence population equilibrium density, resulting in spatiotemporal variations in foraging behavior.

Keywords Capture · Carrying capacity · Diet · Diving · Epibenthic · Foraging · Generalist · Infauna · Mega-invertebrate · Prey · Sea otter · Specialist · Tactile · Time budget · Tool · Vision

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4.1 Sea Otters: Marine Specialists But Diet Generalists

An animal forages to remain in energy balance, grow, and reproduce. As a result, foraging is a prominent behavior, although the amount of time devoted to it will vary among species. Sea otters, which are marine specialists but diet generalists, feed primarily on benthic mega-invertebrates (i.e., body dimension >1 cm), such as mollusks, crustaceans, echinoderms, and cephalopod, although they also feed opportunistically on slow-moving demersal fishes, the egg cases of rays, and herring roe on kelp. They locate and capture epibenthic and infaunal prey with their forepaws by relying on vision and tactile sensitivity during short-duration dives (routine dives <2 min) in shallow water (routine dives <30 m and maximum dive depth ~100 m) in the littoral zone (see Sect. 3.2.3; Bodkin et al. 2004; Wolt et al. 2012; Thometz et al. 2016; Davis 2019). Because of their elevated basal metabolic rate (i.e., 2.9-fold higher than a terrestrial mammal of similar size) and food consumption (i.e., 25% of body mass daily; see Sect. 3.3.4), sea otters have a significant top-down effect on benthic mega-invertebrates, which affects littoral community structure (see Chap. 8; Estes and Palmisano 1974; Kenyon 1969; Estes and Duggins 1995; Estes 2015; Davis 2019).

4.2 Evolution of Sea Otter Foraging Behavior

The Lutrinae subfamily of otters exhibits two types of prey capture: hand-oriented and mouth-oriented. Hand-oriented otters (e.g., *Enhydra* and *Aonyx*) feed primarily on benthic invertebrates, which they capture and manipulate with their forepaws, sometimes using stones as tools for opening hard-shelled bivalves (Estes et al. 2009; Timm-Davis et al. 2015, 2017). Mouth-oriented otters (e.g., *Lutra*, *Lontra*, and *Pteronura*) feed primarily on fishes, which they capture (grasp) with their teeth. These two foraging behaviors are reflected in the morphology of the skull and teeth of sea otters and North American river otters (*Lontra canadensis*), respectively. Sea otters are durophagous (from Latin durus [hard] + −phagy [feeding on]) and feed primarily on mega-invertebrates with a shell (mollusks), exoskeleton (crustaceans), or test (sea urchins), although they feed opportunistically on other prey without an exoskeleton (e.g., octopuses). They have short, blunt skulls and postcanines with rounded or conical cusps (bunodont dentition) and large occlusal surfaces for crushing hard prey (Fig. 4.1a–d; see Sect. 3.1.1; Fisher 1941). In contrast, North American river otters are primarily piscivorous, and their teeth are adapted for grasping, piercing, tearing, and shearing soft prey, such as fish (Fig. 4.1e–h).

The ancestors of sea otters (*Enhydra*) diverged from other Eurasian otters in the early Pliocene (~5 Mya). One lineage was *Enhydritherium*, which dispersed from Europe around the northern rim of the North Atlantic Ocean and into the Gulf of Mexico ~2 Mya, where the first fossils of *Enhydritherium terraenovae* appeared in Florida (see Sect. 2.4). *E. terraenovae* and extant sea otters were similar in size, with a body mass of ~22 kg (Lambert 1997). However, according to the

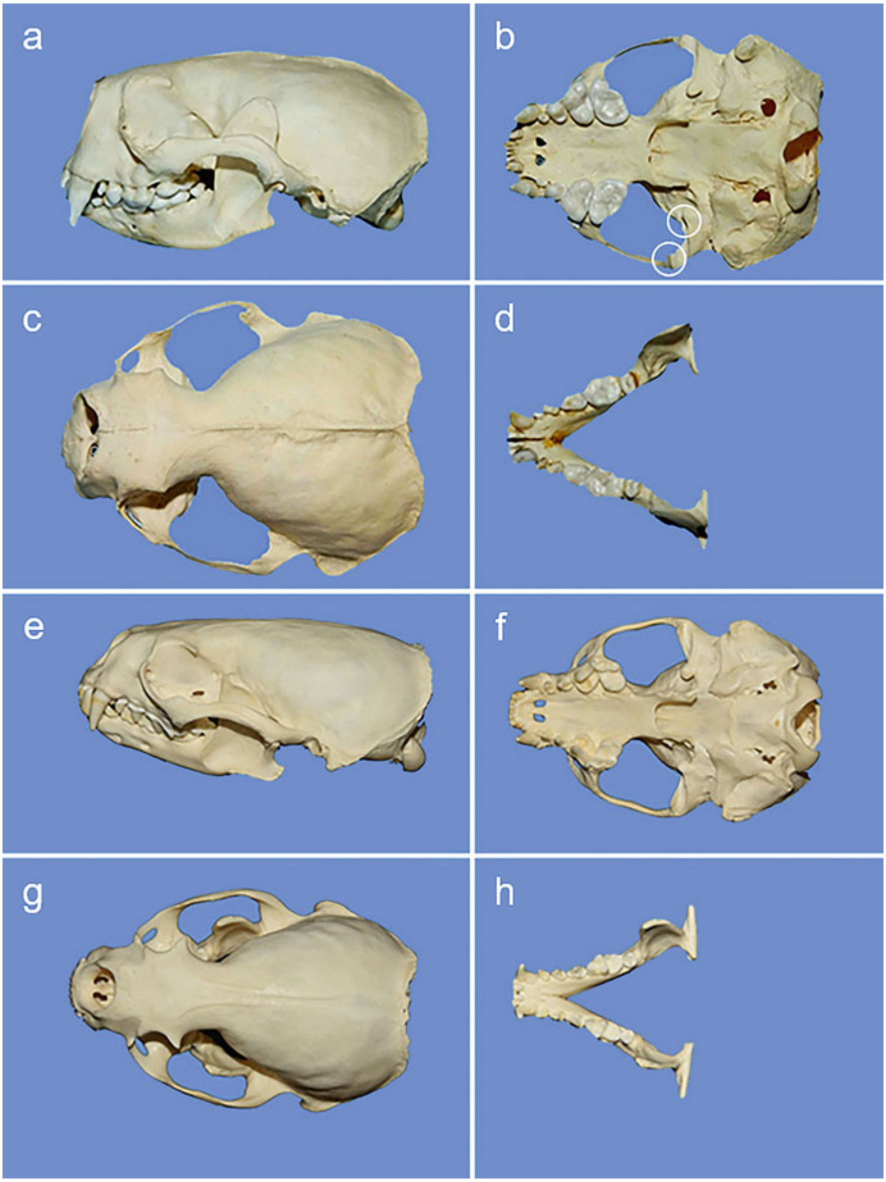

Fig. 4.1 Skull and jaw of a sea otter (**a**–**d**) and river otter (**e**–**h**). Circles in (**b**) identify the pre-articular and postglenoid processes, which partially surround the mandibular fossa and condyle that prevent transverse movement of the jaw

paleoenvironment of the fossil sites in Florida, *E. terraenovae* inhabited both nearshore marine and inland freshwater environments, whereas sea otters are restricted to marine habitats. Because it had morphological characteristics of both river otters and modern sea otters, it is likely that *E. terraenovae* was transitional between mouth-oriented and hand-oriented prey capture. The diet of *E. terraenovae* likely consisted of hard prey, such as mollusks (similar to sea otters), because of the thick, heavily worn cusps on the carnassial teeth. However, their diet most likely included fish when in freshwater environments, indicating a habitat generalist rather than a marine specialist. The events leading to the dispersal of *Enhydritherium* into the Pacific Ocean through the Central American Seaway, where presumably it gave rise to *Enhydra* (3–1 Mya), remain uncertain and will require additional fossil evidence. We know that *Enhydritherium* became extinct in the Atlantic, and *Enhydra* dispersed around the North Pacific Rim, where it became adapted to a durophagus diet of marine invertebrates.

4.3 Foraging Dives

All otters feed primarily on aquatic prey, which they capture during short, shallow dives. Most otters are semi-aquatic and occupy a variety of habitats, including lakes, streams, rivers, marshes, swamp forests, estuaries, and coastal waters, where they feed primarily on fish and small invertebrates. In contrast, sea otters are marine specialists, which feed primarily on mega-invertebrates but occasionally sessile fish (Watt et al. 2000; Wolt et al. 2012). When swimming on the surface in a prone (belly down) position or while diving, sea otters use dorsoventral undulation with simultaneous pelvic paddling at speeds $<1.4\ \mathrm{m\ s^{-1}}$ (Fig. 4.2; see Sect. 3.1.2.3; Williams 1989; Davis 2019). The forelimbs are held close to the body to reduce drag and are not used for locomotion. Sea otters are positively buoyant because of a lung volume that is substantially larger (3.3-fold) than in a terrestrial mammal of similar size (Kooyman 1973; see Sect. 3.2.1). Prior to a dive, sea otters hyperventilate to oxygenate blood hemoglobin and muscle myoglobin, which are the primary oxygen stores (Davis 2019). Unlike many marine mammals, the large lungs of sea otters also are a significant (40%) source of oxygen during a dive. Although diving lung volume has not been measured, sea otters inhale prior to a foraging dive, which causes them to float higher in the water, so they may dive on a full lung volume (see Sect. 3.2.1). To overcome positive buoyancy at the beginning of a foraging dive, a sea otter may leap out of the water with a powerful kick of the hind flippers, arch its back, and descend (Fig. 4.3).

Positive buoyancy means that sea otters must actively stroke with their hind flippers when descending during a dive. Assuming a full lung volume, sea otters reach neutral buoyancy at a depth of ~35 m (see Sect. 3.2.1). This is deeper than most foraging dives (<30 m) made by sea otters in Alaska and California (Bodkin et al. 2004; Tinker et al. 2007; Wolt et al. 2012; Thometz et al. 2016). Hence, sea otters must actively stroke to remain submerged while capturing epibenthic and infaunal prey during routine dives less than ~35 m deep, although this analysis does not include changes in buoyancy resulting from the gradual loss of air (bubbles) from the fur (Fig. 4.4b). When they are ready to ascend, sea otters stop stroking and

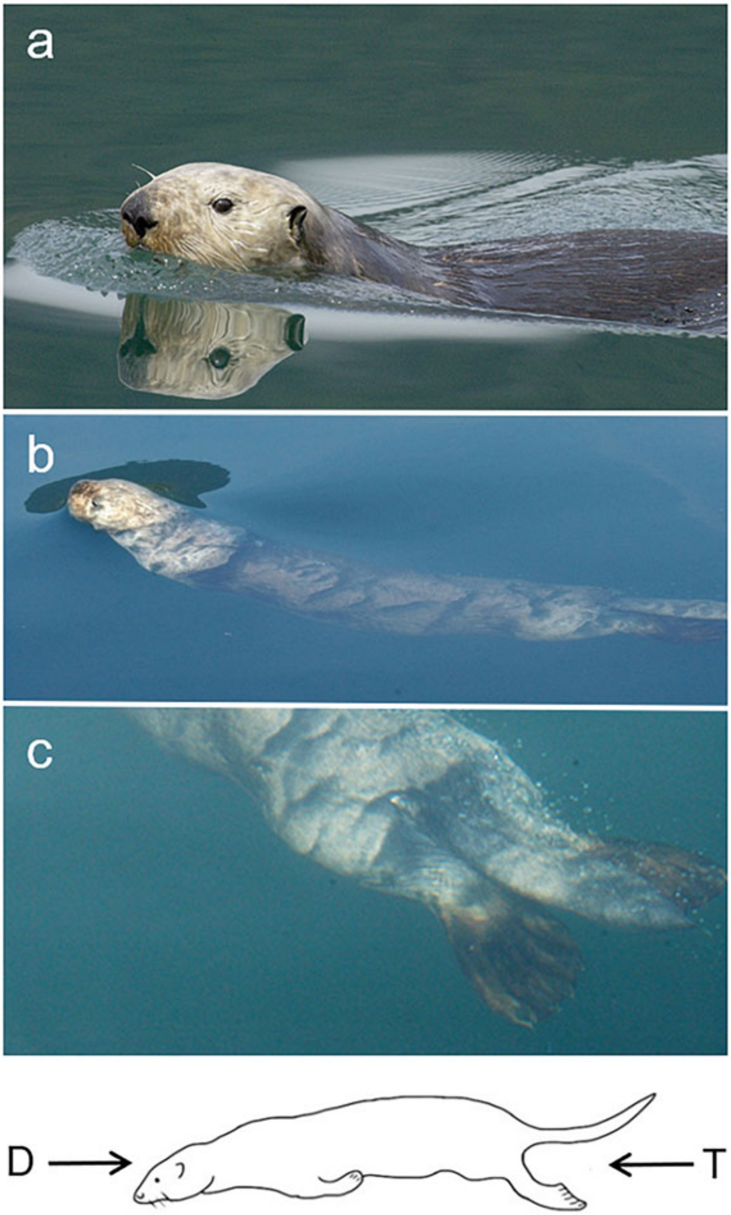

Fig. 4.2 Sea otters use their hind flippers when (**a**) swimming on the surface in a prone position and (**b**) swimming submerged. In both cases, sea otters use dorsoventral undulation and simultaneous pelvic paddling with their webbed hind feet (**c**), which generate thrust (T) to overcome drag (D) (**d**). The fore limbs are held close to the body to reduce drag and are not used for locomotion. Images (**a**–**c**) were obtained under USFWS Permit Nos. MA-043219 and MA-078744 to R. Davis

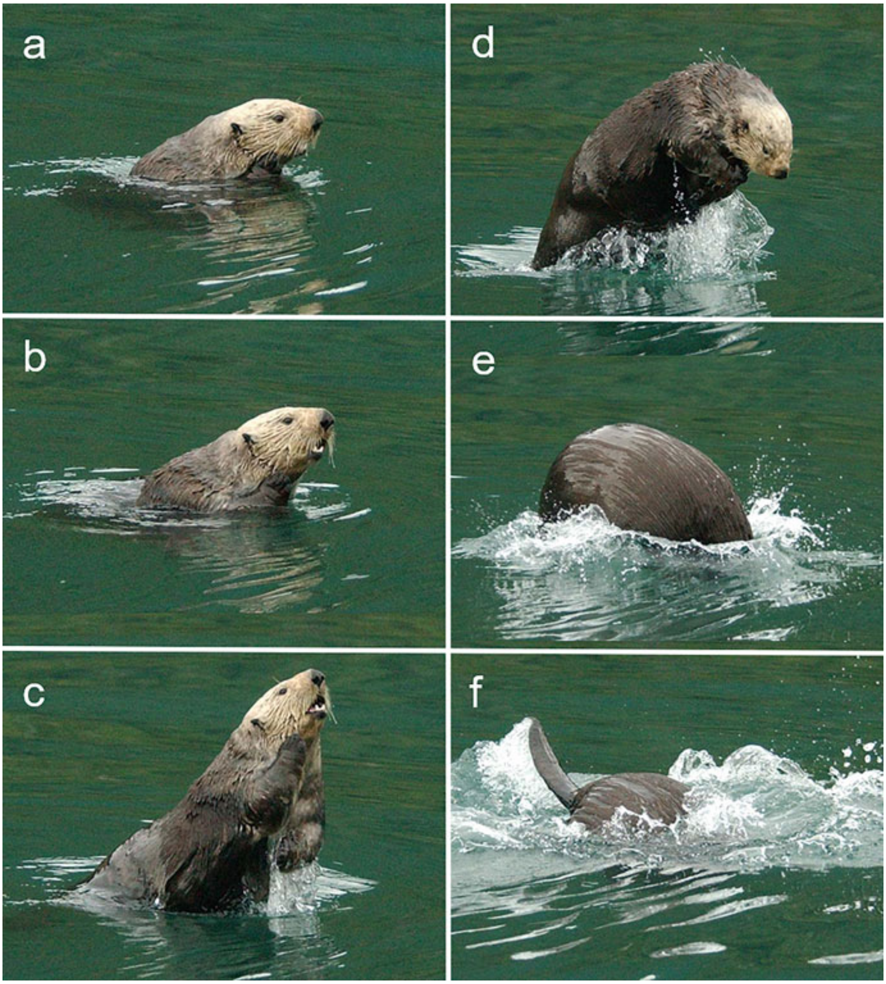

Fig. 4.3 Sea otter leaping out of the water at the beginning of a foraging dive. Images (**a**–**f**) were obtained under USFWS Permit No. MA84799B to R. Davis

rise passively to the surface, although ascent may be augmented with additional stroking to increase speed. At the maximum recorded dive depth of ~100 m, which is rare, a 25 kg sea otter is negatively buoyant, so stroking would be required during initial ascent until it becomes positively buoyant above a depth of ~35 m (Bodkin et al. 2004). Except for very deep dives, the mode of locomotion during a dive changes from active swimming during descent and benthic foraging to passive gliding during most of the ascent.

With a mean diving metabolic rate of 21.5 ml O_2 min^{-1} kg^{-1}, a 25 kg sea otter has an aerobic dive limit (ADL) of ~3.7 min (see Sect. 3.2.3; Yeates et al. 2007; Cortez et al. 2016; Thometz et al. 2015; Davis 2019). This limits routine dive depth and available foraging habitat to nearshore, shallow (<30 m) waters (Kenyon 1969;

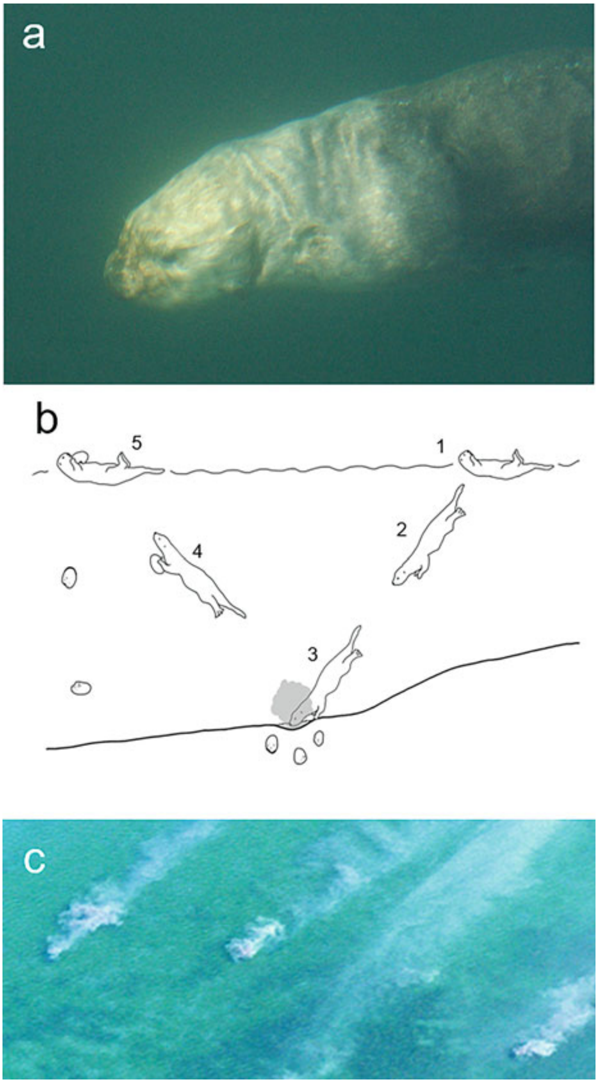

Fig. 4.4 (**a**) Sea otter during a dive with open eyes. (**b**) Sequence of events during a foraging dive for clams in a soft-sediment benthic habitat: (1) hyperventilate at surface, (2) dive to the seafloor, (3) excavate soft sediments with forepaws using tactile sense (vision not possible because of turbidity) to distinguish clams from gravel, (4) return to the surface with a clam, (5) consume clam and discard shell. (**c**) Aerial image of sea otters digging in soft sediments in Prince William Sound, Alaska. Image (a) was obtained under USFWS Permit No. MA-043219 to R. Davis

Calkins 1978; Riedman and Estes 1990; Bodkin et al. 2004; Tinker et al. 2007; Wolt et al. 2012; Esslinger et al. 2014). Although deeper dives occur, they are rare (Newby 1975; Bodkin et al. 2004, 2012; Wolt et al. 2012). In Southeast Alaska, only 0.003% of dives were > 90 m, and in Prince William Sound, Alaska, 0.04% of foraging dives were >50 m (Bodkin et al. 2004, 2007). The mean duration of foraging dives for all sea otters is about 2 min, with a maximum duration of ~8 min (Bodkin et al. 2004; Wolt et al. 2012; Thometz et al. 2016).

In Simpson Bay, Alaska, the average depth of foraging dives is 27 m with no significant difference between males and females (Fig. 4.5a; Osterrieder and Davis

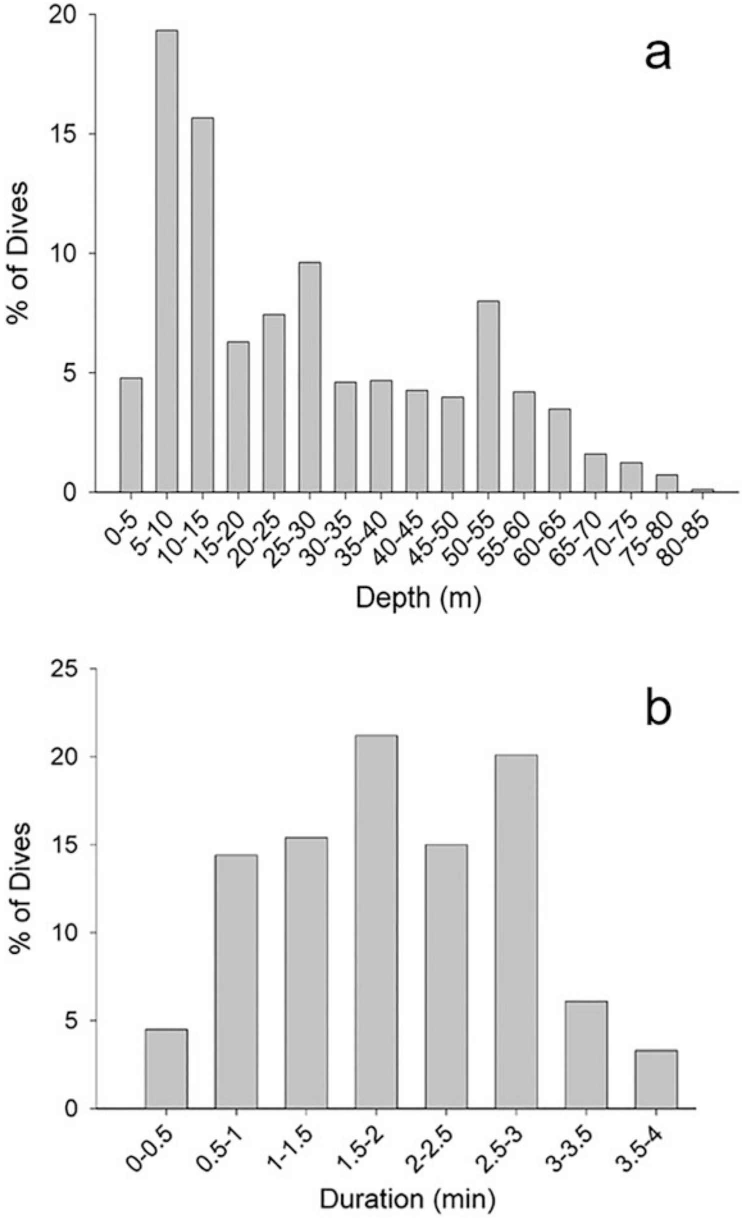

Fig. 4.5 Distribution of foraging dive (**a**) depths and (**b**) durations for adult male and female sea otters in Simpson Bay, Prince William Sound, Alaska (Wolt et al. 2012)

2009; Wolt et al. 2012). Nevertheless, sea otters exploit all of Simpson Bay proportional to the bathymetry (i.e., percentage of the bay within a depth range) down to a depth of 82 m, although there is a preference for shallower depths in the

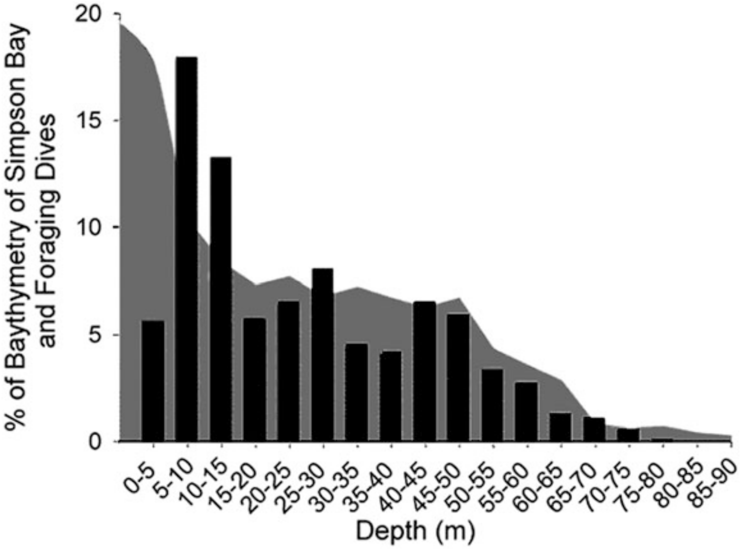

Fig. 4.6 Distribution of sea otter foraging dive depths (bars) and the percentage of the seafloor within each depth range (shaded area) for Simpson Bay, Alaska (Wolt et al. 2012)

range of 5–15 m (Fig. 4.6; Osterrieder and Davis 2009; Wolt et al. 2012). The mean foraging dive duration is 1.9 min with a normal distribution from 0 to 4 min and a peak at 1.5–2.0 min (Fig. 4.5b). There is a positive relationship between dive duration and depth because of the ADL, but shallow dives can be as long as deep dives (Fig. 4.7; Wolt et al. 2012; Thometz et al. 2016). In Western Prince William Sound, the mean duration of shallow foraging dives (<10 m in depth) is 0.7 min, while the mean duration of deeper dives (>15 m) is 1.6 min (Bodkin et al. 2007).

In Southeast Alaska, the mean depth and duration of foraging dives are 19 m and 1.4 min, respectively, with a preference for the depth range of 0–20 m relative to available benthic habitat (Kvitek et al. 1993; Bodkin et al. 2004). Males in Southeast Alaska and Western Prince William Sound exhibit this bimodal pattern, while females routinely forage at the shallower depths (Fig. 4.8). On average, males make more deep dives (>30 m) than females. In Washington State, mean foraging dive duration is 0.92 min, with a maximum of ~5 min (Laidre and Jameson 2006). In California, bimodal foraging behavior is not evident, although males generally forage at deeper depths than females (Thometz et al. 2016). Foraging in shallow water is associated with a large number (>200 day^{-1}) of short duration (~1 min) dives, with a high percentage (~70%) of each dive spent searching for prey on the seafloor (Bodkin et al. 2012). Foraging success is high among habitats, ranging from 70–90%, although the energy content of pre can vary (Kvitek et al. 1992, 1993; Doroff and Bodkin 1994; Dean et al. 2002; Wolt et al. 2012; Coletti et al. 2016).

Water depth is the defining characteristic of sea otter benthic habitat. Throughout their range, sea otters historically occupied littoral habitats from estuaries to exposed coastlines within their diving ability. For example, large numbers of sea otters occur more than 50 km offshore in the Bering Sea, where the bathymetry is within routine

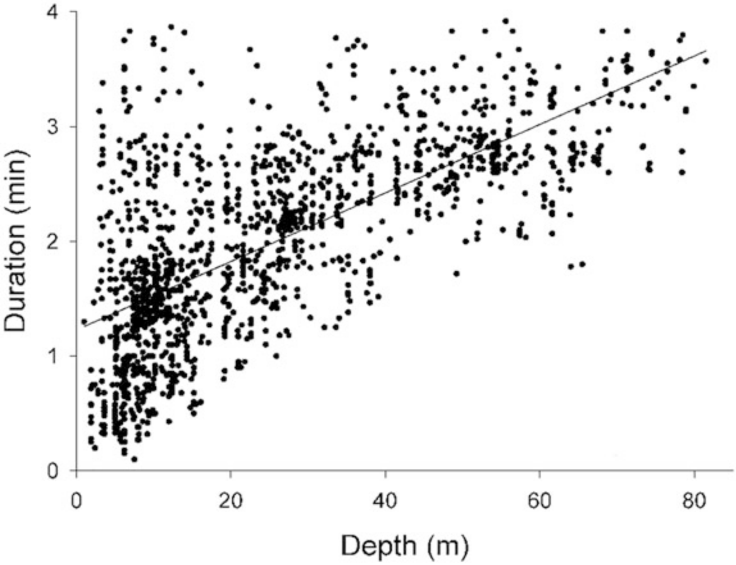

Fig. 4.7 Successful foraging dive depth as a function of dive duration (Wolt et al. 2012)

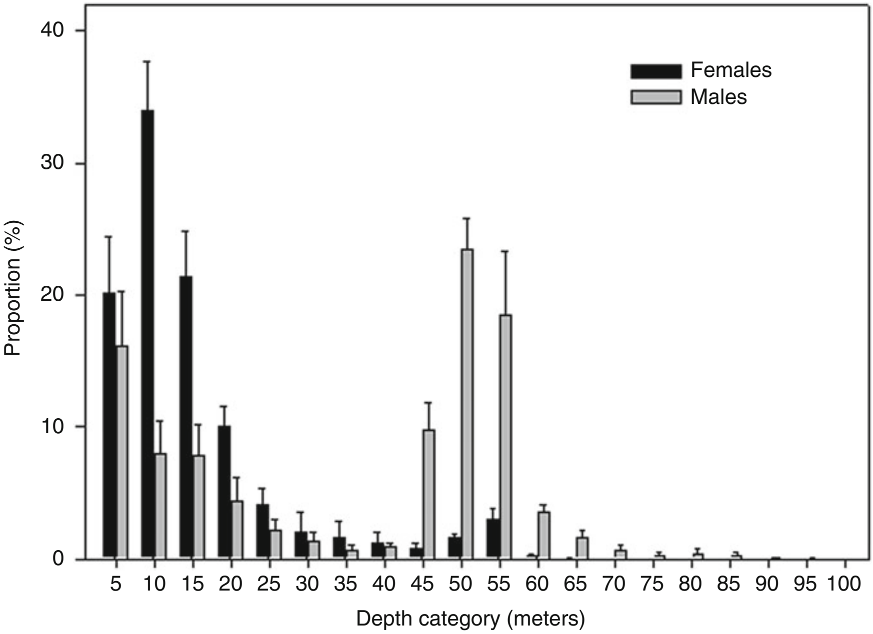

Fig. 4.8 Distribution of dive depths for sea otters in Southeast Alaska and Prince William Sound, Alaska

foraging depths (Bruggeman et al. 1988). In general, the depth and duration of foraging dives reflect the local variation in bathymetry and seafloor habitat.

4.4 Diet

Sea otters are diet generalists and feed primarily on mega-invertebrates, such as mollusks (e.g., clams, scallops, mussels, abalone, turban snails, and chitons), crustaceans (e.g., crabs, shrimp, and barnacles), echinoderms (e.g., sea urchins, sea cucumbers, and sea stars) and cephalopods (e.g., octopuses and squid) (Fig. 4.9; Williams 1938; Murie 1940; Barabash-Nikiforov 1947; Hall and Schallar 1964; Kenyon 1969; Estes et al. 1982; Kvitek and Oliver 1988; Kvitek et al. 1988, 1993;

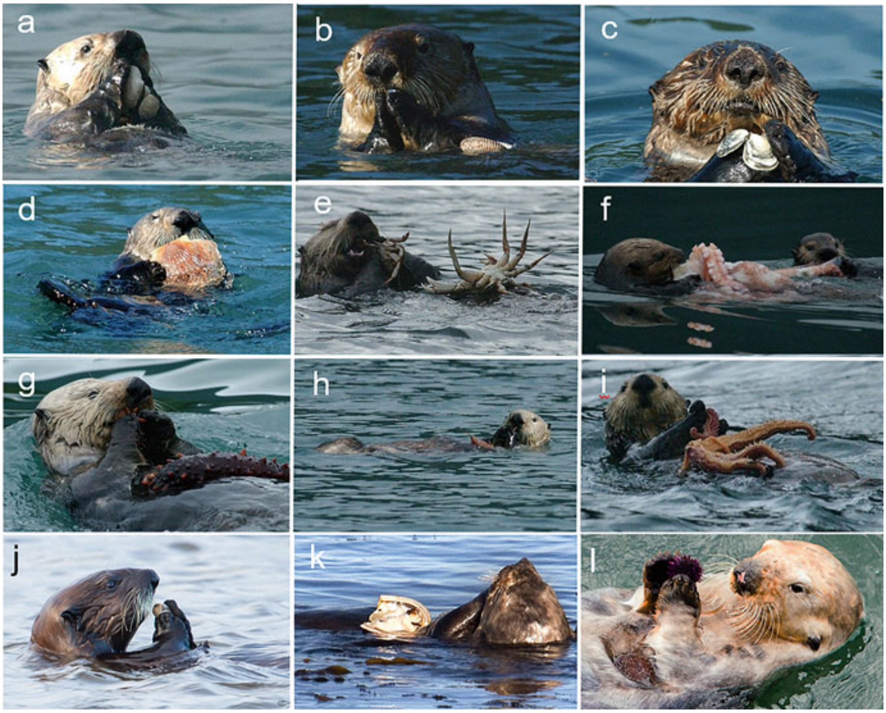

Fig. 4.9 Some prey species of sea otters in Alaska (**a**–**i**) and California (**j**–**l**): (**a**) butter clam (*Saxidomus gigantea*), (**b**) Nuttall's cockle (*Clinocardium nuttallii*), (**c**) stained macoma (*Macoma inquinata*), (**d**) weathervane scallop (*Patinopecten caurinus*), (**e**) Dungeness crab (*Metacarcinus magister*), (**f**) giant Pacific octopus (*Enteroctopus dofleini*), (**g**) California sea cucumber (*Parastichopus californicus*), (**h**) Alaska spoonworm (*Echiurus echiurus alaskanus*), (**i**) sea star (probably *Evasterias echinosoma*), (**j**) Lewis' moon snail (*Neverita lewisii*), (**k**) red abalone (*Haliotis rufescens*), and (**l**) Pacific purple sea urchin (*Strongylocentrotus purpuratus*). Images (**a**–**i**) were obtained under USFWS Permit No. MA84799B to R. Davis. Images (**j**) and (**l**) courtesy of J. Tomoleoni. Image (**k**) courtesy of N. La Roche

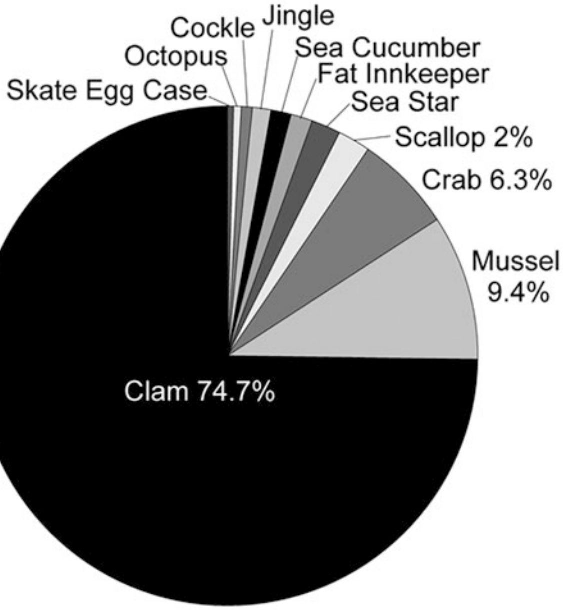

Fig. 4.10 Percent distribution of identified prey for sea otters in Simpson Bay, Alaska (Wolt et al. 2012)

Watt et al. 2000; Dean et al. 2002; Estes et al. 2009; Wolt et al. 2012; Tinker 2015; Coletti et al. 2016). However, they also feed opportunistically on slow-moving benthic fishes, the egg cases of rays, and herring roe on kelp (Kenyon 1969; Estes et al. 1982; Monson et al. 2000; Lee et al. 2009). Dietary analysis is based on stomach contents, fecal remains (spraint), and direct observations, and the method used can influence the results. Some prey, such as small mussels, are more commonly detected in spraint but are difficult to observe with binoculars or a spotting scope.

When sea otters have occupied an area for an extended period (i.e., >25 years), distinct diets are associated with two types of habitat. One diet, which is dominated by clams supplemented with mussels and crabs, is associated with unconsolidated or mixed sediments (e.g., mixed mud, sand, and gravel), often with a gently sloping bathymetry (Fig. 4.10; Barabash-Nikiforov 1947; Kenyon 1969; Calkins 1978; Kvitek et al. 1988, 1993; Dean et al. 2002; Laidre and Jameson 2006; Wolt et al. 2012; Hale et al. 2019). Sand lance (*Ammodytes hexapterus*) also may occur in the diet of sea otters in the Aleutian Islands and the Gulf of Alaska (Estes et al. 2009). The second diet, which is dominated by sea urchins (up to 90% *Strongylocentrotus* spp.) and various species of crabs, snails, and mussels, is associated with rocky-reef habitats, which often support both canopy and understory kelp forests (Barabash-Nikiforov 1947; Kenyon 1969; Estes et al. 1982; Estes and Duggins 1995; Watt et al. 2000; Tinker et al. 2007). In these rocky, kelp forest habitats, rock greenling (*Hexagrammos lagocephalus*) and Atka mackerel (*Pleurogrammus monopterygius*) may contribute significantly to the diet (Estes et al. 1982; Watt et al. 2000). The dichotomous diet associated with these two habitats is apparent for sea otters in the Strait of Juan de Fuca (Washington State) (Laidre and Jameson 2006). In areas with a steep, rocky shoreline, the diet is dominated by red and purple sea urchins (up to >90%), whereas clams (63%) are the predominant prey in adjacent, soft-sediment habitats.

Foraging behavior and preferred prey can vary temporally in two contexts. One pertains specifically to sea otters recolonizing formerly occupied habitat in which prey species increased in abundance and size after the near extirpation of sea otters during the Maritime Fur Trade in the eighteenth and nineteenth centuries (see Chap. 10). As sea otters reoccupy historic habitat, large and easily captured prey (e.g., epibenthic abalone, sea urchins, and crabs) are consumed, resulting in reduced abundance and size (Lowery and Pearse 1973; Estes and Palmisano 1974; Kvitek et al. 1988). In some cases, this is followed by intraspecific dietary diversification (i.e., individual specialization) as foraging effort and prey become less energetically profitable because of their smaller size. As a result, some sea otters concentrate on certain prey using specialized foraging techniques, which may be transferred matrilineally (Tinker et al. 2007, 2008).

The other temporal context of sea otter prey preference, which may be independent of population density, is associated with seasonal, annual, decadal, or episodic changes in prey availability or energy content. For example, on Amchitka Island in the Aleutian Islands, Alaska, sea otters began to prey on the smooth lumpsucker (*Aptocyclus ventricosus*), an oceanic fish that became a novel and significant part of the diet during winter and spring of a two-year study (Watt et al. 2000). In Prince William Sound, sea otters prey on small but numerous Pacific herring (*Clupea pallasii*) eggs, which are deposited as a thin layer on kelp during the spring spawn (Lee et al. 2009). Along the Katmai coast in Alaska, mussels are important (i.e., 34% occurrence in spraint) prey during winter and spring when they are gravid, but less important (5% occurrence) during summer (Coletti et al. 2016). Finally, there is a seasonal shift toward shallow water foraging in Prince William Sound, which is coincident with reproduction and increased energy density of intertidal bivalves (Bodkin et al. 2012).

4.5 Prey Capture

Sea otters are grouped with other raptorial predators even though they capture and manipulate prey with their forepaws (hand-oriented capture or prehension) rather than using their mouth (Werth 2000; Timm-Davis et al. 2015, 2017). This contrasts with the raptorial feeding behavior of mouth-oriented North American river otters, which feed primarily on fish. Unlike other carnivorous marine mammals, sea otters consume their prey at the surface rather than underwater (Figs. 4.4b and 4.9). As a result, they ingest and masticate food with rounded premolars and molars similar to those in terrestrial omnivores and carnivores (Fig. 4.1a–d; Reilly and Lauder 1990; Hiiemae and Crompton 1985; Markey and Marshall 2007; Timm-Davis et al. 2017). In contrast, Odontoceti (toothed whales) and Pinnipedia (seals, sea lions, fur seals,

Fig. 4.11 Sea otter using a stone as an anvil to open a butter clam. Image obtained under USFWS Permit No. MA-043219 to R. Davis

and walruses) capture and consume small prey underwater using either raptorial biting and/or suction without mastication, or slashing and tearing off pieces from larger prey that are small enough to swallow without further processing in the oral cavity (Kooyman and Davis 1986; Davis et al. 2013; Davis 2019).

Sea otters have foreshortened forelimbs, which they use to capture and manipulate prey and to grasp tools (e.g., rocks) to open hard-shelled prey, but not for locomotion (Figs. 4.9 and 4.11; see Sect. 3.1.2.2; Hall and Schallar 1964; Estes 1990; Fujii et al. 2015). Stones may be used as hammers to open hard prey at the surface or underwater. Because the phalanges are encased within the paws (i.e., the phalanges are not separate) and provide no independent movement or dexterity, rocks or prey must be held between the paws (Fig. 4.11; Pocock 1928; Howard 1975). Alternatively, a rock placed on the chest may serve as an anvil. A rock may be retained during foraging bouts and used multiple times by storing it beneath a flap of skin under the arm, which indicates anticipation and planning (Hall and Schallar 1964). The prevalence of tool use by sea otters varies geographically and may be passed culturally from females to offspring during the six-month dependency period (Mann and Patterson 2018; Estes et al. 2003). This behavior, which is more prevalent in sea otters along the coast of California and in Southeast Alaska than the Kuril Islands, Aleutian Islands, and Southcentral Alaska, may depend on diet specialization (e.g., turban snails) (Hall and Schallar 1964; Fujii et al. 2015, 2017). However, if sea otters from areas that normally do not use tools are given rocks or other hard objects while in captivity, they often pound the walls of their enclosure, sometimes causing significant damage (Kenyon 1969; R. Davis unpub. obs). This indicates that tool use may be an inherent behavior in sea otters, which manifests only when ecologically or behaviorally required.

To locate prey, sea otters use vision and the tactile sensitivity in their forepaws (Kenyon 1969). The eyes of sea otters are small and similar to those in diurnal terrestrial mammals, but with better accommodation underwater (Fig. 4.4a; see Sect.

3.3.1; Mass and Supin 2007). Underwater vision is emmetropic (focused), with a visual acuity similar to that in other marine mammals and the aerial acuity of many terrestrial mammals (see Sect. 3.3.1; Mass and Supin 2018). The eyes of sea otters differ from other marine mammals because the iris is attached to the frontal surface of the lens, so contraction and dilation of the iris significantly influences the curvature of the lens, allowing for emmetropic vision in air and underwater. However, there is no evidence for low-light adapted vision, which occurs in some Pinnipedia (Davis 2019). Hence, sea otters probably use vision to locate epibenthic prey under daylight conditions. However, tactile sensitivity may assist sea otters in locating epibenthic prey under low-light conditions, in rocky crevices, and under rocks (Shimek 1977; Kvitek and Oliver 1992). During the summer in Alaska, sea otters forage throughout the day because there is little change in diel light levels but transition to pronounced diurnal foraging during winter. This transition indicates the use of vision to locate epibenthic prey, although tactile sensitivity also may be important (Shimek 1977; Wolt et al. 2012; Esslinger et al. 2014).

Sea otters use their teeth or stone tools to access the flesh of mega-invertebrates with a shell, exoskeleton, or test. When sea otters capture decapod crabs, they consume the limbs with the exoskeleton, while the body is consumed after removing the carapace (dorsal section of the exoskeleton) with the canine teeth (Fig. 4.9e). Abalone (*Haliotis* spp.), which are detached from rocks, are consumed by grasping and tearing pieces of the muscular foot and other organs with the upper and lower incisors and canine teeth. In some cases, sea otters may repeatedly strike an attached abalone with a rock, which facilitates capture by fracturing or jarring it loose (Hall and Schallar 1964; Houk and Geibel 1974; Hines and Loughlin 1980). Likewise, a stone tool may be used to crack the shells of moon snails (*Neverita lewisii*) and turban snails (*Tegula* spp.). To open sea urchins (i.e., *Mesocentrotus franciscanus*, *Strongylocentrotus droebachiensis*, *Strongylocentrotus purpuratus*), sea otters use their lower canine teeth to break the test from the ventral surface where the spines are shorter or use a stone to crack the test, then consume the yellow, fatty roe. When sea otters kill a Giant Pacific octopus (*Enteroctopus dofleini*), they consume the muscular legs and discard the head, but how they capture and handle these large (body mass ~15 kg with a radial arm span of up to four m) cephalopods underwater is a mystery (Fig. 4.9f; R. Davis, unpub. obs.). Small, epibenthic scallops (e.g., *Chlamys rubida*) and mussels (e.g., *Mytilus trossulus*) are eaten whole, while the shells of larger species (e.g., *Pecten caurinus*) are opened with the teeth (Fig. 4.9d). Sea cucumbers (e.g., *Parastichopus californicus*), Alaska spoonworms (e.g., *Echiurus echiurus alaskanus*), and sea stars (e.g., *Evasterias echinosoma*) are consumed whole (Fig. 4.9g, h, i). Sea otters consume fronds of kelp (e.g., *Saccharina latissima*) that are covered with the eggs of Pacific herring, which spawn during the spring in Alaska (Lee et al. 2009). Sessile benthic fish, such as kelp greenling (*Hexagrammos decagrammus*), Atka mackerel (*Pleurogrammus monopterygius*), Masked greenling (*Hexagrammos octogrammus*), and lumpfish (*Aptocyclus* sp.) also may be consumed (Kenyon 1969; Monson et al. 2000), but not moribund salmon after spawning (R. Davis unpub. obs.).

When searching for clams and other infaunal prey (e.g., *Saxidomus gigantea*, *Leukoma staminea*, *Macoma inquinata*, *Clinocardium ciliatum*, *Urechis caupo*), it is uncertain if sea otters search the seafloor for holes or siphons using vision (Hines and Loughlin 1980). Previous success may inform a sea otter on where to dig or to enlarge an existing hole. Once digging begins, sea otters excavate soft sediments (mud and mud-gravel) with their forepaws, creating foraging pits or trenches (i.e., 20–150 cm in diameter and 10–50 cm deep), although they may be enlarged during multiple dives (Figs. 4.4b and 4.12; Shimek 1977; Hines and Loughlin 1980; Kvitek et al. 1992, 1993; R. Davis unpub. obs.). This digging activity creates a plume of sediments and limits vision because of turbidity, so sea otters use the tactile sensitivity in their forepaws to locate clams and other infaunal prey (Fig. 4.4b, c; Shimek 1977; Hines and Loughlin 1980; R. Davis unpub. obs.). The threshold for tactile surface discrimination (i.e., alternating grooves) is ≤0.5 mm with a very rapid (< 1 s) response time, which is consistent with the enlarged somatosensory cortex representing the paws (see Sect. 3.3.3; Radinsky 1968; Strobel et al. 2018). This gives sea otters good tactile sensitivity to differentiate between clams and gravel, and their foraging dives are ~87% successful (Shimek 1977; Kvitek et al. 1993; Wolt et al. 2012). In some cases, sea otters may bring more than one prey item to the surface by placing them under a flap of skin (pouch) in the armpit (Mann and Patterson 2018). The role of vibrissae in prey detection is uncertain (see Sect. 3.3.3).

To extract the tissue from small bivalves (e.g., clams and mussels), prey is placed in the back of the mouth between the upper and lower premolars and molars, which requires a wide gape. In sea otters, gape angle ranges between 61–66° with a maximum angle of 82°, which is greater than the maximum gape angle (55–65°) for other carnivorans (Herring and Herring 1974; Timm-Davis et al. 2017). The jaws are closed and the shell is cracked or crushed with a bite force of up to 554 Newtons (125 pounds) (Timm 2013). The shells of otter-predated clams and other hard-shelled bivalves are commonly found along beaches and typically have one broken valve and one intact valve joined at the hinge (Fig. 4.13b, d). When a hard-shelled clam or cockle is cracked, the broken piece distal from the hinge is discarded, and the otter then opens the bivalve and scoops out the flesh with its lower incisors and canines (Fig. 4.9a). Soft-shelled clams (e.g., Macomas) are easily crushed into multiple pieces and discarded or partially consumed (Fig. 4.9c), while the broken shell and flesh of small mussels (e.g., *Mytilus* sp.) can be ingested entirely.

Because of their durophagous mode of feeding, the primary occlusal area provided by the enlarged, upper third premolars and lower first molars shows the greatest wear, breakage, and infection, which may limit longevity (Fig. 4.14; Fisher 1941; Kenyon 1969). In addition, significant malocclusion of the postcanine teeth may occur in recently weaned pups feeding on hard prey but whose deciduous teeth have not been replaced. When sea otters can no longer feed efficiently, they die rapidly of starvation because of their elevated basal metabolic rate (see Sect. 3.2.4).

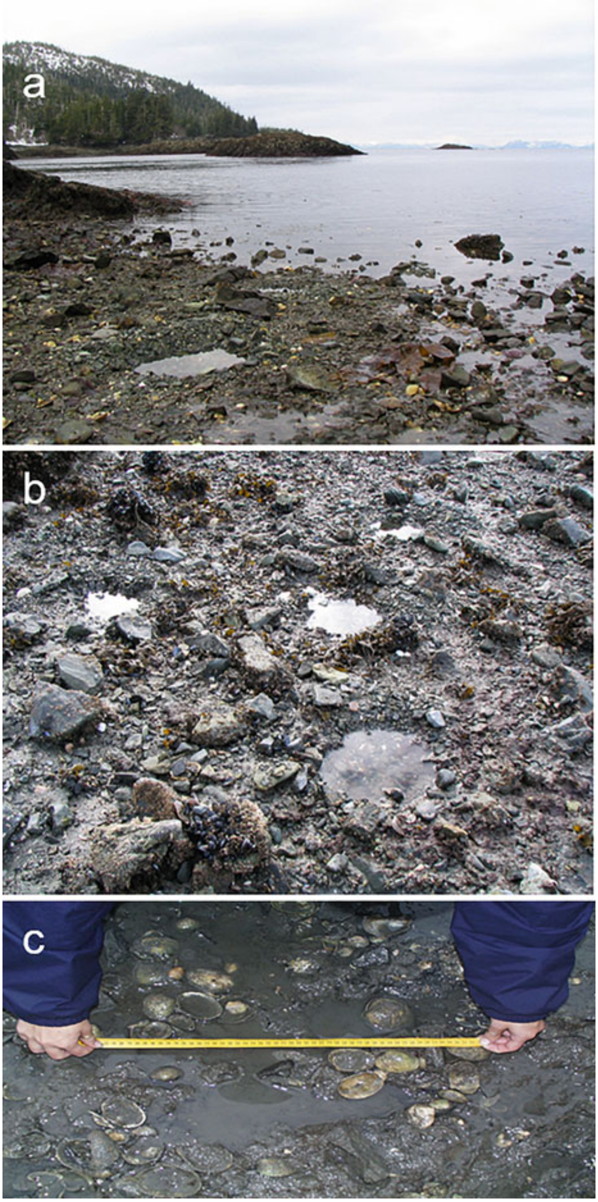

Fig. 4.12 (**a** and **b**) Sea otter foraging pits, Prince William Sound, Alaska. (**c**) Sea otter foraging pit (~20 cm in diameter, 8 cm deep) in the intertidal

4.6 Daily Foraging Duration

Foraging dives often occur in bouts (i.e., two or more consecutive dives) with 1–2 min between dives depending on foraging success and prey handling (Bodkin et al. 2004; Wolt et al. 2012). Depending on the number of consecutive dives, bouts may be several hours in duration (Thometz et al. 2016). The amount of time that sea

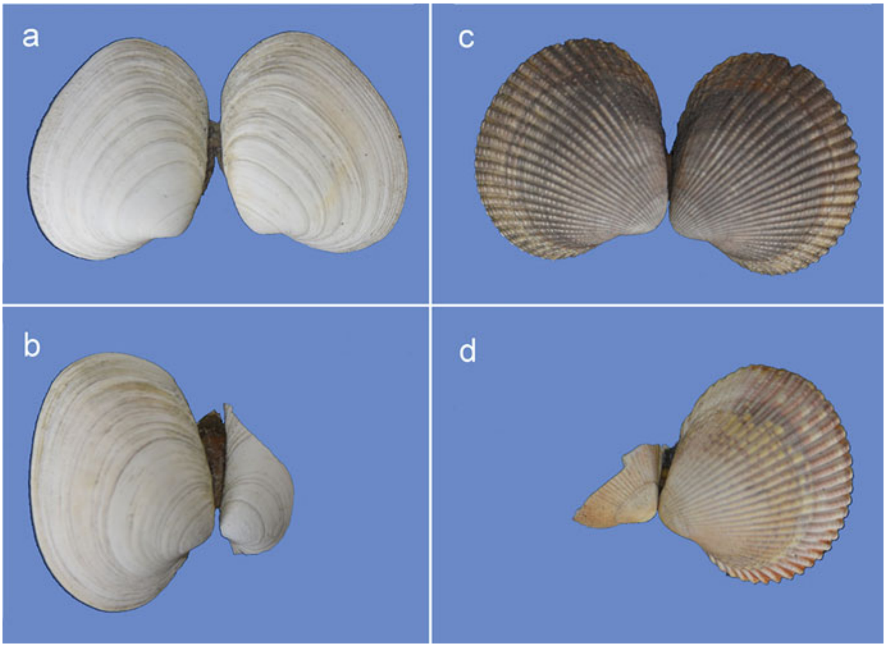

Fig. 4.13 Butter clams (*Saxidomus gigantea*) with (**a**) intact hinged valves and (**b**) one broken valve resulting from sea otter predation. Nuttall cockles (*Clinocardium nuttallii*) with (**c**) intact hinged valves and (**d**) one broken valve resulting from sea otter predation

otters devote to foraging depends on age, sex, reproductive status, presence of a pup, time of year, and prey availability (which varies geographically, seasonally, and episodically) (Shimek and Monk 1977; Monson et al. 2000; Dean et al. 2002; Esslinger et al. 2014; Tinker 2015; Coletti et al. 2016; Cortez et al. 2016). In addition, variation may result from the sampling method (direct observation vs. radio telemetry and time-depth recorders), diel period (daylight hours only vs. 24-h monitoring), and seasonality (summer vs. annual) (Loughlin 1980; Garshelis et al. 1986; Ralls and Siniff 1990; Gelatt et al. 2002; Bodkin et al. 2007; Tinker et al. 2007, 2008; Esslinger et al. 2014; Cortez et al. 2016). Unlike other marine mammals, sea otters have small or no energy reserves in the form of blubber, so they feed frequently (i.e., every 3–4 h). If feeding is interrupted, they enter a fasting state within 4–8 h and a state of starvation within 24 h. Hence, foraging is a daily activity that cannot be postponed, although it appears to be reduced in females with neonatal pups during the first 3 weeks postpartum (Gelatt et al. 2002; Esslinger et al. 2014; Thometz et al. 2014, 2016; Cortez et al. 2016).

Adult female sea otters demonstrate distinctive feeding behavior during pup rearing, which is independent of prey availability (Thometz et al. 2016). Female sea otters with pups <4 weeks of age (mean body mass = 1.8 kg) reduce (but do not eliminate) foraging effort to protect their altricial pups from predation by bald eagles (*Haliaeetus leucocephalus*) and other threats (Fig. 4.15; see also Sect. 7.4; Sherrod

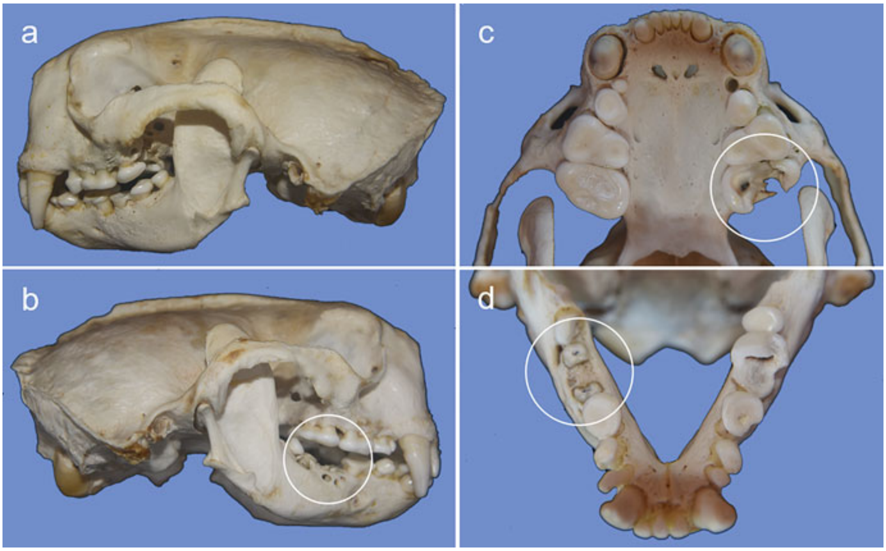

Fig. 4.14 The left (**a**) and right (**b**) side of the skull and the upper jaw (**c**) and lower jaw (**d**) from an adult sea otter skeleton that was found above the high tide line in Simpson Bay, Alaska. The teeth were heavily worn, and one upper and one lower molar (circles) were broken or missing. Bone necrosis was evident around the broken teeth and may have resulted from periapical abscesses (Kenyon 1969)

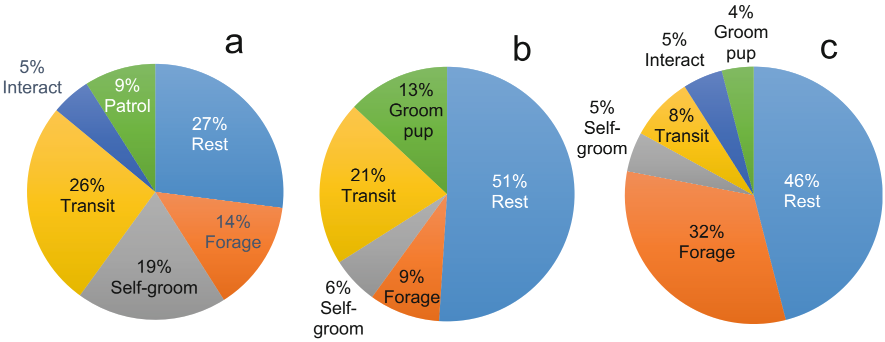

Fig. 4.15 Average 24-h activity budgets sea otters: (**a**) male, (**b**) female with pup <4 weeks old, and (**c**) female with pup 8–12 weeks old. Resting behavior includes sleeping on the water's surface. Foraging behavior includes the time submerged and while handling prey at the surface between dives. Self-groom refers to felting the fur to maintain an air layer. Groomed refers to the pup being groomed by the female Transit refers to is directed swimming at the surface, usually in the supine position (belly up with head facing backward) using alternate or simultaneous pelvic paddling. Nursing refers to the percentage of time spent suckling. Interact refers to socializing with other otters and, in the female, occasional mating behavior. Data for females with pups were collected simultaneously in Simpson Bay, Alaska during the summer months of June to August (Cortez et al. 2016)

Table 4.1 Daily foraging effort (% of 24-h period) of sea otters in Alaska and California. Estimates were based on either direct observation, radio telemetry, time-depth recorders, or a combination of methods. Results are for adult and subadult males and females. Some of the females may have been pregnant or had pups. The Aleutian Islands and Prince William Sound are located in Alaska

Food Limited (%)	Non-Food Limited (%)	Location	References
40	29	Southeast Alaska	Bodkin et al. (2007)
55	17	Aleutian Islands	Estes et al. (1982)
50	37	Prince William Sound	Garshelis et al. (1986)
42	25	California	Tinker et al. (2008)
49	41	Prince William Sound	Dean et al. (2002)
44	37	California	Thometz et al. (2015)
Mean			
46.7	31.0		

et al. 1975; Esslinger et al. 2014; Gelatt et al. 2002; Thometz et al. 2016; Cortez et al. 2016). To remain in energy balance and lactate during this period, females rely on small fat deposits, which they acquire during gestation but deplete within 3 weeks (see Sect. 7.3). As the pup increases in size, so does the female's foraging effort. By the time a pup is 8–12 weeks of age (mean body mass = 5.8 kg), the female devotes 32–48% of the day to foraging to support her own metabolic needs and provide food (milk and prey) to the growing pup (Thometz et al. 2014, 2016; Cortez et al. 2016). As the pup approaches adult size (15–20 kg) at the weaning age of six months, the female may spend up to 50% of the day foraging (Estes et al. 1982). This leaves the remaining time for essential body maintenance behaviors, such as resting (~45%) and self-grooming (~5%), which may be a minimum for good health. At some point, the energetic demands may exceed the foraging ability of the female, reduce the time for body maintenance behaviors, and cause a decrease in body condition, which can lead to pup abandonment, early weaning, or mortality in severe cases (see Sect. 7.4; Chinn et al. 2016).

Although various factors influence the amount of time that sea otters forage, it generally increases as prey availability decreases and a population approaches carrying capacity (Table 4.1; Eberhardt and Siniff 1977; Estes et al. 1982; Garshelis et al. 1986; Dean et al. 2002; Bodkin et al. 2007; Tinker et al. 2008; Thometz et al. 2016). A comparison among seven studies showed that sea otters spent 46% (11.0 h) of each day foraging in areas that were food limited and 31% (7.4 h) in areas where it was not, although duration of reoccupation did not always correlate with food availability (Loughlin 1980; Estes et al. 1986; Bowlby et al. 1988; Ralls and Siniff 1990; Gelatt et al. 2002; Walker et al. 2008). In addition to the percentage of time spent foraging, the rate of energy intake has been used as a metric for prey availability (see Sect. 8.6). Along the Katmai coast of Southwest Alaska, sea otters had an energy intake rate of 12 kcal min^{-1} (50 kJ min^{-1}) in 2006 when the population was growing (Coletti et al. 2016). By 2015, the energy intake rate had declined 62% after the sea otter population reached an equilibrium density (Fig. 8.5). As a result, sea otters spent more time foraging to remain in energy balance.

Sea otters in Prince William Sound show seasonal differences in foraging behavior (Esslinger et al. 2014). Females and males spend less time foraging during summer months compared to the remainder of the year. In addition, they spend more time foraging during daylight hours in the winter, which indicates that vision is important for prey detection.

4.7 Carrying Capacity and Foraging Behavior

As sea otters reoccupy an area from which they were extirpated, enhanced populations of epifaunal prey, such as sea urchins, crabs, and abalone, generally decline first, followed by infaunal species, such as bivalves, depending on the type of habitat (Kimker 1982: Ostfeld 1982; Kvitek and Oliver 1988, 1992; Kvitek et al. 1988, 1992, 1993; Coletti et al. 2016). In rocky habitats with thriving kelp forests where herbivorous mega-invertebrates have declined because of predation, sea otters may exhibit intraspecific diet diversity (i.e., diet specialization among individuals within a population) associated with density-dependent competition for food (Estes et al. 1982; Tinker et al. 2007). Sea otters in the Aleutian Archipelago increased consumption of demersal fish as sea urchin populations declined because of predation (Estes 1990; Watt et al. 2000). Similar to tool use, diet specialization as a response to competition for diminishing prey may be a learned behavior passed from females to their offspring, although it does not occur in all populations (Wolt et al. 2012; Thometz et al. 2016). For sea otters in soft-and mixed-sediment benthic habitats with low densities of epifaunal invertebrates, prey switching may not occur as bivalve densities decline. For example, in Prince William Sound, Alaska, foraging success rates remained high over many decades for a diet dominated by clams (Calkins 1978; Garshelis et al. 1986; Dean et al. 2002; Wolt et al. 2012; Cortez et al. 2016).

The exploitation of abundant mega-invertebrates by sea otters as they reoccupy historic habitat has increased our understanding of their role in the community structure of nearshore habitats (Estes and Palmisano 1974; Estes and Duggins 1995). As sea otter population density approaches carrying capacity, other extrinsic factors may influence population equilibrium. For example, killer whale predation on sea otters in the Aleutian Islands since the 1980s allowed sea urchin populations to recover and thrive as they did when sea otters were hunted to near-extinction during the Maritime Fur Trade (see Chap. 10; Estes et al. 1998). As sea otter abundance declined by ~90%, sea urchin populations increased and kelp forests disappeared, creating sea urchin barrens. Sea otters that remained were no longer food-limited and established a new equilibrium density regulated by killer whale predation (Tinker 2015).

Food availability is known to influence the equilibrium density of sea otter populations, and the amount of time that sea otters forage is an important indicator of the population status (Tinker 2015). However, each population has its own combination of intrinsic (territoriality, emigration) and extrinsic (food availability, predators, disease, human-related mortality, weather, episodic environmental events) factors affecting equilibrium density. Hence, a single factor (e.g., food availability) regulating population density may not necessarily predominate or may vary over time to produce a complex interaction among the effects of various factors influencing foraging behavior (Fowler 1987; Davis et al. 2019; Watt et al. 2000; Smith et al. 2021).

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Chapter 5
Social Structure of Marine Otters: Inter and Intraspecific Variation

Adi Barocas and Merav Ben-David

Abstract Otters are a semiaquatic clade that stands out among carnivorans. Of 13 otter species, only three are known to cooperate, although most species exhibit some form of sociality. The observed variation in social structure among species, especially those in marine environments, makes this taxon suitable for studying the proximate and ultimate factors underpinning sociality. Here we review evidence for social behavior in otters with an emphasis on two species: the North American river otter (an inland and coastal generalist) and the sea otter (a marine specialist). In addition, we provide new information on a marine population of river otters in coastal Alaska using telemetry, camera traps, and social network analysis. Our results provide new insight into the contexts for river otter social behavior, confirm previous observations on individual variation in social behavior, and highlight differences between males and females. We additionally review the published data on sea otter social behavior. We discuss potential directions for hypothesis testing in otter social systems with an emphasis on drivers of individual variation in social behavior, especially potential insights from the fields of sociogenomics and proteomics.

Keywords Allogrooming · Behavior · Cooperation · Fitness · Hierarchy · Interaction · Latrine · Lutrinae · Marine · Network · Sea otter · Sociality

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5.1 Patterns of Social Behavior and Cooperation in Otters

Numerous species of mammals live in social groups, a life history strategy that has diverse advantages (Krause and Ruxton 2002). Close associations with conspecifics can provide individuals with increased protection from predation, facilitate access to resources, and enhance mating opportunities (Silk 2007). In addition, sociality can be advantageous because larger groups can better defend territories, forage more efficiently, and facilitate the transfer of knowledge among relatives and conspecifics (Aureli et al. 2008; Clutton-Brock et al. 2010; Markham et al. 2015; Merkle et al. 2015; Jesmer et al. 2018). The conditions that led to the independent evolution of sociality in multiple taxa and the causes and consequences of variation in social relationships among animals continue to be of interest. New analytical tools, such as game cameras, GPS tracking, and proximity tags, and network analyses have provided fine-scale analysis of multilevel social interactions among animals (Krause et al. 2013; Kays et al. 2015). These advances have renewed scientific interest in assessing the quantity, quality, and diversity of relationships within social units and their consequences for the survival and fitness of individuals (Silk et al. 2003, 2010; Barocas et al. 2011).

The majority of species in the Order Carnivora (hereafter referred to as carnivorans) are solitary (Lukas and Clutton-Brock 2012). Cooperation for non-breeding purposes includes group foraging, predator vigilance, and alloparenting. However, such behaviors are relatively uncommon among carnivorans, as only 10–15% of all species aggregate outside of the breeding season (Gittleman 1986). Two taxonomic families, Canidae (dog-like carnivorans) and Herpestidae (mongooses), are the exception because they demonstrate at least one type of cooperation (Gittleman 1989; Smith et al. 2012). In larger carnivorans that feed mainly on ungulates, sociality and cooperation are favored because of the need to capture large prey and defend carcasses. For example, spotted hyenas (*Crocuta crocuta*) form subgroups to protect kills from other hyenas or predators, such as lions (*Panthera leo*). However, resource limitation may constrain group size because individuals may gain more energy when foraging in smaller groups (Smith et al. 2008).

Factors favoring cooperation in carnivorans can be divided into two categories: ecological and life history. A phylogenetic analysis suggests that carnivorans that engage in cursorial hunting of large-bodied prey are most likely to cooperate (Smith et al. 2012). Moreover, morphological traits that enhance hunting (e.g., body mass and shoulder height) and reduce male-male competition (e.g., reduced sexual dimorphism) are most common in highly cooperative species. In addition, species of carnivorans that are more cooperative in breeding generally have larger relative brain sizes and greater reproductive investment than did non-cooperative carnivorans. Species that wean offspring at older ages (enhanced reproductive investment) and live in large groups (presumably in areas with clumped resources) are more likely to cooperate in defense against predators (Smith et al. 2012). Thus, large prey that require cooperative hunting effort with many individuals promote cooperation among carnivorans.

Of the carnivore families considered asocial, the mustelids stand out with a relatively high level of cooperation among species (Smith et al. 2012). This conclusion is based on a few well-studied species, such as the Eurasian badger (*Meles meles*) and the North American river otter (*Lontra canadensis*). The social organization of most mustelids is based primarily on intra-sexual territoriality, with male home ranges overlapping those of several females. Such spatial segregation may limit the opportunities for social interactions (Powell 1979). In contrast, the Eurasian badger has consistent social groupings with well-structured territories delimited by latrines (Woodroffe and Macdonald 1993). Badgers are solitary foragers, but individuals show a high frequency of interaction with group members (Böhm et al. 2008).

Among the Lutrinae, which is a subfamily within the Mustelidae, Eurasian otters (*Lutra lutra*), giant otters (*Pteronura brasiliensis*), North American river otters, and sea otters (*Enhydra lutris*) have been well studied. Other species are understudied because of their evasive behavior and challenging aquatic habitats. Although many of the 13 otter species exhibit social behaviors and live in groups (Table 5.1), forms of cooperation were unequivocally documented in only two (Koepfli et al. 2008; Smith et al. 2012). The giant otter, which according to molecular analyses, forms a distinct clade from other members of the family, is the only lutrine that lives in consistent family groups with a socially dominant reproductive couple (Leuchtenberger and Mourão 2008). When hunting for fish and defending against predators, giant otters exhibit cooperative behavior, including coordinated aggression and harsh vocalizations. In addition, they demonstrate active territory defense from conspecifics through aggression and scent marking (Leuchtenberger and Mourão 2009; Groenendijk et al. 2015; Leuchtenberger et al. 2015). North American river otters exhibit a flexible social system where group size and associations among individuals depend on population density and resource availability. High-density marine populations show cooperative foraging for schooling fish, although cooperation also was observed in freshwater systems (Blundell et al. 2002a; Gorman et al. 2006). In one study, four river otters herded a school of white suckers (*Catostomus commersonii*) in the Upper Tunkhannock Creek in northwestern Pennsylvania (Serfass 1995). During live-trapping in Yellowstone Lake in 2005, another study observed a group of three otters attempting to protect a captured individual from the researchers (Crait et al. 2006). More limited cooperation occurs in sea otters, which aggregate in rafts of up to hundreds of animals, with the largest groups usually formed by males (Garshelis et al. 1984). Rafting may be a form of group vigilance against predators when resting on the water's surface. Despite close spatial proximity in rafts, individuals do not frequently interact. The main form of cooperation is alloparenting by females, which is infrequently observed in wild populations (Staedler and Riedman 1989; Riedman and Estes 1990).

Evidence of explicit cooperation in other species is lacking. However, sociality occurs in several species, including the small-clawed otter (*Amblonyx cinereus*) and the smooth-coated otter (*Lutrogale perspicillata*) (Table 5.1). Both species

Table 5.1 Summary of sociality and cooperation among the 13 species of otters. Sources are cited in the text

Common name	Scientific name	Marine populations	Diet	Sociality	Cooperation
Sea otters	*Enhydra lutris*	Only	Mostly marine invertebrates	Yes, but low levels of interaction	Alloparenting; solitary foraging
Eurasian otter	*Lutra lutra*	Yes	Mostly fish	Females with young	No
Hairy-nosed otter	*Lutra sumatrana*	Yes (mangrove swamps)	Fish and aquatic invertebrates	Unknown	Unknown
Smooth-coated otter	*Lutrogale perspicillata*	Yes (estuaries and marshes)	Fish and aquatic invertebrates	Extended family groups; bi-parental care	Unknown but presumed
Small-clawed otter	*Amblonyx cinereus*	Yes (mangrove swamps)	Mostly aquatic invertebrates	Yes	Unknown but presumed
Spotted-neck otter	*Hydrictis maculicollis*	No	Fish and aquatic invertebrates	Yes, separate male and female groups	Unknown but presumed
African clawless otters	*Aonyx capensis*	Yes	Mostly crustaceans and fish	Usually solitary	Unknown
Congo clawless otter	*Aonyx congicus*	No	Mostly crustaceans and amphibians	Unknown	Unknown
Giant otter	*Pteronura brasiliensis*	No	Mostly fish	Extended family groups	Yes
Marine otter	*Lontra felina*	Yes	Mostly aquatic invertebrates	Yes, mostly small family groups	Unknown
Neotropical otter	*Lontra longicaudis*	Yes (estuaries and marshes)	Mostly fish	No	No
Southern river otter	*Lontra provocax*	Yes	Fish and aquatic invertebrates	Females with young	Unknown
North America river otter	*Lontra canadensis*	Yes	Fish and aquatic invertebrates	Yes	Yes

aggregate in larger groups in coastal areas where resources are abundant (Sivasothi and Nor 1994; Abdul-Patah et al. 2014). Typical smooth-coated otter groups are familial units, which consist of both parents and their young, whereas small-clawed otter sociality can extend beyond the family group structure. This species can form larger groups of up to eight adults throughout its range and exhibit frequent social interaction (Hussain 1996). Similar to North-American river otters, small-clawed otter group sizes vary according to resource availability and may number up to 15 (Kruuk 2006; Perinchery et al. 2011).

Temporary social assemblies coinciding with a predominantly solitary lifestyle occur in other otter species. In both inland and marine Eurasian otter populations, male home ranges overlap, sometimes simultaneously, and males can occur in pairs. In contrast, female territories are predominantly exclusive, and close kin avoid each other even when mothers share parts of their home-ranges with their daughters (Kruuk and Moorhouse 1991; Kruuk 2006; Quaglietta et al. 2014). Similar spatial and social dynamics were observed in a lake population of spotted-necked otters (*Hydrictis maculicollis*), where aggregations of up to 12 individuals were documented (Reed-Smith et al. 2014). African clawless otters (*Aonyx capensis*) form social groups but forage alone to reduce intraspecific competition when hunting crustaceans (Butler and Marshall 1996). Similar patterns of spatial and social dynamics occur in the South American marine otter (*Lontra felina*). Although they form family groups, individuals are solitary hunters that feed on mollusks, crustaceans, and benthic fishes along rocky coasts. Association patterns in this species are likely influenced by increased vulnerability to predation and a strong dependence on safe, rocky shelters (Medina-Vogel et al. 2007; Valqui 2012).

The recurring tendency of otters to form groups and interact socially when resources are not limiting indicates behavioral flexibility and suggests that other forms of cooperation may be prevalent in Lutrinae. The tendency to associate with conspecifics is intriguing given that the majority of species achieve higher densities in marine environments (Kruuk 2006).

5.2 Marine Otters

Excluding those using estuaries, at least six of the 13 known otter species have marine populations (Table 5.1; Estes et al. 2009). Specifically, at higher latitudes, a number of freshwater otter populations have secondarily entered the sea in response to higher productivity in coastal compared to inland habitats. Shetland Eurasian otters and coastal otter populations—namely river otters along the North America Pacific and Atlantic coasts, southern river otters (*Lontra provocax*) in Patagonia—spend less time foraging and achieve higher population densities (Sepúlveda et al. 2015; A. Valenzuela, *personal communication*). These species also inhabit freshwater ecosystems, but they exhibit lower densities (Kruuk 2006; Estes et al. 2009). The increased presence of conspecifics implies that individuals of these marine populations have more opportunities to interact with others, although the inter- and intraspecific variation in sociality and cooperation suggest an underlying predisposition for such behaviors. This is especially evident for Eurasian otters in Shetland Islands. Although males in this population have overlapping home ranges, they are solitary foragers (Kruuk and Moorhouse 1991). Both sexes deposit scent marks, which are composed of urine, feces, and excretions from the anal gland, throughout their range. Parts of these markings are ephemeral as they get washed away by the tides (Kruuk 1992). Thus, although densities along the Shetland coast are higher than in freshwater systems, social interactions are limited, and cooperation does not seem to exist.

In the sections below, we focus on two case studies of marine otters with distinctly different social systems: the North American river otter and the sea otter. We review the available evidence documenting their social structure and current data describing the behavior and interactions of North American river otters. We also discuss directions for future studies in these and additional otter species.

5.3 North American River Otter Sociality

Coastal river otters in Alaska exhibit a flexible social system, where males spend approximately 50% of their time in groups of up to 18 individuals, but females are mostly solitary (Blundell et al. 2002a; Barocas et al. 2016). Individual river otters vary in several measures of sociality, including spatial interactions, frequency of association, and home range overlap (Bowyer et al. 1995; Blundell et al. 2004).

5.3.1 Social Interactions Among Males

The primary social interaction in male river otters is cooperative foraging for pelagic schooling fish, which provide substantial energetic benefits (Blundell et al. 2002a; Ben-David et al. 2005; Kruuk 2006). Tracking data from telemetry and proximity tags indicate that male river otters exhibit fusion-fission dynamics, separating from and then recoalescing into foraging groups (Blundell et al. 2002a; Barocas et al. 2016). This conclusion was corroborated by direct observations conducted in Prince William Sound, Alaska, following the *Exxon Valdez* oil spill in 1989. Throughout the summer of 1991, we used a skiff to follow groups of otters (for 24 h) that included at least one individual implanted with a radio transmitter (Bowyer et al. 2003). Data on group size, distance from shore, and prey capture success were recorded (Bowyer and Ben-David, unpub.obs.). Foraging was solitary or occurred in groups of up to eight, and most of the fish captured were either sandlance (*Ammodytes americanus*) or capelin (*Mallotus villosus*). These observations also corroborated telemetry data suggesting that some males and most females rarely join groups (Bowyer and Ben-David, unpub. Obs.). Observations of 15 captive male river otters (Alaska SeaLife Center, Seward) in 1998–99 also indicated that some individuals rarely exhibit affiliative social behaviors, whereas others are very interactive (Hansen et al. 2009).

Further support for the conclusion that male otter groups are largely driven by cooperative foraging is provided by differences in diet between social and asocial individuals (Bowyer et al. 2003; Ben-David et al. 2005). Diet analyses of otter feces as well as stable isotope analysis indicate the prevalence of schooling pelagic fish in diet of social otters and especially males (Ben-David et al. 2005). Furthermore, a spatially-explicit individual-based model, which simulated foraging behaviors of males and females without any explicit coding for affiliation or conspecific attraction, generated virtual groups similar in size to those observed from radio telemetry (Albeke et al. 2015).

Finally, genetic data collected from 125 individuals in Prince William Sound revealed that river otter groups are composed of both relatives and non-kin and largely form based on familiarity (i.e., previous knowledge; Blundell et al. 2004; Hansen et al. 2009). In addition, sociality neither enhances reproductive success nor increases inclusive fitness, especially for males (Blundell et al. 2004). This may result from the limited mating season in Alaska (~1 month) and the tendency for older males to move long distances from their social groups, which reduces competition for mating opportunities (Blundell et al. 2002b). Under such circumstances, mating success is unaffected by group affiliation. At the end of the mating season, these older males return to their original social groups, which have been largely maintained during their absence by less dominant individuals (Blundell et al. 2002b; Hansen et al. 2009). Overall, the nutritional benefits that male river otters accrue from joint foraging and mating migrations may offset male-male competition, which is ubiquitous in other mating systems (Emlen and Oring 1977).

Male North American river otters use scent marking, haptics (tactile allogrooming, co-rubbing, playing, and wrestling), and acoustic interactions to form and maintain social networks and reduce aggression. During 284 h of observation of captive river otters (Alaska SeaLife Center), only 79 occurrences of negative interactions among 15 males were recorded in a 10 month period, compared with 1451 positive ones (Hansen et al. 2009). These mostly included ignoring social advances from other individuals, screaming, and mounting, with only one fight (Hansen et al. 2009). Even in captivity, river otter males established a clear social hierarchy based on scent marking behaviors. It has been observed that dominant males in captivity investigate the feces of other males (familiar and non-familiar ones) more often than subordinate ones (Rostain et al. 2004).

5.3.2 Social Interactions Among Females

Female river otters in coastal Alaska show significantly lower levels of sociality than males (Blundell et al. 2002a, 2004; Barocas et al. 2016). Although females occasionally join male foraging groups, they rarely spend extended periods interacting with them (Blundell et al. 2002a). Assuming that cooperative foraging offers access to high-quality food during lactation, it is unclear why females so rarely join male groups. One explanation is the risk of infanticide, although such behavior has not been observed. Alternatively, it is possible that the tendency of pelagic fish-schools to move long distances within a short time reduces their accessibility to females, which restrict their movements to the vicinity of maternal dens or because of their need to defend a territory (Ben-David et al. 2005).

Based on the behavior of captive river otters, placing females together often causes aggression (Reed-Smith et al. 2014). In the wild, researchers studying river otters in Herring Bay, Alaska, observed a fight between two females (E. Rock unpub. obs.). A female with a pup approached a salmon stream where another female was fishing with her two pups. A brief, loud fight erupted, after which the mother of the singleton left without her offspring, who joined the other two pups and their mother. Nevertheless, this was described as a close association between two radio-implanted female otters, which appeared to rear pups together in Esther Passage, Alaska (Rock et al. 1994). The authors assumed these were mother and daughter as the younger animal was a subadult when captured the year before. We made a similar observation of two unmarked adult females caring for three pups in Kenai Fjords National Park. In a marsh in San Francisco Bay, California, several females were observed protecting multiple pups from coyotes (*Canis latrans*; Rostain 2000). Although alloparenting may exist among female river otters, avoidance and territoriality are more common. Indeed, seven females instrumented with proximity tags in the Kenai Fjords and Prince William Sound failed to show interactions with either males or other females (Barocas et al. 2016).

5.3.3 The Role of Latrines in River Otter Sociality

The social system of coastal river otters is largely mediated by olfactory communication at latrines (a communal site for defecation; Ben-David et al. 1998). From a landscape perspective, the sites selected for social behavior and scent marking are characterized by high shoreline convexity (i.e., a promontory) and increased proximity to suitable foraging habitat (Albeke et al. 2010; Crowley et al. 2012). In addition, latrines vary in size and shape and can be broadly characterized as crossover sites (where long, overland trails connect two bodies of water) and piazza-style sites (where all trails from the water lead into one large open space). Some latrines occur near holts (i.e., dens) and freshwater pools (Bowyer et al. 2003). Social activity is more prevalent near piazza-style latrines, whereas crossover sites are commonly visited by larger groups (Barocas et al. 2016). At latrines, male river otters frequently groom, allogroom, touch, and play. They also spend a considerable part of their time rubbing and scent marking on vegetation (Bowyer et al. 2003).

Studies based on radio telemetry suggest that social otters, especially males, use a small number of available latrines with high intensity. These communication hotspots change location seasonally and annually, suggesting that scent marking functions convey information within and between male social units (Ben-David et al. 2005). High-resolution tracking indicates that fission and fusion events are temporally associated with latrine visits, suggesting feedback between olfactory information and grouping decisions. This relationship also holds in the spatial dimension, where individuals whose home ranges overlap are more likely to be found together (Barocas et al. 2016). Thus, while the primary factor encouraging the formation of male river otter groups is cooperative hunting, group formation and maintenance also rely on scent marking at latrines (Blundell et al. 2002a).

Females rarely associate with males or visit latrines frequented by large groups (Blundell et al. 2004; Barocas et al. 2016). Instead, they visit multiple latrines infrequently, largely to assert territorial boundaries (Ben-David et al. 2005; Albeke et al. 2015). However, females bring their pups to latrines used by male otters (Barocas and Ben-David, unpub. obs.), presumably to expose them to the scent marks of resident males. Because males typically do not disperse from their natal range except during the mating season, and because groups form based on familiarity, introducing pups to resident male groups may facilitate their acceptance into these social units (Blundell et al. 2002b; Hansen et al. 2009).

5.3.4 Social Behavior at Latrines

River otters do not possess a thick layer of subcutaneous fat. Similar to other otter species, they rely on longer guard hairs to cover and shield the underhairs, creating a protective water-resistant outer layer (Weisel et al. 2005; Liwanag et al. 2012). The hair density in the fur of North American river otters (up to 585 underhairs mm^{-1}) is similar to fur seals (up to 444 underhairs mm^{-1}) but less than sea otters (up to 1189 underhairs mm^{-1}). However, in all cases, the size and shape of cuticular scales on underhairs play an important role in trapping air next to the skin (Davis 2019; see Sect. 3.2.2). To maintain the insulating air layer, river otters groom and blow air into their fur. As otters groom their fur, the interstices between the underhairs become so small that water does not penetrate because of the high surface tension of water, and an air layer is created that provides most of the thermal insulation.

While grooming is essential to maintain an air layer in the fur, it also is one of their main forms of social interactions. Otters will occasionally self-groom, but as in primates, allogrooming can establish and strengthen social relationships (Henzi et al. 2009). When allogrooming, otters use their mouths to gnaw gently at each other's head and shoulders. In a detailed study of river otter behavior in captivity, individuals showed consistent allogrooming (Hansen et al. 2009). In the wild, allogrooming frequency varies by latrine type. In piazza-style sites, river otters exhibit higher positive social interactions (32%) compared to trail-based latrines (12%). In general, grooming and allogrooming were especially common near latrines where fresh water pools were available, possibly associated with rinsing in fresh water and fur maintenance (Barocas et al. 2016).

To further understand the social component of allogrooming, we deployed camera traps from May–August 2016 at 43 coastal latrines in Prince William Sound, yielding 1806 videos with river otter behavior (Barocas et al. 2020). We focused our analysis on latrine visits in which full behavioral sequences for each individual otter could be evaluated based on an established ethogram. All social interactions, including grooming (Fig. 5.1a) and joint rolling on the ground

Fig. 5.1 Examples of North American river otters performing social behaviors related to fur maintenance. Allogrooming (**a**) and rolling (**b**) behavior in a marine population in Prince William Sound, Alaska

(Fig. 5.1b), were recorded. We found that per capita, allogrooming frequency during group visits is significantly higher compared to self-grooming. In addition, grooming frequency was higher in piazza-style (18.5%) compared to crossover (3.6%) latrines (Fig. 5.2a). In contrast, rubbing and rolling on the ground was unaffected by social context, as both solitary and social animals performed the behavior in comparable frequencies (solitary = 38.3%; group = 39.9%; Fig. 5.2b). As with allogrooming, this behavior was more common near piazza-style than at crossovers latrines (piazza-style = 48.4%; crossover = 28.6%; Fig. 5.2b), likely as a result of the trail-dominated structure of crossovers. These observations corroborate the conclusion that allogrooming plays an important role in maintaining group cohesion. Further analysis, including behavioral data collected from captive river otters, may reveal whether allogrooming conveys information on dominance within otter social groups, similar to that in primates (Barrett et al. 2002; Hansen et al. 2009).

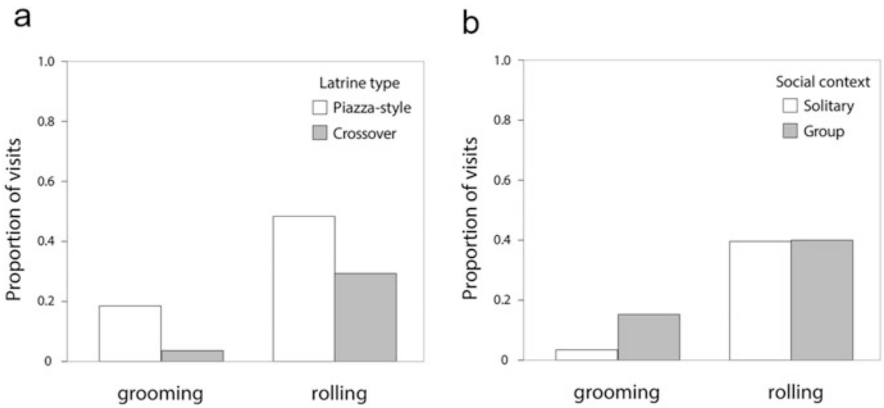


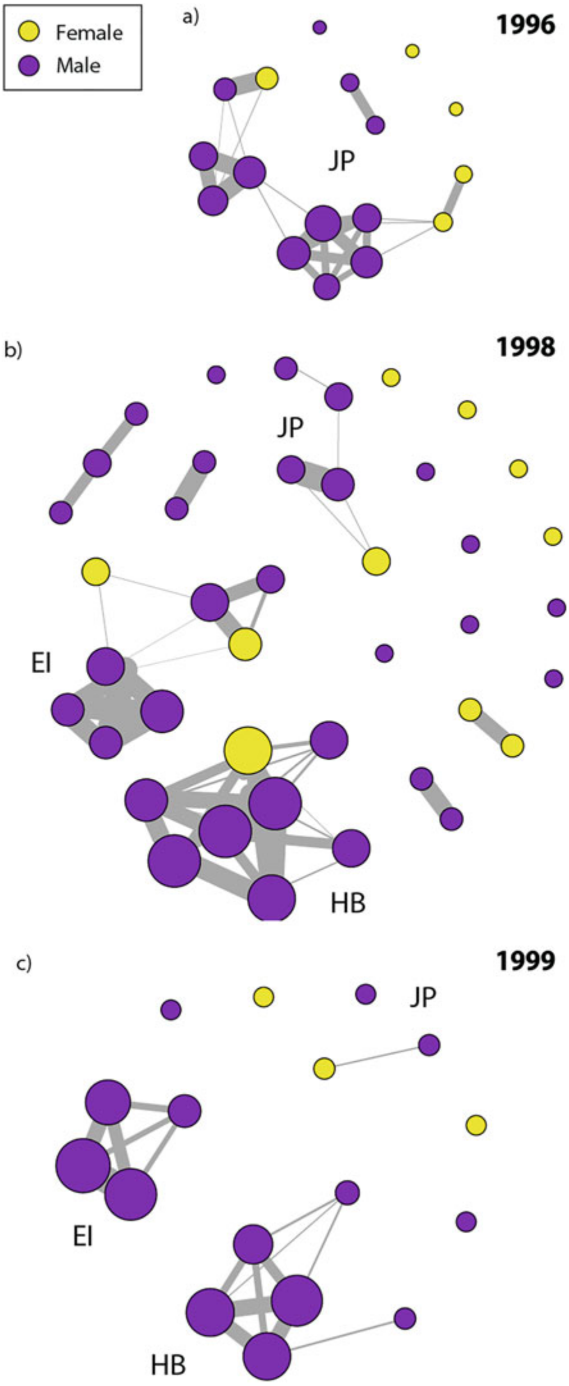
Fig. 5.2 Proportions of social behaviors performed by river otters during latrine visits and different contexts. Data represent behavioral bouts collected from camera traps deployed during the summer of 2016 in Prince William Sound, Alaska

5.3.5 River Otter Social Network Structure

From 1996–99, 55 river otters were captured in three areas and fitted with VHF radio transmitters in Prince William Sound (Blundell et al. 2002a). Associations among tagged otters were inferred from telemetry and direct observations, and we used these inferred associations to build social networks (Croft et al. 2008). Because the duration of periods when otters were found together was unknown, the ties between individuals represented a summation of all events when each pair of individuals was detected together, using the 'gambit of the group' method (i.e., if more than two individuals are observed together, reciprocal spatial associations are inferred among all individuals; Croft et al. 2008). Individual otters were represented in the networks as nodes and the strength of association between them as edges. Because the majority of otters were observed both alone and in the company of other individuals, and because the sampling effort was heterogeneous, we chose the Simple Ratio association index, which accounts for total observations (Farine and Whitehead 2015).

We initially plotted the networks to visualize patterns and assess the number of components. The 1996 network, in which all tagged animals were from the same area, Jackpot Bay (JP), created one large component that included 12 individuals (75% male) and several smaller ones (Fig. 5.3a). The 1998 network, which included individuals from separate areas (JP, Herring Bay [HB], and Eleanor Island [EI]), was more fragmented. Individuals from each area formed a distinct component, with the strongest ties among otters from HB (88% males). In HB, where sampling efforts were the highest, there were two additional dyads disconnected from other components (Fig. 5.3b). The lack of association among individuals from HB and EI suggests spatial segregation among these areas, whereas JP is spatially more remote from both of the other populations. Similarly, the 1999 network was formed by two

Fig. 5.3 River otter social networks based on associations. Node sizes are proportional to strength centrality, and edge widths are proportional to the Simple Ratio association index (see text for details). Data was inferred from VHF radio telemetry between summers 1996 and 1999, in Prince William Sound, Alaska



main components in HB and JP (all composed of males) and a smaller, fragmented one in EI (Fig. 5.3c).

In animal social networks, node connectivity reflects the social position of an individual. Because we were interested in quantifying such positions for males and females, we calculated three node-based centrality metrics for each individual: (1) Degree centrality—the number of direct ties an individual has, (2) Strength centrality—the weighted equivalent of binary degree (i.e., the sum of all edge weights connected to each node, (3) Clustering coefficient—the density of the subnetwork of a focal individual's neighbors, calculated by the number of ties between neighbors divided by the maximal possible number of ties between them (Wasserman and Faust 1994; Wey et al. 2008; Farine and Whitehead 2015).

Overall, network centrality metrics that measured the number and strength of direct contacts were considerably higher for males compared to females (Table 5.2). This pattern was not significant for degree centrality (1996: Kruskal-Wallis $\chi^2 = 3.5$, $P = 0.06$; 1998: $\chi^2 = 1.33$, $P = 0.25$; 1999: $\chi^2 = 3.3$, $P = 0.07$) but did receive stronger support in one of the years and was overall closer to significance for strength centrality (1996: Kruskal-Wallis $\chi^2 = 5.4$, $P = 0.02$; 1998: $\chi^2 = 3.46$, $P = 0.06$; 1999: $\chi^2 = 3.42$, $P = 0.06$). These results indicate that males have higher numbers of direct connections and their connections are stronger compared to females, but the difference in the strength of connections is more accentuated. This finding is in line with results from a study that observed that females occasionally associate with males and join them on foraging bouts, but they rarely spend extended periods in social groups (Blundell et al. 2002a). It also highlighted the fact that not all males in the population join social groups. There were no evident differences in clustering coefficients in the two years when comparison was possible, suggesting that the cohesion of social neighborhoods of males and females was similar (1996: Kruskal-Wallis $\chi^2 = 0.01$, $P = 0.9$; 1998: $\chi^2 = 0.13$, $P = 0.71$; Table 5.2).

Research on the networks of social animals suggests that individuals can have positions in their groups that are consistent over time and among contexts (Lusseau and Newman 2004; Aplin et al. 2015). We did not have a sufficient sample size for which detailed group structure was known over multiple years. However, among the five individuals in the HB group, four did show consistency in their network positions (i.e., similar relative connectivity) among the occasions measured (Fig. 5.4). Recent evidence on the consistency of social positions suggests that intrinsic factors, such as the animal's 'social phenotype', may be as important in determining social structure as other factors, such as age, sex, and resource availability (Farine et al. 2015; Krause et al. 2017). Other studies indicate a relationship between the behavioral types of individuals and their network positions (Aplin et al. 2013; Snijders et al. 2014). Whether river otter patterns of sociality are in line with this evidence is an intriguing research direction, which can be explored in the future with the increase of long-term data collection.

Table 5.2 Social network node metrics for male and female river otters in Prince William Sound, Alaska, during the summers of 1996–99. Values are means and standard errors

Year	Females				Males			
	n	Degree	Strength	Clustering coefficient	n	Degree	Strength	Clustering coefficient
1996	5	1.40 ± 0.75	0.19 ± 0.09	0.75 ± 0.16	12	3.42 ± 0.57	0.67 ± 0.10	0.71 ± 0.07
1998	9	1.56 ± 0.67	0.28 ± 0.17	0.63 ± 0.15	32	2.44 ± 0.4	0.85 ± 0.17	0.69 ± 0.06
1999	3	0.33 ± 0.33	0.02 ± 0.02		15	2.36 ± 0.43	0.53 ± 0.13	0.89 ± 0.05

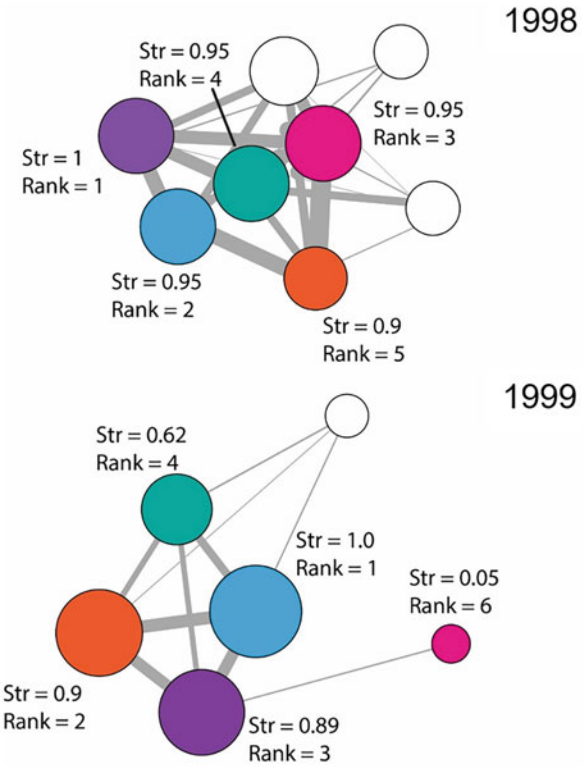


Fig. 5.4 River otter social networks in the Herring Bay, Alaska. Individuals that were present in both years have the same colors. Node sizes are proportional to strength centrality and edge widths are proportional to the Simple Ratio association index (see text for details). Each individual's strength centrality and rank within the group are presented. Data were inferred from VHF radio telemetry during the summers of 1998 and 1999 in Prince William Sound, Alaska

5.4 Sea Otter Sociality

Sea otters exhibit a social system that is unique among lutrines specifically and carnivorans in general. Throughout their range, males and females form aggregations that are spatially segregated, designated as 'male areas' or 'female areas' (Schneider 1978). Home ranges of both sexes are small (<20 km of shoreline), and females show high philopatry, although they occasionally shift their core activity areas (Estes et al. 2009; Tarjan and Tinker 2016). Younger sea otters occasionally move longer distances, and some males adopt a mobile lifestyle throughout their lives (Jameson 1989).

The reproductive system of sea otters is resource defense polygyny, where dominant males actively search for estrous females or establish territories within female areas (see Chap. 6; Jameson 1989; Tinker et al. 2018). Males aggressively exclude other males from their breeding territories, although home ranges of females often overlap those of several males (Pearson et al. 2006). The number of males within female areas varies seasonally, likely as a function of female receptivity. Males return to their original areas presumably because they offer higher food availability (Tinker et al. 2018). As a result of male territoriality, younger or non-competing males are excluded from female areas. These non-breeding males often congregate in large bachelor rafts or emigrate to new areas. Territorial males will occasionally return to male areas after breeding and integrate into these bachelor rafts. Male territoriality has a significant influence on the equilibrium density of sea otter populations (Davis 2019). In stable sea otter populations, male and female ranges are consistent through time and differ in some habitat features, including wave exposure. In expanding populations, new foraging and resting areas are initially occupied by males, whereas females usually arrive later (Garshelis et al. 1984; Pearson and Davis 2005).

The formation of sea otter aggregations is likely the result of a combination of factors, the first of which is the mating system described above. The second is the avoidance of predators, although large rafts may be attractive to marine predators, such as killer whales (*Orcinus orca;* see Chap. 9; Estes et al. 1998. It is possible that this behavioral pattern resulted from hunting by humans, as groups of sea otters may alert conspecifics to the presence of surface predators. Human hunting was a significant mortality factor during the Maritime Fur Trade in the eighteenth and nineteenth centuries, and it likely exerted strong selection pressure on sea otters (see Chap. 10; Larson et al. 2002). Alternatively, spatial distribution of suitable habitat may contribute to the tendency of otters to form aggregations. When rearing young pups, female otters often leave them in kelp beds or sheltered areas to ensure they do not drift with the tides and winds (Tinker et al. 2018). Limited availability of such features may result in female aggregations. Finally, gregariousness may facilitate foraging through the acquirement of valuable information regarding resource availability (Ward and Zahavi 1973). This may be true for male sea otters for which exploration and movement among feeding areas are frequently documented, whereas females may acquire knowledge on high-quality foraging areas from their mothers (Garshelis et al. 1984; Lee et al. 2009; Novak and Tinker 2015).

5.4.1 Interactions Among Males

Male rafts—consisting of up to several hundred individuals—commonly form after early morning foraging sessions; they are fluid in their composition, with several fission and fusion events occurring each day (Garshelis et al. 1984). Variation in group size is likely influenced by population density. Despite the consistent spatial proximity, social interactions are uncommon (5–11% of observations; Garshelis et al. 1984; Pearson and Davis 2005; Finerty et al. 2009). These behaviors include mock fights and copulations, especially involving juveniles. Allogrooming among males has not been reported. In contrast, agonistic interactions are often observed among territorial males (67% frequency; Pearson and Davis 2005). Compared with river otters, the low frequency of social interactions may be a consequence of the more aquatic lifestyle of sea otters, as the reduced time on land provides less opportunity for social activity.

5.4.2 Interactions Among Females

Females usually aggregate in smaller groups than males (Garshelis et al. 1984). They mostly interact with their young pups, especially in the first three months of life (Cortez et al. 2016). Females give birth on the water's surface and carry their altricial pup on their abdomen for about a month before the pup begins to develop swimming skills. In addition to nursing, providing solid food, and protecting their pups from predators and other sea otters, females allocate a considerable proportion of time to grooming their pups (4–13% of their time; Cortez et al. 2016). This is the only form of allogrooming recorded in sea otters and results from the pup's inability to effectively self-groom, especially in the first eight weeks after birth. Whereas river otter females exclude each other from their territories and remain solitary, sea otter females likely aggregate because they carry their pup with them and are not spatially constrained by a natal holt.

5.4.3 Sea Otter Social Structure

Despite extensive data on the spatial distribution of sea otters, formal assessment of social network formation and maintenance have not been performed, largely because researchers assumed that rafts were composed of randomly assembled collections of individuals that aggregated after solitary foraging (Estes, unpub. obs.). A preliminary analysis of long-term spatial associations between tagged sea otters in Monterey Bay, California, indicates that several distinct clusters occur within the large aggregations (Tinker, unpub. obs). In addition, some individuals (male-female mated pairs and reproductively-synchronous females) show consistent associations over many years. As a result, formal network analyses for sea otters may reveal important information on sociality that revises our understanding of the species' mating system, dispersal patterns, and reproductive success.

Differences in social structure between sea otters and marine North American river otters likely result from their foraging modes, mating systems, and habitat. Whereas marine river otters can forage in a group, spend a significant proportion of time on land, and have more opportunities for social interactions, sea otters are solitary foragers and primarily aquatic. However, if sea otter male and female spatial associations show consistency (associations with the same individuals over time), it would be interesting to examine whether they—like river otters—are affected by kinship, age, social status, or familiarity. In addition, because the resources available to sea otter populations vary throughout their range, density may be an important driver of aggregation sizes and cohesiveness, which varies geographically and in areas recently reoccupied since the maritime fur trade.

5.5 Conclusions and Future Directions

Since the advent of social network analysis as a tool to study animal sociality and advances in the ability to collect and analyze larger datasets, researchers have moved beyond the description of social systems to more mechanistic approaches, including hypothesis testing with null models and network dynamics (Croft et al. 2016). As a result, current research on social behavior includes (1) the temporal and spatial dynamics of social networks, (2) spatial structuring of social interactions, (3) communication and transfer of information within social networks, and (4) various forms of feedbacks between social structure and demography (Pinter-Wollman et al. 2013; Ilany et al. 2015; Firth and Sheldon 2016; Snijders and Naguib 2017; Shizuka and Johnson 2020). Our network analysis of North American river otters provides examples of how these approaches can be used in the study of lutrine ethology and ecology. These approaches can provide new information on sea otter behavior.

The case studies reviewed here show how animal social systems can present common patterns, such as differences in sociality among sexes, links to resource availability, and dependence on spatial behavior. They also provide insights into the ecology of North American river otters and sea otters associated with differences in mating systems, foraging behavior, and amphibious vs. aquatic living. The social systems that are influenced by factors such as habitat, diet, sex, reproductive status, and population density offer opportunities to explore the causes and consequences of variation in sociality among mammals.

Nevertheless, none of the mentioned factors could fully explain the differences in social interactions among individual river otters in coastal Alaska and between species (e.g., marine *Lontra canadensis* vs. *Lutra lutra*). In our attempt to understand the role of inheritance in determining social tendencies, researchers are using genomic tools, including transcriptomics (gene expression) and proteomics (protein translation) to link genes with specific behaviors (Robinson 1999; Robinson et al. 2005). In the lutrines, social interactions could be further shaped by maternal teaching (e.g., exposure to male scent at latrines in *Lontra canadensis*), social standing in the hierarchy, and more. We anticipate that with the emergence of technological advances in the application of proximity tags, remotely operated video cameras, genomics and network analyses, lutrines will be at the center of research on the factors underlying variation in social behavior.

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Chapter 6
Reproductive Behavior of Male Sea Otters

Heidi C. Pearson and Randall W. Davis

Abstract The reproductive system of sea otters 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 ~3 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. The reproductive system of sea otters is more similar to some species of Phocidae (true seals) than to other species of otters, likely because mating occurs at sea.

Keywords Consortship · Copulation · Mating behavior · Resource defense polygyny · Segregation · Sea otter · Sexual segregation · Territoriality

6.1 Male Sea Otters: Morphologic, Physiologic and Behavioral Traits

Beyond differences in sexual organs, male and female sea otters are similar in appearance, physiology, and sensory abilities (see Chap. 3). Although they are sexually dimorphic in size, there is significant overlap in the body mass of adult males and females depending on subspecies, geographic location, and prey

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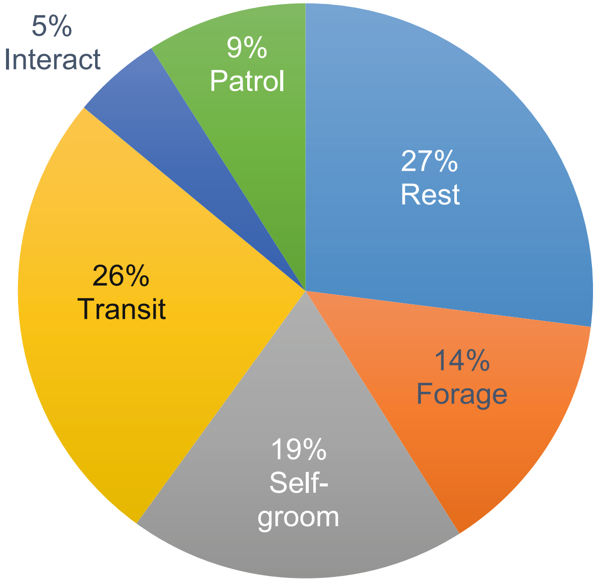

Fig. 6.1 Mean 24-hr activity budget for territorial male sea otters. Resting behavior includes sleeping on the water's surface. Foraging behavior includes the time submerged and while handling prey at the surface between dives. Self-groom refers to felting the fur to maintain an air layer. Transit refers to directed swimming at the surface, usually in the supine position (belly up with head facing backwards) using alternate or simultaneous pelvic paddling. Patrol refers to swimming at the surface in the prone position (belly down with head facing forwards). Interacting includes social and mating behavior. Data were collected in Simpson Bay, Alaska, during the summer months of June to August. Data adapted from Finerty et al. (2009)

availability (Kenyon 1969). Male sea otters range in mass from 22-45 kg and females from 14-33 kg.

Male and female sea otters exhibit similar behaviors, including resting, foraging, transiting, grooming, and socializing/mating (Figs. 6.1, 6.2, and 7.1; Pearson and Davis 2005; Finerty et al. 2009). For territorial males, patrolling (searching for sexually receptive females and excluding other males) is an additional behavior that does not occur in females. These behaviors occur almost exclusively in the marine environment. While sea otters occasionally haul out on shore to rest, this is not necessary, and they typically rest on the water's surface (Estes 1989).

In this chapter, we review male sea otter reproductive behavior. We begin with male sea otter reproductive anatomy and physiology and then discuss the evolution of their mating system (resource defense polygyny), territorial behavior, mating behavior, and comparisons with other marine mammals and otters. For a comparable review of female reproductive behavior, see Chap. 7.

6.2 Anatomy and Physiology of Male Reproduction

Male sea otters become sexually mature at 5–6 years of age, although social maturity (i.e., the ability to defend a territory and mate) may not occur for several more years (Estes 1989). Male sea otter reproductive anatomy is similar to that of other carnivorans (i.e., species of the Order Carnivora). A vascular penis is reinforced with a baculum (penile bone), which has a ligamentous attachment to the ischium (Kenyon 1969; Orbach 2018). The baculum aids coitus by maintaining sufficient stiffness during intromission (Miller 2018a). When floating supine (belly up with head facing backward) on the water's surface, a penile ridge formed by the baculum and a scrotum containing the paired testes are visible (Fig. 6.3). During mating, ejaculation is similar to other male mammals, and sperm production exhibits mild

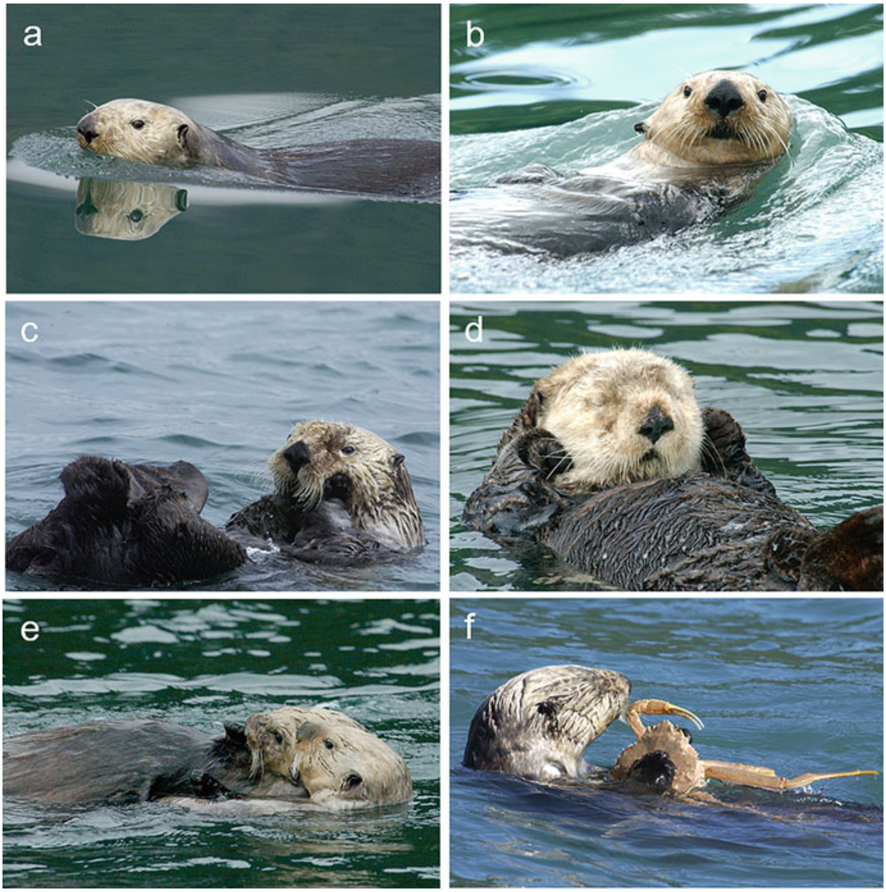

Fig. 6.2 Behaviors of male sea otters: (**a**) patrolling, (**b**) transiting, (**c**) self-grooming, (**d**) resting/ sleeping, (**e**) interacting with a female and (**f**) foraging. Images obtained under USFWS Marine Mammal Permit Nos. MA-043219 and MA-078744 to R. Davis

Fig. 6.3 External male reproductive anatomy showing a penile ridge and scrotum. Image obtained under USFWS Marine Mammal Permit No. MA-043219 to R. Davis

periodicity, indicating a weakly expressed breeding season (Orbach 2018). There is no evidence for reproductive senescence, probably because longevity is <20 years and often limited by tooth wear, predation, and disease (Fig. 3.6; Kenyon 1969). As with other Mustelidae, female sea otters are reflex ovulators (see Sect. 7.2). Copulation stimulates ovulation by means of a post-coitus rise in luteinizing hormone (Carroll et al. 1985). The persistence of semen in the female reproductive tract for prolonged periods (up to 120 hr in ferrets, *Mustela putorius furo*) likely facilitates fertilization (Amstislavsky and Ternovskaya 2000).

In mammals, androgens (i.e., the male sex hormones testosterone and androstenedione) induce male sexual behaviors, including scent-marking, copulation, and intermale aggression (Fig. 6.4; Hart 1974). Male sea otter reproductive behavior is likely influenced by chemoreception, which involves pheromones and the vomeronasal system (see Sect. 3.3.4). In sea otters, the vomeronasal organ is a bilaterally symmetrical, blind diverticulum (or pouch), located at the base of the anterior nasal cavity, which opens into the oral cavity through the anterior incisive ducts (the two large foramina behind the incisors) behind the upper incisors (Fig. 3.3b; Davis 2019). It detects volatile and nonvolatile pheromones released by individuals of the same species that convey social or sexual (endocrine) cues, which can influence behavior and reproductive physiology (Chamero et al. 2007; Liberles 2009; Thewissen 2018). The vomeronasal organ likely functions in precopulatory behavior when males nose the anogenital region of females before copulation (see below and Fig. 6.4b). As observed in other carnivorans (e.g., dogs), this behavior enables the male to assess estrous state by pulling pheromones contained in the female's urine and vulvar and anal secretions into the vomeronasal organ (Kustritz 2005).

Fig. 6.4 Male reproductive behavior: (**a**) male tests female's sexual receptivity, (**b**) anogenital nosing associated with the detection of pheromones by the vomeronasal organ and other olfactory cues, (**c**) male grasps female from behind, (**d**) male grasps female's nose, (**e**) mating on the surface of the water, (**f**) male penis prior to coitus. Images obtained under USFWS Marine Mammal Permit Nos. MA-043219 and MA-078744 to R. Davis

6.3 Evolution of the Sea Otter Mating System

The reproductive system of sea otters is resource defense polygyny. Dominant males divide geographical areas used by females into territories, which they aggressively defend from other males (Figs. 6.5 and 6.6). This type of reproductive system arises when there is no male paternal care, female ranges are not defendable, and female groups are unstable (Clutton-Brock 1989). In addition, it results in a social system in which males and females segregate into geographically discrete areas. Male areas are occupied almost exclusively by males of all ages (Kenyon 1969; Garshelis et al. 1984; Monnett 1988). In contrast, female areas contain a few territorial males and

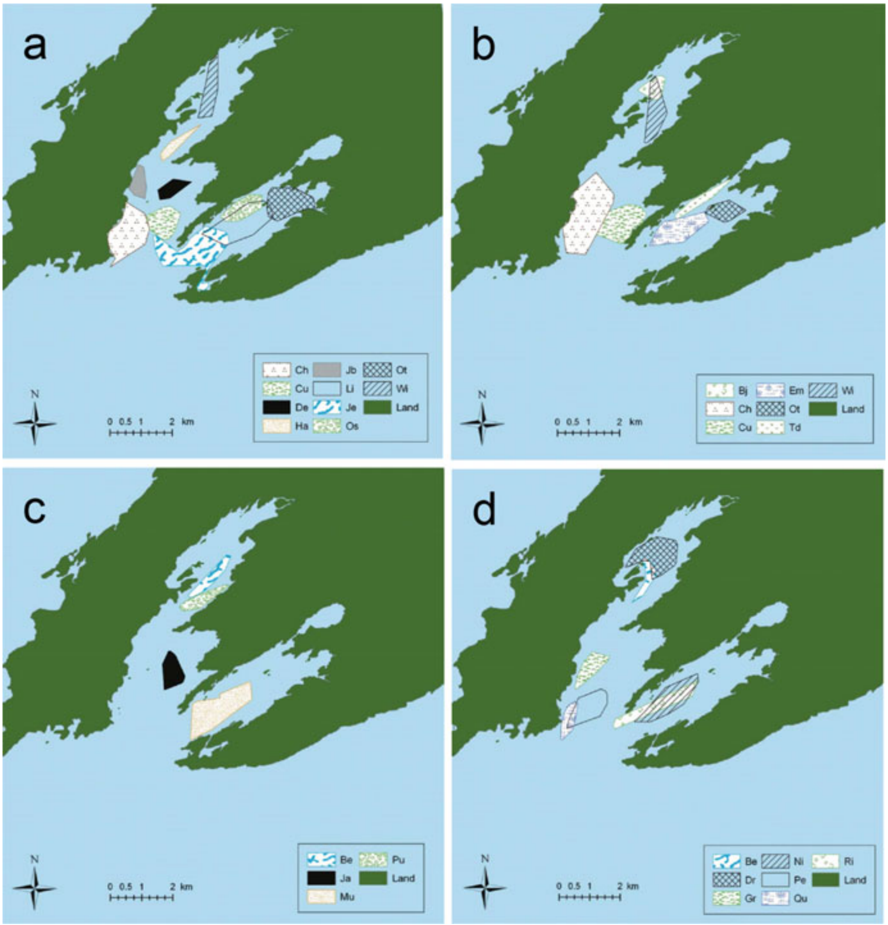

Fig. 6.5 Male sea otter territories in Simpson Bay, Prince William Sound, Alaska, during the summers of (**a**) 2003, (**b**) 2004, (**c**) 2005, and (**d**) 2006

females of all ages (Garshelis et al. 1984; Monnett 1988). Other males are excluded from female areas, making emigration (or reduced immigration) of males, especially subadults, an important factor in regulating population density (Monnett 1988; Garshelis et al. 1984; Ralls et al. 1996; Wolff 1997; Bodkin et al. 2000). As sea otter populations expand, non-territorial males are the first to explore and occupy new habitats resulting in range expansion (Garshelis et al. 1984). In addition, as prey resources decrease in established areas and competition increases, young females follow males into new areas and produce pups, thereby perpetuating the cycle of range expansion (Garshelis et al. 1984; Lafferty and Tinker 2014).

These dispersal patterns also have implications for sex-specific differences in ranging patterns. Adult females have relatively stable home ranges with unstable aggregations, making it challenging for males to defend females or influence their

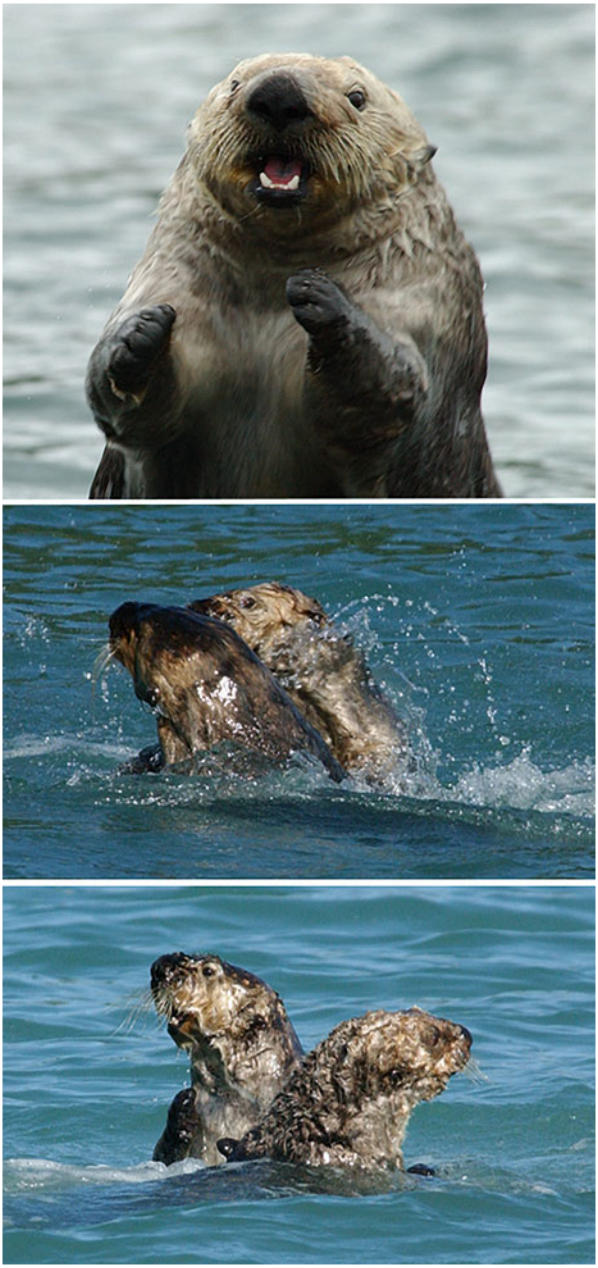

Fig. 6.6 Male sea otters fighting at the surface. Images obtained under USFWS Marine Mammal Permit Nos. MA-043219 and MA-078744 to R. Davis

movements. Consequently, adult males enhance mating opportunities by defending territories containing resources important to females. Males have larger annual ranges as they move between female and male areas during the breeding and non-breeding seasons, respectively, while females have smaller annual ranges and aggregate in female areas (Garshelis et al. 1984; Monnett 1988; Jameson 1989; Ralls et al. 1996). Subadult males and females have much larger ranges than adults, with subadult males having the largest (Monnett 1988; Ralls et al. 1996).

6.4 Male Territorial Behavior

Unlike most species in the Family Mustelidae, adult male sea otters are territorial (Chap. 5; Kenyon 1969; Calkins and Lent 1975; Loughlin 1980; Garshelis et al. 1984; Estes 1989; Jameson 1989; Pearson et al. 2006). Territoriality occurs in mating systems spanning wide taxonomic ranks, including invertebrates and nearly every vertebrate class, with its definition originally rooted in descriptions of display behaviors of birds (Brown and Orians 1970; Kaufmann 1983). Most definitions of a territory describe it as the exclusive, fixed area of an individual (or group) home range containing important (oftentimes scarce) resources that are aggressively defended (contest competition) against members of the same sex and (typically) the same species (Brown and Orians 1970; Maher and Lott 1995). A key aspect of territoriality is the spacing of individuals within a habitat for optimum reproductive density (Pitelka 1959). Territoriality is a form of spatially localized social dominance, whereby the territory holder has priority of access to resources (e.g., food, shelter, mates) important for survival and/or reproductive success (Owen-Smith 1977; Kaufmann 1983; Maher and Lott 1995).

A territorial male sea otter excludes conspecific males, enabling uninterrupted mating privileges with females, enhanced reproductive success, and fewer intrasexual agonistic encounters (Welty and Baptista 1988). Territories generally are non-overlapping, which decreases population density and competition for food (Fig. 6.5). Maintaining a territory is energetically expensive. Territory holders (1) increase their energy expenditure during mating, displaying, and defense activities, (2) decrease the amount of time available for foraging and resting, and (3) face an increased risk of injury or death during agonistic encounters (Fig. 6.6; Brown 1964; Owen-Smith 1977; Kodric-Brown and Brown 1978; Apollonio et al. 1989; Vehrencamp et al. 1989; Isvaran and Jhala 2000). When animals defend territories to protect resources, energetic profitability will depend on the quality and spatiotemporal distribution of resources and intraspecific competition (Davies and Houston 1981; Houston et al. 1985). When territoriality no longer enhances fitness, another mating strategy will prevail (Gill and Wolf 1975; Lott 1984).

Sea otters are an excellent species for examining territorial behavior in the marine environment. Their regular presence on the water's surface and their distinguishing facial features (e.g., nose scars) enable image-identification and behavioral observations of known individuals for focal follows (Fig. 6.7; Foote 1970; Calkins and Lent 1975; Loughlin 1980; Mann 1999; Pearson and Davis 2005; Pearson et al. 2006; Finerty et al. 2007; Gilkinson et al. 2007). In addition, sea otters often occur in shallow (<100 m) nearshore waters because their foraging dives are short (<4 min

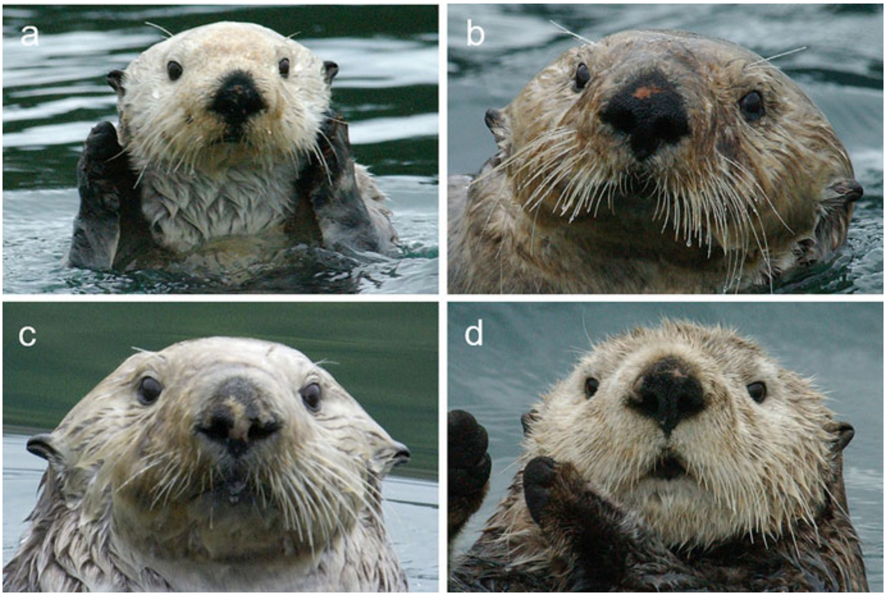

Fig. 6.7 Territorial male sea otters showing distinct nasal markings or scars, which may have resulted from fights with other males. These scars and other facial features enable individuals to be identified and tracked (Finerty et al. 2007). Images obtained under USFWS Marine Mammal Permit No. MA-043219 to R. Davis

in duration), which facilitates observation from shore or small vessels (Bodkin et al. 2004).[1]

Male sea otters defend territories in female areas with resources (Calkins and Lent 1975; Loughlin 1980; Garshelis et al. 1984; Jameson 1989; Pearson and Davis 2005; Pearson et al. 2006; Finerty et al. 2009, 2010). Territoriality is not present in male areas because they do not compete for estrous females during the non-breeding season (Garshelis et al. 1984; Jameson 1989). Thus, males may switch from being territorial during the breeding season to having undefended home ranges throughout the remainder of the year.

The seasonal occurrence and duration of male sea otter territoriality coincides with the peak breeding season during late summer (California) and autumn (Alaska) (Garshelis et al. 1984; Jameson 1989). However, breeding can occur at any time of the year, and some males are present in their territories year-round (Kenyon 1969; Sandegren et al. 1973; Loughlin 1980; Garshelis et al. 1984; Jameson 1989; Riedman et al. 1994). Furthermore, some males may maintain the same territory for consecutive years, although the boundaries may change seasonally or annually (Garshelis et al. 1984; Finerty et al. 2010). For example, in Simpson Bay, Alaska,

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[1] However, in regions where subsistence hunting is prevalent (e.g., Southeast Alaska), individuals appear to associate small vessels with hunting risk and close approach is typically not possible (Raymond et al. 2019; H. Pearson unpub. obs.).

five males maintained territories in the same area for two consecutive years (Fig. 6.5; Garshelis et al. 1984; Finerty et al. 2010). Territory size in Simpson Bay averaged 0.95 km^2 as compared with an average size of 0.23 km^2 in Gibbon Anchorage (Alaska), 0.35 km^2 near Monterey Bay (California), and 0.40 km^2 in a region from Ragged Point to San Simeon Creek (California) (Loughlin 1980; Garshelis et al. 1984; Jameson 1989; Finerty et al. 2010).

The aquatic environment precludes passive means of territorial defense (e.g., scent-marking; see Chap. 5; Owen-Smith 1977). Thus, sea otters actively defend their territories by patrolling, behavioral displays, and agonistic interactions with other males (Figs. 6.2a and 6.6). When patrolling, a male typically swims at the surface in the prone position (belly down) with its head facing forward just above the water's surface. This posture enables a male to scan the horizon in search of sexually receptive females and intruding males. Patrolling along territorial boundaries deters other males and may be accompanied by exaggerated kicking, splashing, and grooming (Kenyon 1969; Calkins and Lent 1975). Patrolling comprises 9% of the 24-h summer activity budget of territorial males, although this may be an underestimate because it can be combined with transiting (26%) and simultaneous grooming behavior (19%) (Fig. 6.1; Finerty et al. 2009). Unless they are resting or sleeping (Fig. 6.2d; see Sect. 3.2.5), territorial males are alert to any receptive female or intruding male.

If a territorial male encounters another male, a fight may ensue (Fig. 6.6). Aggressive interactions include wrestling, boxing, and biting (Calkins and Lent 1975; Garshelis et al. 1984; Pearson and Davis 2005; Finerty et al. 2010). Broken bacula can result during fights, and broken limb bones also have been observed (Miller 2018a; Davis unpub. obs.). However, fighting is risky and energetically expensive, so the territory holder commonly will chase the intruder out of the area, sometimes at high speed involving porpoising at the surface (Miller 2018b).

Females are attracted to areas based on size, prey availability, accessibility, and the amount of protected shoreline for resting (Fig. 6.5). For example, a large territory at the entrance of a bay with extensive shoreline enclosure and protected coves may attract females with pups because of its easy access, shallow feeding areas, and protection from wind and waves (Garshelis et al. 1984; Pearson et al. 2006; Finerty et al. 2010). In Gibbon Anchorage, the highest quality territories had (1) large areas, (2) abundant prey, (3) land on 1–2 sides, and (4) unobstructed entrances. In Simpson Bay, the highest quality territories had (1) large areas, (2) abundant prey, (3) entrances partially obstructed by other territories, and (4) land on fewer than two sides. Unlike Gibbon Anchorage, high-quality territories in Simpson Bay had entrances partially blocked by other territories, increasing the likelihood of females entering from neighboring territories (Garshelis et al. 1984; Pearson et al. 2006; Finerty et al. 2010). The maximum number of territories was higher in Simpson Bay (10) than Gibbon Anchorage (6), offering one potential explanation for this difference. However, there is significant interannual variation.

While most territories are abandoned during the winter, males have been observed in female areas during the winter, thereby increasing mating opportunities (Loughlin 1980; Garshelis et al. 1984). As territories with females approach carrying capacity, males may leave for short periods, presumably on foraging excursions to meet their energetic requirements (Garshelis et al. 1984). Compared with males holding higher quality territories with abundant prey, males holding lower quality territories with less prey tend to occupy them for shorter periods of time (Garshelis et al. 1984).

Optimality models predict a positive correlation between territory quality and reproductive success (Krebs and Davies 1993). In Gibbon Anchorage, territory quality was positively correlated with the annual mean number of copulations[2] with different females and the annual observed number of pair bonds formed with females within each territory. Based on studies of lekking males, optimality models further predict that males holding higher quality territories (i.e., those more attractive to females) should spend more time in territory maintenance behaviors (e.g., patrolling and interacting with females; Figs. 6.2 and 6.4) rather than body maintenance behaviors (e.g., grooming, resting and feeding; Fig. 6.2c, d, f) (Isvaran and Jhala 2000; Pearson et al. 2006). However, this was not the case for males in Simpson Bay. Potential reasons for this include (1) high-quality territories with more shoreline enclosure may not require additional patrolling, (2) the study occurred prior to the peak breeding season when males may not expend extra effort in territory maintenance, (3) the maintenance of body condition may be just as important as maintaining a territory for reproductive success, and (4) the high metabolic rate of sea otters may necessitate a minimum level of body maintenance that cannot be sacrificed for territory maintenance (Pearson et al. 2006).

6.5 Male Mating Behavior

Males attempt to mate with females that enter their territories to forage, rest, or transit to other areas (Loughlin 1980; Garshelis et al. 1984; Pearson et al. 2006). A male that encounters a female uses chemoreception to determine estrus (Fig. 6.4b; see Sect. 6.2). This behavior may occur even if the female has a pup and is not sexually receptive. If a female is not in estrus, these encounters are often brief and involve rolling and failed attempts at coitus before the male disengages and continues patrolling, often stealing any prey from the female (Pearson and Davis 2005). Sometimes, a male will associate with a female and her pup for extended periods. Although the male may be sexually motivated and engage in rough play with the female, the female may not be receptive.

A female that is in estrus and is sexually receptive may form a consortship with a male, which typically lasts ~3 days (Box 6.1; Kenyon 1969; Calkins and Lent 1975; Garshelis et al. 1984; Pearson and Davis 2005; Pearson et al. 2006). Consortships occur in mammals that lack long-term mating relationships or shared parenting. During a sea otter consortship, the pair swim and forage in synchrony, usually led by

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[2] As mating behavior may not result in fertilization, copulations were used as a proxy for reproductive success.

the female (Kenyon 1969). During this time, the male exerts exclusive mating rights to the estrous female with frequent (e.g., hourly at the beginning of the consortship) copulations that decrease over time. Mating may occur near a rocky shore or reef (i.e., hauling-out rock), which becomes the center for their activities and is used for resting between copulations (Kenyon 1969). When resting onshore, the female and male nuzzle and fondle each other.

Like other mustelids, sea otter copulatory behavior is aggressive, which may induce ovulation (Tinker et al. 2018). The mating sequence involves the mating-hold, whereby the male and female are ventrodorsally joined, respectively, with the male's forearms wrapped around the female's chest (Fig. 6.4c). Attaining this mating-hold often involves wrestling, thrashing, and rolling at and below the surface. In addition, the mating-hold typically involves nose-biting, where the male grabs hold of the female's nose with its teeth (Fig. 6.4d; Kenyon 1969; Foote 1970). The already extruded penis is inserted as the male rests against the female's back (Fig. 6.4e, f). Copulation may be short or last to 30–60 min (Garshelis et al. 1984). Occasionally, mating is fatal to the female (Foote 1970; Krueder et al. 2003; Harris et al. 2010). This occurs more often (or at least has been better documented) in Southern sea otters along the California coast (Krueder et al. 2003; Harris et al. 2010). One study reported mating trauma to be a primary or contributing factor to cause of death in 11% of sea otter carcasses examined over a 3-year period in Monterey Bay, California (Krueder et al. 2003). In Simpson Bay, a freshly killed (body temperature above ambient water temperature) female sea otter was found in good body condition with no signs of injury. Necropsy indicated that death was by drowning, perhaps during mating (R. Davis unpub. obs). At the end of the consortship, the female deserts the male and is unlikely to mate again that season, thus ensuring paternity.[3] However, within this polygynous system, males mate with other estrous females that enter their territories (Garshelis et al. 1984; Riedman and Estes 1990). While males may attempt to prevent estrous females from leaving their territories without mating, it is impossible for them to control a female's movements, indicating the possibility of female mate choice (Kenyon 1969; Calkins and Lent 1975; Garshelis et al. 1984).

Maladaptive mating behavior has been observed in California, where some male sea otters have copulated with female and male juvenile harbor seals (*Phoca vitulina*; Hatfield et al. 1994; Harris et al. 2010). These interactions are aggressive and can cause trauma (e.g., vaginal and colorectal perforation) and death. In some cases, males were observed guarding and attempting to copulate with carcasses, a behavior observed with female sea otter carcasses that likely has origins in consortship behavior (Harris et al. 2010). There are at least two possible explanations for this behavior. Androgen-mediated, reflexive, and sometimes indiscriminate mating behavior may occur in male tetrapods. Thus, young harbor seals may be easy and

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[3] While females have been observed to copulate with more than one male during estrus, it is unknown if fertilization was successful (Riedman and Estes 1990). The presence of sperm competition in sea otters is unknown.

opportunistic targets for especially aggressive male sea otters or those that are unsuccessful in holding territories (Harris et al. 2010). Conspecific (i.e., indiscriminate) necrophilia may result from similar causes (Dickerman 1960). An additional explanation is that a sudden decline in mean survival rates for prime-aged adult females may have reduced the number of receptive females, perhaps leading subdominant males to misdirect mating behavior towards harbor seals (Tinker et al. 2006; Harris et al. 2010).

Box 6.1 Case Study of Consortship Behavior During our study of territorial male behavior in Simpson Bay during the summers of 2002–2003, we observed three consortships. Two were formed between territorial males and single females, while the third was formed between a male and female with a pup (Pearson and Davis 2005). We describe one of these consortships here.

From July 15–17, 2002, territorial male 608 and single female 609 formed a consortship and moved to a small cove. Our initial observation of the male occurred during copulation, so the consortship probably commenced prior to this. In addition to behaviors typically associated with mating (Fig. 6.4), the pair engaged in synchronous swimming (often with the female leading), diving, and hauling out on a rock to rest between consecutive copulations (Kenyon 1969). We observed multiple copulations on the first and second days of the consortship.

On the third day, the female terminated the consortship. Initially, the male and female engaged in synchronous swimming and diving, similar to that during the previous two days. Termination of the consortship was initiated by female aggression towards the male, asynchronous diving behavior, and desertion while the male was submerged. The male responded by swimming around the cove, searching and calling loudly for the female, which we could see swimming up the bay and within hearing range. After an hour, the male stopped searching and began foraging.

6.6 Comparisons with Other Marine Mammals and Otters

Because most male mammals do not participate in rearing offspring, mating systems are predisposed to polygyny. Females invest considerable resources (gestation, lactation, and parental care) in rearing a few offspring during their lives, whereas males compete for access to as many females as possible. The occurrence of polygyny depends on the spatiotemporal distribution (e.g., dispersed or aggregated) of adult females. In many marine mammals, natal philopatry (i.e., the tendency to breed at or near their place of birth) results in spatial clustering in aquatic breeding grounds or terrestrial rookeries, both of which are influenced by environmental conditions, food availability, and predators (Mesnick and Ralls 2018). Large rookeries with seasonal reproductive synchrony may result in female defense polygyny.

In the aquatic environment where females are mobile, there may arise resource defense polygyny, lekking (male display sites), scramble or contest competition, ambush mating, polygynandry (multifemale-multimale), roving, and temporary or serial monogamy (consortship or sequential female defense polygyny) (Bowen 2018; Mesnick and Ralls 2018). Sperm competition also may occur in some species, which is associated with seasonal enlargement of the testes. These mating systems are not mutually exclusive, and combinations may arise.

Among Otariidae (sea lions, fur seals, and walruses), dense female aggregations and terrestrial mating results in polygyny and sexual dimorphism (Gentry 1998; Mesnick and Ralls 2018). Females aggregate on rookeries suitable for parturition, thermoregulation, and access to offshore prey, so the mating system has been described as resource defense polygyny, although it may resemble female defense polygyny in some species. Among Phocidae (true seals), most species copulate in water. Females often are dispersed or occur in small colonies. The mating system is moderately polygynous, with the males of some species producing underwater vocalizations (e.g., in Weddell seals, *Leptonychotes weddellii*), which are thought to be part of male-male competitive displays. Resource defense polygyny occurs in some male ice-breeding seals, but other species appear to use sequential female defense polygyny (Mesnick and Ralls 2018). Elephant seals (*Mirounga* spp.) are unusual in that they copulate on land and display extreme sexual dimorphism and female defense polygyny (Le Boeuf and Mesnick 1990). Walruses, which are also strongly polygynous and copulate in water, exhibit resource defense polygyny or a lek-like mating system (Bowen 2018; Mesnick and Ralls 2018).

Odontoceti (toothed whales) exhibit complex, social-sexual groupings and a diversity of mating strategies, including consortships, hierarchical alliances of cooperating males aggressively herding females, scramble or contest competition, polyandry, ambush mating, and roving. Males may exhibit morphological and behavioral secondary sexual characteristics (Mesnick and Ralls 2018). Seasonal enlargement of the testes in some species indicates sperm competition. Among Mysticeti (baleen whales), mating systems include consortships, lekking, scramble or contest competition, and promiscuity (roving), none of which are mutually exclusive. In Sirenia (dugongs and manatees), solitary males may search for females over large areas or form mating herds of males that pursue females.

Compared with other otter species, the resource defense polygyny in sea otters is unusual. North American river otters (*Lontra canadensis*) and Eurasian otters (*Lutra lutra*) appear to have a promiscuous mating system, while other otter species form pair bonds and tend towards monogamy (Estes 1989; Tinker et al. 2018). Among marine mammals, the mating system of sea otters is similar to those species that exhibit terrestrial and aquatic resource defense polygyny. The reproductive strategies of male Weddell seals may provide the best parallel with sea otters. Males establish territories under shore-fast ice near breathing holes and cracks used by females. Similar to sea otters, mating occurs in the water, and the resource defended by male Weddell seals is access to breathing holes around rookeries used for pupping (Stirling 1983; Harcourt et al. 2007, 2008). However, unlike sea otters, male Weddell seals attract females through vocalization displays, a behavior also found in lekking systems (Harcourt et al. 2007).

6.7 Conclusions

The combination of surface persistence, coastal habitat, and defense of aquatic, resource-based territories distinguishes the behavior of male sea otters from other marine mammals. Key components of male sea otter reproductive behavior include sexual segregation, resource defense polygyny, aquatic mating, and lack of paternal care of offspring. Because mating occurs at sea, the reproductive system of sea otters is more similar to some species of Phocidae than to other species of otters. Future research avenues include (1) the role of the vomeronasal gland in male reproductive strategies, (2) examination of male reproductive success and its correlation with territory quality and mating strategy (e.g., territorial vs. roaming), and (3) assessing the energetic costs of maintaining a high vs. low-quality territory.

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Chapter 7

Reproductive Behavior of Female Sea Otters and Their Pups

Michelle M. Cortez and Randall W. Davis

Abstract Female sea otters become sexually mature at 2–4 years of age. Birth may occur throughout the year with a normal litter size of one. The reproductive cycle (period of gestation and dependency) is ~12 months, so female sea otters are normally either pregnant or caring for a pup. After birth, the female provides the pup with high-fat milk from two mammary glands on the lower abdomen. Female sea otters are income breeders and must feed daily to maintain milk production, although small fat reserves, which develop during gestation, may reduce the need to forage during the initial 3 weeks post partum. Maternal behavior, which is influenced by hormones and sensory cues, manifests as vigilance against abiotic or biotic threats to neonates, allogrooming (pup grooming provided by the female), and nursing. Sea otters often give birth on the surface of the water, so there is an immediate threat to the pup from drowning, hypothermia, and predation. Pups are altricial and dependent on the female for care (nursing and grooming) and protection, although 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 3 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, this energetic demand may exceed the female's foraging ability and cause a decrease in body condition, which could lead to pup abandonment or early weaning in severe cases. This behavior enables the female to survive and raise future offspring and enhance fitness. As a result, pup survival will vary geographically and annually in synchrony with favorable conditions. After females wean or abandon their pups, mating occurs within a few days to weeks, and the cycle repeats.

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7.1 Female Sea Otters: Morphologic, Physiologic, and Behavioral Traits

Beyond differences in sexual organs, male and female sea otters are similar in appearance, physiology, and sensory abilities (see Chap. 3). Although they are sexually dimorphic in size, there is significant overlap in the body mass of adult males (22–45 kg) and females (14–33 kg) depending on subspecies, geographic location, and prey availability (Kenyon 1969).

Male sea otters do not participate in rearing offspring, but both sexes exhibit many similar behaviors, including resting, foraging, transiting, grooming, and socializing/mating (Figs. 7.1 and 7.2). These behaviors occur almost exclusively in the marine environment, although the female and pup occasionally haul out to rest. For females, protecting, grooming, and provisioning (i.e., with milk and solid food) offspring are additional behaviors that do not occur in males. Females do not exhibit patrolling behavior, which is associated with male territoriality (see Chap. 6).

In this chapter, we review the reproductive and maternal behavior of female sea otters and their pups. We briefly review female sea otter reproductive anatomy and physiology, followed by a discussion of lactation, maternal and pup behavior, and reproductive strategies. The evolution of the sea otter mating system (resource defense polygyny) is discussed in Chap. 6.

7.2 Anatomy, Physiology, and Behavior of Female Reproduction

Female sea otters become sexually mature at 2–4 years of age (Kenyon 1969; Bodkin et al. 1993; Jameson and Johnson 1993; von Biela et al. 2009). The uterus and ovaries are typical of carnivorans (Sinha et al. 1965; Sinha and Conaway 1968). Female sea otters do not have a distinct breeding season. Pups are born in every month of the year, with a peak in the spring for Northern (i.e., Alaska, British Columbia, and Washington State) sea otters (Kenyon 1969; Siniff and Ralls 1991; Riedman et al. 1994). Birth may occur on water or land with a normal litter size of one (Kenyon 1969). Gestation is ~6 months in duration and includes an unimplanted period (embryonic diapause) of 2–3 months and an implanted phase of 4 months (Jameson and Johnson 1993; Riedman et al. 1994). Because sea otter pups are dependent on the female for ~6 months, the reproductive cycle (period of gestation and dependency) is ~12 months.

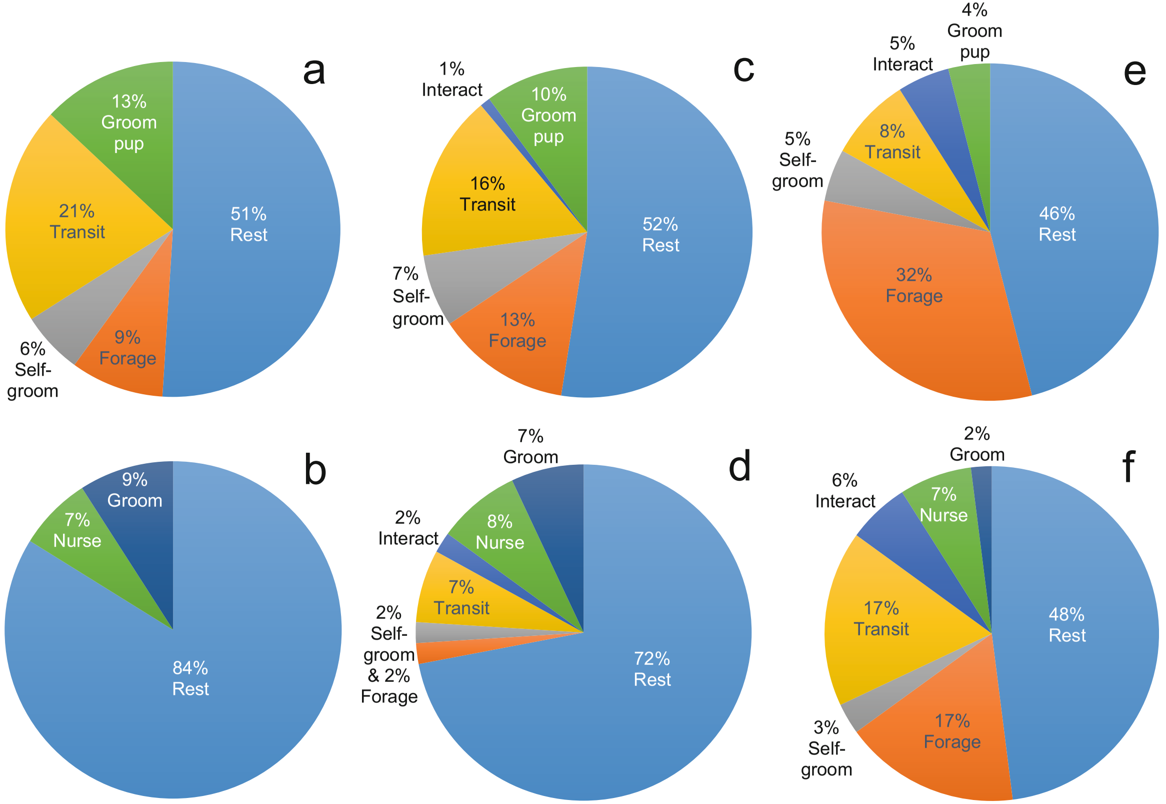

Fig. 7.1 Average 24-h activity budgets for female sea otters with pups of varying ages: (**a**) female with (**b**) pup <4 weeks old; (**c**) female with (**d**) pup 4–8 weeks old, and (**e**) female with (**f**) pup 8–12 weeks old. Resting behavior includes sleeping on the water's surface. Foraging behavior includes the time submerged and while handling prey at the surface between dives. Self-groom refers to felting the fur to maintain an air layer. Groom refers to the pup being

Fig. 7.2 Female and pup behaviors: (**a**) female resting and pup nursing, (**b**) female grooming pup, (**c**) female sharing Giant Pacific octopus with pup, (**d**) female transiting with pup resting, (**e**) female self-grooming, and (**f**) female and pup interacting. Images obtained under USFWS Marine Mammal Permit Nos. MA-043219 and MA-078744 to R. Davis

After females wean their pups at the age of ~6 months, the period of anestrus is short, and coitus occurs within a few days to a few weeks (see Fig. 6.4; Jameson and Johnson 1993; Riedman et al. 1994). Hence, female sea otters are normally (85–90% of the time) either pregnant or caring for a pup (Bodkin et al. 1993; Jameson and Johnson 1993; Eberhardt and Schneider 1994; Riedman et al. 1994). The pre-ovulatory behavior of females reduces aggression towards males so that mating may occur (Takashi 1990). If a female sea otter is in estrus and sexually receptive, she and a male form a consortship, which typically lasts ~3 days (see Sect. 6.5;

Fig. 7.1 (continued) groomed by the female. Transit refers to directed swimming at the surface, usually in the supine position (belly up with head facing backward), while using alternate or simultaneous pelvic paddling. Nursing refers to the percentage of time spent suckling. Interact refers to socializing with other otters and, in the female, occasional mating behavior. Data for females with pups were collected simultaneously in Simpson Bay, Alaska, during the summer months of June to August. Data adapted from Cortez et al. (2016a, b)

Kenyon 1969; Calkins and Lent 1975; Garshelis et al. 1984; Pearson and Davis 2005; Pearson et al. 2006). During a consortship, the pair swim and forage in synchrony, usually led by the female. Mating may occur near a rocky shore or reef (i.e., hauling-out rock), which becomes the center for their activities and is used for resting between copulations (Kenyon 1969). When resting onshore, the female and male nuzzle and fondle each other. The male exerts exclusive mating rights to the estrous female with frequent (hourly at the beginning of the consortship) copulations that decrease over time (Kenyon 1969). As with other mustelids, female sea otters are reflex ovulators, so copulation stimulates ovulation through a post-coitus rise in luteinizing hormone (Carroll et al. 1985). The persistence of semen in the female reproductive tract for prolonged periods (up to 120 h in ferrets, *Mustela putorius furo*) likely facilitates fertilization (Amstislavsky and Ternovskaya 2000). After ~3 days, the female abandons the male, which plays no role in rearing offspring.

In addition to hormonal changes, reproductive behavior in female sea otters may be influenced by pheromones detected by the vomeronasal system (see Sect. 3.3.4). This auxiliary olfactory organ detects volatile and nonvolatile pheromones released by individuals of the same species that convey social or sexual (endocrine) cues, which can influence behavior and reproductive physiology (Chamero et al. 2007; Liberles 2009; Thewissen 2018). Although the vomeronasal organ likely influences precopulatory behavior in males when they nose the anogenital region of females before copulation (see Sect. 6.2 and Fig. 6.4b), its role in the precopulatory behavior of females is uncertain. Female sea otters lick and nose the anogenital region of young pups while nursing. This behavior stimulates urination and defecation in altricial mammals, but it also may involve the detection of pheromones that reinforce maternal behavior (Sandegren et al. 1973).

7.3 Lactation

Parturition initiates the transition of fetal mammals from placental nourishment to the ingestion of milk produced by female exocrine mammary glands, referred to as lactation. Milk is a complex liquid containing variable amounts of water, carbohydrates, amino acids, lipids, electrolytes, vitamins, hormones, and immunological molecules (Davis 2019). Sea otter milk has a high fat content (23%), with an energy density of 10.3 kJ g^{-1} (2.46 kcal g^{-1}), although this varies throughout lactation (Jeness et al. 1981). Milk is produced by two mammary glands located bilaterally and symmetrically on the ventral inguinal region along the embryonic mammary ridges. In terrestrial mammals, the mammary glands are arranged in organs, such as breasts or udders, which protrude from the body. However, in sea otters and other marine mammals, they are relatively flat and lie beneath the blubber or skin. As a result, they conform to the hydrodynamic shape of the body and are not conspicuous. When nursing, young sea otter pups face posteriorly while resting on the female's abdomen as she floats or swims on the surface of the water in a supine position (Fig. 7.2a). Pup vocalization may indicate hunger and initiate nursing (Sandegren et al. 1973). Milk is ejected through the nipple by oxytocin-mediated contraction of myoepithelial cells stimulated by suckling (Koyama et al. 2013). As pups mature, they become too large to rest on the female and nurse while lying prone in the water perpendicular to the female.

Because female mammals initially provision their offspring by lactation, they form a bond that persists until weaning or longer. In contrast, male mammals for most species do not participate in rearing offspring and do not form a bond. As an evolutionary strategy, lactation enables mammals to transfer dietary or stored energy and nutrients from the female to the offspring until they can feed on their own, a dependency period that varies among species. There is a range of lactation strategies (i.e., mixed strategies) exemplified by two extremes. Species that provision their young while feeding daily are referred to as income breeders, while those that provision their young using stored energy (fat) and nutrients accumulated at an earlier time and fast during lactation are referred to as capital breeders (Drent and Daan 1980; Houston et al. 2007). Among marine mammals, Mytsiceti (baleen whales) and Phocidae (seals) are capital breeders, while Odontoceti (toothed whales), Otariidae (sea lions and fur seals), Odobenidae (walruses), and Sirenia (dugongs and manatees) are income breeders, although this varies among species (Davis 2019).

With their small size, high metabolic rate, and lack of blubber for thermal insulation, sea otters are income breeders for most of the pup dependency period. However, pregnant females develop transient fat deposits in the subcutaneous dorsal caudal area, omental bursa, around the kidneys, and in the inguinal area (Cortez et al. 2016b). This fat supplements the female's energetic requirements and contributes to milk production during the first 2–4 weeks postpartum when foraging is reduced (but not eliminated) to protect the pup from predation and other threats. During early lactation, sea otters resemble capital breeders, which rely on fat reserves for milk production (Gelatt et al. 2002; Davis 2019). However, a lactating female sea otter's small fat reserves are exhausted after several weeks, and foraging becomes the sole source of energy for metabolism and milk production, which is characteristic of income breeders.

7.4 Maternal and Pup Behavior

Maternal behavior is initiated by pregnancy hormones produced or regulated during fetal development, which inhibit sexual behavior while stimulating feeding and enlargement of mammary glands (Broad et al. 2006). The maintenance of maternal behavior after parturition is influenced by: (1) hormones, (2) visual, auditory, tactile, and olfactory cues from offspring, and (3) experience acquired over the reproductive life of a female (Eisenberg and Kleiman 1972; Rosenblatt and Siegel 1981; Riedman et al. 1994). These influences on maternal behavior enhance bonding with the pup and influence female conspecific and heterospecific aggression (Sandegren et al. 1973).

Synchronization of maternal behavior and lactation after parturition enhances the survival of offspring (Corona and Levy 2015). In most mammals, this manifests as vigilance against abiotic or biotic threats to neonates, allogrooming, and nursing. For sea otters, birth often occurs on the surface of the water, so there is an immediate threat of drowning, hypothermia, and predation. Because sea otter pups are altricial, the female must provide care and protection during the initial months after birth. Neonatal sea otters cannot swim, making them highly susceptible to drowning. As a result, the female swims at the surface in a supine position while carrying the neonate on her abdomen until it develops the strength and coordination to swim on its own at ~1–2 months of age (Fig. 7.2d). While the female is foraging, a very young pup rests effortlessly at the surface of the water, buoyed by air trapped in the pup's lanugo (i.e., neonatal fur) (see Sect. 3.2.4). Leaving a neonatal pup at the surface unattended makes it vulnerable to predation (e.g., bald eagles [*Haliaeetus leucocephalus*]), so the female reduces the amount of time spent feeding during the first 3 weeks after parturition and relies on stored fat to remain in energy balance (Monson et al. 2000; Gelatt et al. 2002; Esslinger et al. 2014; Cortez et al. 2016a, b). An unattended pup also is at risk of drowning from wind and waves, so females with young pups often move to sheltered areas of coastline or bays, which become nursery areas (Sandegren et al. 1973). In California, inclement weather is a significant cause of pup mortality, and this is true in parts of Alaska, especially during the winter (Kenyon 1969; Jameson and Johnson 1993).

Sea otters rely on fur for thermal insulation in water, which has a thermal conductivity 23-fold greater than in air (see Sect. 3.2.4). To be an effective insulator in water, the fur must be waterproof and trap an air layer next to the skin, which provides 70% of the sea otter's thermal insulation (Williams et al. 1988). Sea otters create this air layer by grooming (felting) and blowing air into their fur through their nostrils. When a sea otter is born on the surface of the water, its fur is wet and provides little thermal insulation, and the pup's large surface-to-volume ratio further enhances heat loss. Because altricial sea otter pups are unable to groom their fur, the female must perform this vital function by grooming the pup's lanugo to create an insulating air layer (Fig. 7.2b; Sandegren et al. 1973). This behavior is so important that a female spends about 13% of each day grooming the pup, which gradually decreases as the pup learns to groom itself over the next 2–3 months (Fig. 7.1a, c, d; Cortez et al. 2016a).

Sea otters are susceptible to predation by killer whales (*Orcinus orca*) and sharks (e.g., *Carcharodon carcharias* and *Lamna ditropis*), and neonates in the northern populations are susceptible to predation by bald eagles (see Chap. 9; Sherrod et al. 1975; Estes et al. 1998; Kreuder et al. 2003; Anthony et al. 2008). In parts of Alaska, female sea otters with neonates spend a significant amount (21%) of each day transiting (i.e., surface swimming) with their pup, often meandering without any apparent reason (Figs. 7.1a and 7.2d; Cortez et al. 2016a). The purpose of this behavior is unknown, but by reducing the time that newborn pups are left unattended at the surface and by moving around the nursery area, females may be engaging in predator avoidance (Sandegren et al. 1973). In California, females with young pups respond to adverse weather conditions by swimming in large ovals within a defined area. This behavior may be a response to indications of distress by the pup (Sandegren et al. 1973). Female vigilance for possible danger has been documented in other marine mammals (Hill et al. 2008). This swimming behavior decreases after several weeks as pups become larger and the potential threat of bald eagle (and other) predation diminishes.

As pups mature and develop their own survival behaviors and abilities, the female's behavior changes (Gelatt et al. 2002; Osterrieder and Davis 2009; Cortez et al. 2016a; Thometz et al. 2016). Hence, the behaviors of females and pups are complementary (i.e., combining in such a way as to enhance pup survival) but constantly changing as pups mature towards weaning and independence at the age of ~6 months. Research in Simpson Bay, Alaska, shows the progressive changes in maternal and pup behavior during the first 3 months postpartum (Fig. 7.1; Cortez et al. 2016a). During the first month of life, sea otter pups (mean body mass 1.8 kg; Cortez et al. 2016b) sleep most (84%) of the day with the remainder of their time nursing (7%) and being groomed by the female (9%) (Figs. 7.1b, 7.2a and 7.3a). The female's behavior is one of vigilance, and she carries the pup on her abdomen while resting (51%), transiting (21%), self-grooming (6%), or grooming the pup (13%), and these behaviors occur throughout the day (i.e., 24-h period) (Figs. 7.1a and 7.2). The only time the female leaves the pup on the surface of the water unattended is while foraging (9%), which is reduced in duration to prevent predation, primarily by bald eagles (see Sect. 9.3). In addition, female sea otters in Alaska may switch to nocturnal foraging when accompanied by small pups, presumably as a defense against bald eagle predation (Gelatt et al. 2002). Similar activity patterns occur in Southern (California) sea otters (Sandegren et al. 1973). An adult female sea otter normally ingests 24% of her body mass in food daily, and this increases to an average of 29% during the first month postpartum. Most of the additional energy in the female's diet goes into milk production (134 ml of milk day^{-1}), which represents 10% of the energy ingested by the female (Cortez et al. 2016b; Davis 2019). During this time, neither the female nor pup socially interacts with other sea otters, although they often associate with other mom-pup pairs in nursery rafts, which may be a form of group vigilance against predators (see Sect. 5.1). Female conspecific aggression may occur in areas used to shelter from wind and waves (Sandegren et al. 1973).

During the second month of life, pups double in size (mean body mass 3.6 kg) and exhibit new behaviors (Figs. 7.1d and 7.3b). They still sleep most (72%) of the day with little change in the percentage of time nursing (8%) and being groomed by the female (7%). Emerging behaviors include self-grooming (2%), transiting (7%), foraging (2%), and interacting (2%) with the female or other moms with pups. Swimming alongside the female and self-grooming are associated with increased muscular strength and coordination. This also is true for foraging behavior, but the pup only mimics the female when she dives and is unable to find its own food. Instead, the pup is reliant on the female for milk and prey that she brings to the surface (Fig. 7.2c). After a foraging dive, the pup climbs onto the female's chest and solicits food. When the female begins a foraging dive, the pup may follow but has a limited breath-hold ability and remains submerged for less than 30 s. In addition, air trapped in the lanugo makes the pup very buoyant, which further limits diving

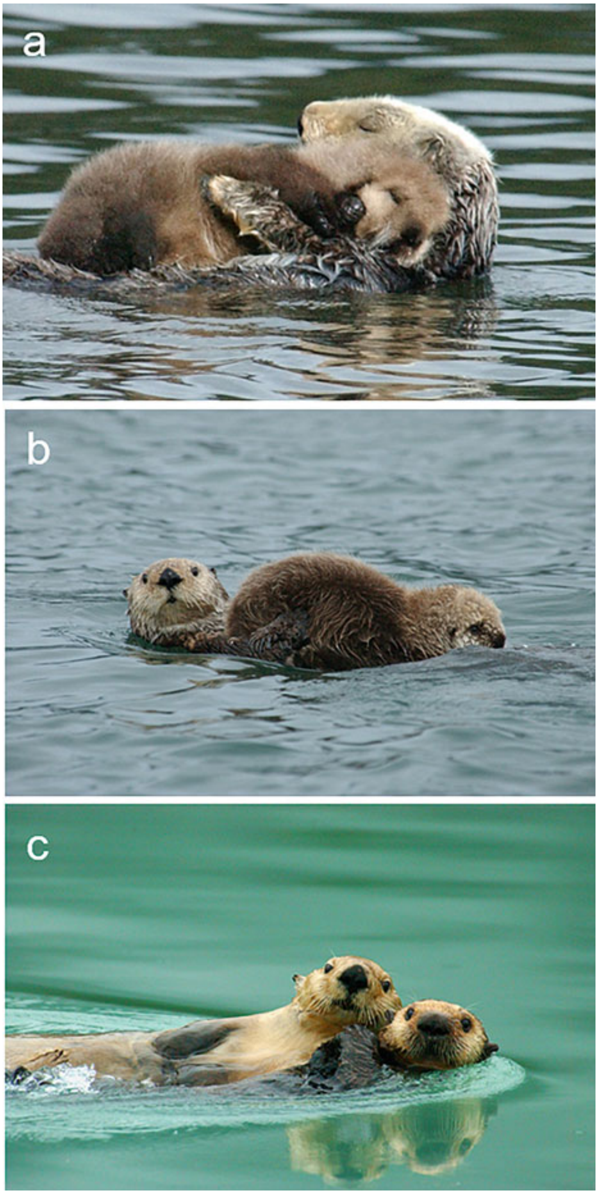

Fig. 7.3 Sea otter pup age classes: (**a**) 0–4 weeks, (**b**) 4–8 weeks, and (**c**) 8–12 weeks. Image (**c**) courtesy of R. Wolt. Images obtained under USFWS Marine Mammal Permit Nos. MA-043219 and MA-078744 to R. Davis

ability. While the female is diving, the pup may wander and interact with other sea otters, which is the first indication of social interaction. This sometimes results in separation from the female when she returns to the surface. Adult females and pups produce loud screams (frequency range 3–6 kHz), which can be heard over long distances (up to 1 km), especially when a female and pup are separated (see Sect. 3.3.2; Sandegren et al. 1973). Whether a pup and female recognize each other's vocalizations is unknown, but they will continue vocalizing until reunited.

During the second month postpartum, the female remains vigilant as she carries the pup on her abdomen while resting (52%), self-grooming (7%), and while grooming the pup (10%) throughout the day (Figs. 7.1c and 7.3b). As the threat of bald eagle predation lessens, there is a decrease in meandering swimming (16%) and an increase in foraging (13%) to provide milk for the rapidly growing pup. On average, the female ingests 32% of her body mass daily during the second month postpartum. Most of the additional energy in the female's diet goes into milk production (266 ml of milk day^{-1}), which represents 18% of the energy ingested by the female (Cortez et al. 2016b; Davis 2019). There is still little interaction (1%) of the female with other sea otters except for the unsuccessful mating attempts by territorial males. While nursing, females with pups are not sexually receptive and any interactions with males are brief.

By the third month of life, a pup is too large (mean body mass = 5.8 kg) to rest on the female's abdomen (Fig. 7.3c). The pup now sleeps or rests about the same percentage (46%) of the day as the female, but the amount to time devoted to nursing (7%) is similar to the previous 2 months (Fig. 7.1f). Self-grooming (3%) increases, but grooming by the female (2%) is still required to maintain the thermal insulation of the lanugo, which is replaced by adult pelage as the pup molts. The pup is now strong enough to swim (17%) alongside the female and begin foraging (17%). However, the pup is still dependent on milk and prey provided by the female (Fig. 7.2f). The pup spends more of the day (6%) interacting with the female and other sea otters.

By the time that the pup is 3 months of age, the female still rests (46%) and self-grooms (5%), about the same percentage of the day (24-h period) as during the previous 2 months (Fig. 7.1e), which may be the minimum requirement for good health and maintenance of the fur for thermal insulation. The remainder of the day is dominated by foraging (32%) to provide energy for herself and the rapidly growing pup (Fig. 7.2c). Similar activity patterns occur in Southern sea otters (Sandegren et al. 1973). Remarkably, the female now ingests 39% of her body mass daily. Most of the additional energy in the female's diet goes into milk production (468 ml of milk day^{-1}), which represents 26% of the energy ingested by the female (Cortez et al. 2016b; Davis 2019). The remaining time is divided among pup grooming (4%), transiting (8%), and interacting (5%), primarily with the pup and territorial males.

We do not have detailed activity budgets for females and pups between the ages of 4–6 months. However, the diving and foraging abilities of the pup improve as it approaches adult size (~15 kg) around the time of weaning (Riedman et al. 1994; Laidre et al. 2006; Esslinger et al. 2014). The pup's energetic needs are provided by the female (milk and prey) and its own foraging success. However, this is a difficult time for the female as she attempts to satisfy her own energetic requirements and those of the pup, which may require the female to spend 50% of the day foraging (Estes et al. 1982; Watt et al. 2000; Esslinger et al. 2014). This leaves the remaining time for the essential body maintenance behaviors of resting (~45%) and self-grooming (~5%). At some point, this energetic demand may exceed the foraging ability of the female, reduce time for body maintenance behaviors (i.e., sleep and self-grooming), and cause a decrease in body condition, which could lead to pup abandonment or early weaning in severe cases (Chinn et al. 2016; Thometz et al. 2016). Weaning success depends on many factors, including the age and experience of the female, prey availability, seasonal weather, sea conditions, and episodic environmental change (e.g., El Niño events) (Riedman et al. 1994; Monson et al. 2000). Postweaning survival of pups also depends on prey availability and the severity of winter weather, and mortality can be high (>50%) in the first year (Monson et al. 2000).

7.5 Female Reproductive Strategy

Strategies of parental care ultimately influence fitness. In ecology, *r* and *K* strategies of reproduction refer to trade-offs between quantity and quality of offspring (Klopfer 1981). An r-strategist produces a large number of offspring at the expense of individual parental investment, whereas a *K*-strategist produces few offspring with increased parental investment. Large mammals with a long life expectancy are *K*-strategists, live at densities close to carrying capacity, and invest more heavily in fewer offspring to enhance the probability of surviving to adulthood. Sea otters are a *K*-selected mammalian species. Because of their elevated resting metabolic rate and 6-month dependency period, the energetic cost of reproduction in female sea otters is high (Thometz et al. 2014, 2016; Cortez et al. 2016b; Davis 2019). When combined with reduced body fat, reproductive success is critically dependent on prey availability, especially in areas where the population is at or near carrying capacity. Episodic environmental events that influence prey availability strongly affect pup mortality (Monson et al. 2000). Reduced prey availability may cause the female to abandon the pup (i.e., reduce reproductive effort) if her health and survival are jeopardized (Chinn et al. 2016). If the female loses the pup, the period of anestrus is short, and coitus occurs within a few weeks (Jameson and Johnson 1993; Riedman et al. 1994). This behavior enables the female to survive and raise future offspring, which enhances fitness. However, pup survival will vary geographically and annually in synchrony with favorable conditions, characteristic of bet-hedging species (Monson et al. 2000).

7.6 Conclusions

Female sea otters are primarily income breeders because of their high resting metabolic rate, 6-month dependency period, and lack of blubber, which serves as an energy reserve in most other marine mammals. The offspring of Cetacea and Sirenia are precocial and can swim at birth. For Pinnipedia, altricial offspring are born on land or ice and undergo a period of maturation before they enter the water. Sea otters are the only marine mammal that gives birth to altricial offspring on the water, so female care and vigilance are required to wean the pup. The high metabolic rates of the female and growing pup also mean that the female must devote increasing amounts of time to foraging, sometimes requiring up to 50% of the day. Towards the end of the dependency period, the effort to support herself and the pup may exceed her foraging ability and cause a decrease in body condition, which could lead to pup abandonment or early weaning. Hence, the reproductive success of female sea otters is critically dependent on the geographical, seasonal and annual availability of prey, and pup survival varies in synchrony with favorable conditions.

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Chapter 8
Sea Otter Behavior and Its Influence on Littoral Community Structure

Heather A. Coletti

Abstract The near extirpation and subsequent recovery of sea otters throughout much of their historic range provides an opportunity to examine the influence of a large marine carnivore on littoral habitats. In this review of the sea otters' role in nearshore community structure, I provide examples that compare and contrast shifts in prey communities among varying habitats, which reflect inherent productivity, prey availability, sea otter population density, and foraging behavior. Considered together, these variables can aid in sea otter management. Many coastal areas in the North Pacific Rim are still recovering as sea otters return to the nearshore marine ecosystem as a keystone predator. In their absence, what was considered a natural state must be re-evaluated as direct and cascading effects become apparent. Questions remain as to the full range and persistence of ecosystem-level effects of sea otters in a variety of habitats: What does a natural system with sea otters look like?

Keywords Abundance · Benthic · Bottom-up effects · Community · Ecosystem dynamics · Food web · Habitat · Infauna · Invertebrate · Littoral · Nearshore · Prey · Sea otter · Top-down effects

8.1 Sea Otters: A Littoral Predator

Sea otters are marine specialists but diet generalists, which feed primarily on benthic mega-invertebrates, such as mollusks (e.g., clams and mussels), crustaceans (e.g., crabs), and echinoderms (e.g., sea urchins), although they feed opportunistically on other prey, such as sea cucumbers, octopuses, slow-moving benthic fishes, the egg cases of rays, and herring roe on kelp (see Chap. 4). They locate and capture infaunal and epibenthic prey with their forepaws by relying on vision and tactile sensitivity

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during dives <4 min in duration (see Sect. 3.3.3). Because of their elevated basal metabolic rate (2.9-fold higher than a terrestrial mammal of similar size) and food consumption (see Sect. 3.3.4), sea otters have a significant top-down effect on mega-invertebrates in the littoral (nearshore) zone, which results in a trophic cascade affecting community structure (Kenyon 1969; Estes and Palmisano 1974; Estes and Duggins 1995; Estes 2015). However, this influence is limited to shallow waters (routine dives <30 m and maximum dive depth ~100 m) of the littoral zone because of physiological limits on breath-hold duration (see Sect. 3.2.3; Bodkin et al. 2004; Wolt et al. 2012; Davis 2019).

The historical range of sea otters around the North Pacific Rim from Japan to Baja California includes a range of coastal habitats with varying degrees of productivity. In this chapter, I categorize the seafloor of the littoral zone into two types (1) bedrock or areas of large cobble and boulders (hereafter referred to as rocky) and (2) unconsolidated sediment (i.e., clay and silt, mud, sand, or gravel, often as a mixture and hereafter referred to as soft) (Wentworth 1922; Shepard 1954). Rocky habitats occur along exposed coastlines and in bays and fjords, often with abundant kelp (i.e., macroscopic, multicellular marine algae, such as *Macrocystis* and *Nereocystis*). Soft-sediment habitats include intertidal eelgrass beds and coastlines or bays with a mud, mixed mud and gravel, or sand benthos. Differences in benthic habitat influence invertebrate species composition and community structure (Sebens 1991). Rocky substrates primarily support epibenthic mega-invertebrates (e.g., sea urchins, mussels, snails, crabs). Soft substrates support both epibenthic and infaunal (e.g., clams and polychaetes) mega-invertebrates.

8.2 The Challenge of Sea Otter Ecological Research

In attempting to understand the influence of sea otters on community structure in the littoral zone, we face two challenges. The first is our limited ability to quantify changes in prey distribution and abundance resulting from sea otter predation or its absence. Although sampling subtidal rocky reefs led to the “keystone” designation for sea otters, fewer studies have quantified the influence of sea otters on invertebrate populations in other habitats (Estes and Palmisano 1974). As a result, we often rely on rates of sea otter food consumption to estimate prey abundance and whether a sea otter population has reached an equilibrium density because of food resources (i.e., carrying capacity). Although food availability undoubtedly influences sea otter equilibrium density, other factors—both density-dependent and density-independent—may result in an equilibrium density that is below carrying capacity based on food resources (Ballachey and Bodkin 2015).

The other challenge is historical. The number of sea otters throughout the North Pacific was significantly reduced from ~300,000 to less than ~2000 individuals during the Maritime Fur Trade in the late eighteenth and nineteenth centuries, and this allowed populations of mega-invertebrates (e.g., clams, crabs, sea urchins, etc.)

to flourish in their absence (see Chap. 10). International protection from hunting since 1911 allowed sea otters to recover to ~125,000 individuals and to reoccupy much of their historical habitat, although full reoccupation is decades away (Bodkin 2015). Based on data from translocation studies, sea otters often experience a period of logistic population growth (>20% year^{-1}) when they reoccupy an area (Bodkin 2015). At some point, a population approaches an equilibrium density, although this density is not necessarily stable and may fluctuate (i.e., different population equilibria) inter-annually, decadally, or longer depending on intrinsic and extrinsic factors (Kenyon 1969; Estes 1990; Watt et al. 2000; Bodkin 2015). Assuming a normal reproductive rate, intrinsic factors include territoriality and dispersal, which reduce population density before resource limitation. Extrinsic factors include food availability, predators, disease, human-related mortality, weather, and other environmental variables, which affect survival (Monson and DeGange 1995; Ballachey and Bodkin 2015). The relative effect of these factors varies spatially and temporally, resulting in a mosaic of subpopulations (i.e., local populations) with different densities, rates of growth, and discontinuous distributions. In most cases, we must speculate on the structure of the littoral community before the removal of sea otters and the climax community after prolonged reoccupation.

Nevertheless, there are examples of coastal habitats with sea otter populations that have been relatively stable for at least the past 25 years. These areas serve as examples of systems that have reached a new equilibrium resulting from reoccupation, although this steady state is not necessarily stable and may fluctuate. In this chapter, I summarize studies that compare the influence of sea otters in a variety of littoral habitats. As opposed to a complete summary of past research, I focus on a few studies in which sea otter population density, reoccupation duration, and available prey differ. I use examples from long-term monitoring projects in two Alaskan national parks and compare them with other studies on changes in the littoral zone. Based on this comparison, I discuss the implications for coastal habitats as sea otters continue to reoccupy their historical range.

8.3 Historical Perspective

Ancestors of sea otters (*Enhydra*) diverged from other Eurasian otters ~5 Mya, making them the earliest lineage to diverge within Old World otters (see Sect. 2.5). Two sister groups of modern sea otters occurred in the late Miocene to early Pliocene: *Enhydriodon* and *Enhydritherium*. One hypothesis is that *Enhydritherium* dispersed from Europe around the northern rim of the North Atlantic Ocean into the Gulf of Mexico. From there, *E. terraenovae* dispersed into the Pacific through the Central American Seaway, where 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, possibly from *Enhydritherium,* and entered the North Pacific through the Arctic Ocean and Bering Straits, giving rise to modern sea otters. Regardless of how they appeared in the North Pacific, sea otters have been part of the littoral ecosystem for several million years. This is much longer than the presence of humans around the North Pacific Rim (~15,000 Kya; Erlandson et al. 2007).

Analysis of stable isotopes in archaeofaunal sea otter remains from the late Holocene, which were found in midden sites along the coast of British Colombia, Canada, suggests that sea otters fed primarily on low trophic-level prey, which included sessile benthic mega-invertebrates (Szpak et al. 2012). Based on archaeological records, evidence also exists that ancient indigenous cultures along the Pacific Northwest understood the influence of sea otters on nearshore invertebrate populations, and their numbers were reduced by hunting. In rocky habitats, this allowed for urchin barrens to flourish in close proximity to human population centers while allowing sea otters—and therefore kelp forests—to persist farther from human settlements (Simenstad et al. 1978; Erlandson et al. 2007; Corbett et al. 2008; Salomon et al. 2015). In soft-sediment habitats, the creation of clam gardens (isolated, intertidal regions intended to enhance clam populations through habitat modification and cultivation) were maintained while likely excluding predators, such as sea otters and sea stars (Groesbeck et al. 2014). However, prior to the arrival of Europeans, indigenous sea otter hunting occurred on a much smaller scale than the commercial maritime harvest of the eighteenth and nineteenth centuries, which resulted in the systematic removal of sea otters throughout their range (see Chap. 10; Salomon et al. 2015).

8.4 Current Perspective

Recognition of sea otters as a keystone predator stemmed from research along the rocky coastlines of the Aleutian Archipelago (Estes and Palmisano 1974). Because sea otters had not fully recolonized the entire Archipelago after the Maritime Fur Trade, comparisons of community structure were made among islands with and without sea otters. It became clear that sea otters had a dramatic influence on the nearshore kelp community by reducing sea urchins and releasing kelp from intense urchin grazing. Several studies subsequently investigated the keystone predator hypothesis, and questions remain as to whether sea otters have a similar influence throughout their range (Estes and Duggins 1995). As a result, continuing research has focused on the influence of sea otters on community structure and how it varies with (1) habitat type (rocky or soft), (2) time since reoccupation, (3) sea otter abundance, (4) changes in prey preference over time, and (5) changes in primary productivity (Estes and Duggins 1995). With these variables in mind, I describe several studies, which highlight the variation in community response to sea otter foraging behavior.

Habitat determines the potential prey community available for sea otters. Different habitats can occur in close proximity, allowing the exploitation of a variety of epifaunal and infaunal prey. Factors such as duration since reoccupation, abundance, and subsequent changes in prey availability are interrelated and should be considered together. Sea otters in newly reoccupied areas exploit large, high-energy prey (e.g., epibenthic crabs, sea urchins, abalone), which are abundant and easily accessible. This situation is unsustainable, but the rate at which it shifts to smaller and less accessible prey varies. Sea otters are a generalist predator, able to exploit a wide range of prey (Wolt et al. 2012). However, in rocky habitats with thriving kelp forests where herbivorous mega-invertebrates have declined because of predation, sea otters may exhibit intraspecific diet diversity associated with density-dependent competition for food or become piscivorous and feed on slow-moving benthic fishes, which alters the population carrying capacity based on food resources (Estes 1990; Watt et al. 2000).

As carrying capacity is approached, foraging effort increases as energy intake rates decline, and sea otter abundance reaches an equilibrium density because of food resources, although other intrinsic (e.g., territoriality and dispersal) and extrinsic factors (predators, disease, human-related mortality, weather, and other environmental variables) may be important (Kenyon 1969; Estes 1990; Wolff 1997; Watt et al. 2000; Tinker et al. 2008, 2012; Bodkin 2015; Davis et al. 2019). Finally, seasonal and interannual changes in primary productivity influence the abundance and growth of sea otter prey, which have an important bottom-up effect on the carrying capacity of an area and influence local sea otter densities. Varying temporal and spatial productivity also are influenced by large-scale changes in oceanographic processes and climate change (Menge et al. 2008, 2009; Bodkin et al. 2018; Davis et al. 2019).

8.5 Community Changes in Nearshore Marine Ecosystems

The effects of sea otters on coastal marine ecosystems are well documented across the north Pacific, including both rocky and mixed sediment habitats (Estes and Palmisano 1974; Kvitek et al. 1992; Hughes et al. 2013). The most obvious effect of sea otter predation, particularly during recolonization, is a reduction in densities and sizes of their invertebrate prey (e.g., crabs, clams) and demise of competing shellfisheries (Estes and Van Blaricom 1985; Wendell et al. 1986; Wendell 1994; Watson and Smith 1996; Larson et al. 2013; Hoyt 2015). However, these impacts on prey populations are not always negative. The following examples illustrate the spatiotemporal effects on the nearshore community, both direct and indirect, that are influenced by the variation in the factors described in Sect. 8.4.

8.5.1 Top-Down Effects

The reduction of commercially important mega-invertebrates (e.g., abalone [*Haliotis* sp.], Pismo clams [*Tivela stultorum*], and Dungeness crab [*Cancer magister*]) and subsequent closure of fisheries from California to Alaska have been attributed to sea otter reoccupation (Miller et al. 1975; Estes and Van Blaricom 1985; Garshelis et al. 1986). One of the first conflicts with sea otters involved the California abalone fishery (Carswell et al. 2015). In addition to sea otter predation, excessive commercial and recreational exploitation, disease, and environmental factors (e.g., El Niño events) contributed to the decline and subsequent closure of the abalone fishery in 1997. Although sea otter predation reduced the availability of commercial size abalone, which had become unnaturally abundant after the Maritime Fur Trade, it also had a beneficial effect on abalone populations by reducing sea urchin grazing on canopy-forming kelp, the preferred food of abalone. As a result, sea otter predation on sea urchins contributes to kelp forest formation and habitat for abalone and a more balanced abundance (Raimondi et al. 2015).

Clams are important prey for sea otters throughout their range (Calkins 1978; Estes et al. 1981; Garshelis 1983; Kvitek and Oliver 1988; Kvitek et al. 1988, 1992; Bodkin et al. 2007; Wolt et al. 2012; Coletti et al. 2016). Rapid declines of commercially important species have occurred with the reoccupation of sea otters. One example is the California Pismo clam, which was a viable commercial and recreational fishery until the 1970s (Miller 1974; Miller et al. 1975). Prior to reoccupation of sea otters in central California, Pismo clams were abundant, with an estimated six million tons harvested from 1916–1947 (California Fish. Bulletin 1949). However, they are easily accessible to sea otters in their shallow-water, sandy habitat. The decline of Pismo clams became one of the first documented interactions between sea otters and a commercially and recreationally important species of bivalve.

Commercial Dungeness crab fisheries are not viable in areas with sea otters. In Orca Inlet, Alaska, Dungeness crabs were abundant and commercially harvested. However, the crab fishery collapsed with the arrival of sea otters in the late 1970s. By the mid-1980s, large crabs were rare and represented only 6% of the diet for sea otters in nearby areas, such as Simpson Bay. This low percentage has not changed for the past 30 years, indicating a new equilibrium density in the crab population (Garshelis et al. 1986; Wolt et al. 2012). Dungeness crab surveys conducted in Glacier Bay National Park in southeast Alaska also found significantly lower crab densities in areas with sea otters, suggesting persistent predation in shallow water. Although Dungeness crabs may find refuge from sea otters below a depth of 100 m (maximum sea otter dive depth), they are not common (Shirley et al. 1996).

While there are examples of rapid declines in invertebrate populations in rocky and soft-sediment habitats, the long-term effects of sea otters on infaunal bivalves in soft sediments are poorly understood. Many factors are associated with the top-down effect of sea otters on bivalve populations, including longevity, abundance, distribution, burrowing depth, water depth, and local productivity. For example, sea otters

Fig. 8.1 Remains of butter clams consumed by sea otters in Southeast Alaska with the siphons uneaten, likely because of the presence of saxitoxin, which causes paralytic shellfish poisoning (PSP). Image courtesy of D. Monson, USGS

did not cause a significant decline in butter clam (*Saxidomus nuttalli*) and Pacific gaper clam (*Tresus nuttallii*) populations in Elkhorn Slough, California (Kvitek et al. 1988). Although the time since sea otter reoccupation was only six months, this study indicated that the effects of sea otter predation vary with prey species and habitat. In this example, sea otters preferred smaller bivalves that did not burrow deeply and required less effort to excavate (i.e., lower cost-to-benefit ratio).

Sea otters in Southeast Alaska, which are descendants of translocated sea otters from the Aleutian Islands and Prince William Sound, feed primarily on bivalves, such as butter clams, but only after depleting red sea urchins (*Strongylocentrotus franciscanus*) (Pitcher 1989). During a study conducted in 1989, researchers found that sea otters did not feed on deep-burrowing geoduck clams (*Panopea generosa*), the largest bivalve in the North Pacific, indicating a refuge from sea otters for mollusks in deep sediments (Kvitek et al. 1993). However, in Southeast Alaska, sea otters feed on geoduck clams, indicating that the benefit of excavating deep clams outweighs the energetic costs for some individuals (Hoyt 2015).

Saxitoxin, a potent neurotoxin in dinoflagellates that accumulates in the tissue (especially the siphons) of filter-feeding bivalves and causes paralytic shellfish poisoning (PSP), may secondarily reduce sea otter predation, allowing bivalves to persist (Kvitek and Beitler 1991; Kvitek et al. 1991). In captivity, sea otters avoid clams containing saxitoxin, and this behavior has been observed in wild sea otters, which exclude the siphons when eating clams (Fig. 8.1; H. Coletti and D. Monson unpub. obs.). The occurrence of PSP is associated with environmental factors, such as warm water temperatures, which enhance the productivity of dinoflagellates, often characterized as algal blooms (Vandersea et al. 2018). Although sea otters may avoid clams with saxitoxin, humans have more difficulty. In 1800 during the Maritime Fur Trade, more than 100 Unangan and Sugpiaq sea otter hunters perished from PSP in Southeast Alaska when they gathered mussels on a low tide, and the catastrophe's site became known as Peril Strait (see Chap. 10; Orth 1967).

Similar to kelp forest enhancement in rocky habitats, estuarine primary productivity may benefit from the foraging behavior of sea otters. In California, eelgrass beds in Elkhorn Slough are enhanced by sea otter predation on crabs. Crabs eat mesograzers (e.g., amphipods and isopods), which are small, invertebrate herbivores, which consume epiphytes on the blades of eelgrass thereby enhancing their growth. When sea otters reduce the crab population in an eelgrass bed community, mesograzers flourish, and this trophic interaction allows the eelgrass to thrive in less than ideal conditions (Hughes et al. 2013). Surrounded by commercial agriculture, Elkhorn Slough is subject to heavy nutrient loading and eutrophication, and sea otters mitigate the negative effects of algal formation on eelgrass (Hughes et al. 2013).

An examination of seagrass communities along the central coast of British Columbia, Canada, shows a more complex relationship between sea otters and seagrasses. Shoreline complexity, access to various habitat types (and therefore various prey resources), biodiversity, and time since sea otter reoccupation are factors that influence the effects of sea otter foraging behavior on seagrass communities (Hessing-Lewis et al. 2018). The systems studied along the coast of British Columbia are pristine in comparison to the nutrient-loaded eelgrass beds in Elkhorn Slough. As a result, the effects of sea otters on the seagrass biomass are less apparent in British Columbia, and the difference likely results from the type of habitat (simple vs. complex) and the time since sea otter reoccupation (Hessing-Lewis et al. 2018).

At the onset of sea otter recolonization of Glacier Bay, the population grew rapidly (~50% annually from 1994–2004) as a result of reproduction and immigration (Esslinger and Bodkin 2009). Sampling showed differential effects of sea otter predation on intertidal clam and sea urchin populations depending on the time since reoccupation (i.e., recent to >25 years) (Bodkin et al. 2007). While the prey community responded as expected (lower density, smaller sizes), the response was not uniform among sites, and the results indicated that factors other than sea otter predation influence invertebrate populations (Weitzman 2013).

8.5.2 *Bottom-Up Effects*

Prey abundance and availability depend on primary production, which injects carbon and nutrients into the food web. Seasonal and interannual changes in productivity influence the abundance and growth of sea otter prey, which have an important bottom-up effect on the carrying capacity of an area and influence local sea otter densities.

For example, a small but stable population of sea otters has occupied Simpson Bay, Alaska, since recolonization in the late 1970s (Garshelis 1983). The seafloor of the bay is primarily soft sediment, and clams make up about 75% of sea otter diet, regardless of age or sex (Noll et al. 2008; Gilkinson et al. 2011; Wolt et al. 2012). On average, an estimated 110 adult sea otters (5.2 km^{-2}) have occupied the bay annually since 2001, consuming 176,660 kg of bivalves (Davis 2018). The total mass (standing stock) of the major bivalves (predominately butter clams [*Saxidomus gigantea*] and stained macomas [*Macoma inquinata*]) is 785,730 kg, so adult sea otters consume about 22% annually. Despite these large numbers, <5% of the estimated carbon flux from primary productivity is transferred to sea otters through a four-step cascade: phytoplankton, particulate organic carbon (POC), bivalves, and sea otters. The remainder of the carbon is consumed as phytoplankton by zooplankton or enters a pool of particulate organic carbon (POC), which is (1) consumed by sediment infauna, (2) exported through currents, or (3) buried as sediment organic carbon. Because sea otters in Simpson Bay appear to be consuming clams at or near their replacement rate, any reduction in phytoplankton or bivalve productivity could reduce carrying capacity and the number of otters occupying the bay (Davis 2018).

In a twist to the conventional view of a top-down driven system in the Aleutian Islands, the recent (since the 1980s) *absence* of sea otters throughout the islands since the Maritime Fur Trade also may play a role in structuring prey populations. Without sea otters, local environmental factors likely drove the variation in sea urchin demographics observed in the Aleutian archipelago, indicating that these systems may be more sensitive to environmental perturbations and primary productivity in the absence of sea otters (Weitzman 2020).

8.5.3 Indirect Effects

Sea otters forage nearly exclusively on benthic mega-invertebrates, which are captured and manipulated with their forepaws (see Chap. 4; Kenyon 1969). In soft sediment habitats, their primary prey is clams, which they find by digging pits ~15 cm deep and 20–30 cm wide, although some can be much larger (Fig. 8.2; Kvitek and Oliver 1988). Pits created while digging re-sort sediments and create new habitat for epifaunal and infaunal mega-invertebrates (Fig. 8.3). For example, sunflower sea stars (*Pycnopodia helianthoides*) aggregate around sea otter pits, which provide access to smaller bivalves not consumed by sea otters (Kvitek et al. 1992). Pit persistence is influenced by sediment composition (e.g., clay, silt, sand) and the effects of currents and tides (Bodkin et al. 2011, 2012; Traiger et al. 2016). When digging for clams, sea otters may release contaminants during sediment resuspension. In Prince William Sound, where crude oil from the 1989 *Exxon Valdez* oil spill persisted in shallow sediments for decades, digging for infaunal prey directly exposed sea otters to contaminants through the resuspension of hydrocarbons, which

Fig. 8.2 Aerial image of sea otters digging in soft sediments in Prince William Sound, Alaska. Image courtesy of J. Bodkin, USGS

could have been consumed through grooming, but also likely were present in the prey and therefore directly consumed (Fig. 8.4; Short et al. 2004, 2006, 2007; Bodkin et al. 2012).

Unlike other carnivorous marine mammals, sea otters bring their food to the surface to consume while lying on their backs, rather than consuming it underwater. Sea otters break open a hard-shelled clam (e.g., butter clam) by placing it in the back of the mouth between the upper and lower premolars and molars and biting down with a force that cracks one of the valves (see Sect. 4.5). The cracked valve is discarded, and the otter then opens the clam at the hinge and scoops out the flesh with its lower incisors and canines. Soft-shelled clams (e.g., Macomas) are easily crushed into multiple pieces. Discarded clamshells litter the seafloor and create substrate for the attachment of sessile invertebrates, such as anemones, as well as holdfasts for kelps. Clamshells along with foraging pits influence benthic community structure (Fig. 8.3; Kvitek et al. 1992). When sea otters invert cobble in mixed-sediment habitats, it exposes surfaces that can be colonized by sessile invertebrates.

The influence of sea otter foraging behavior varies among littoral habitats. In the next section, I focus on examples from two Alaskan national parks where long-term monitoring has occurred since 2006 (Dean et al. 2014). Data from these programs have improved our understanding of the effects of sea otter reoccupation on littoral ecosystems, which have been devoid of sea otters for over 100 years. Spatial contrasts between parks, which boarder the Gulf of Alaska, are possible because

Fig. 8.3 Sea otter foraging pits, Prince William Sound, Alaska. Image courtesy of J. Bodkin, USGS

sea otters have small home ranges (few tens of km^2) and do not migrate (Tinker et al. 2008).

Fig. 8.4 Aerial image of sea otter foraging pits along the shore at low tide in Prince William Sound, Alaska. Image courtesy of M. Lindeberg, NOAA

8.6 Contrasting Littoral Communities Along the Gulf of Alaska

Long-duration monitoring is an important aspect of resource management (Oakley et al. 2003; Bennett et al. 2006). Since 2006, monitoring programs in the Katmai National Park and Preserve (KATM) and Kenai Fjords National Park (KEFJ) have provided information for the resource management of littoral habitats affected by sea otter reoccupation (Dean et al. 2014; Coletti et al. 2016). KATM is dominated by low-sloping beaches of sand and mixed-sediments, shallow water extending offshore, and extensive intertidal habitat. Sea otters were extirpated in this area during the Maritime Fur Trade in the nineteenth century (see Chap. 10). However, a remnant population survived at Augustine Island and grew exponentially from $<$100 animals in the mid-1950s to ~7000 by 2015 (Fig. 8.5; Lensink 1960; Kenyon 1969; Prasil 1971; DeGange et al. 1995; Coletti et al. 2016). When monitoring began in 2006, the sea otter diet consisted primarily of clams (63%). The mean energy intake rate was high, indicating that prey were abundant and the population had not reached carrying capacity. By 2015, the energy intake rate had declined 62%, while the sea otter population stabilized (Fig. 8.5). During the same period, the estimated clam biomass declined by $>$50% (Coletti et al. 2018). A stable population size, a decreasing energy intake rate, and decreasing prey availability indicate that KATM has reached carrying capacity because of food limitation (Coletti et al. 2016; Davis et al. 2019).

In contrast to KATM, the KEFJ coastline has deep fjords and rocky headlands shaped by Holocene glaciers. The seafloor is primarily rocky with some areas of soft sediment. The sea otter population is stable at a low density (~0.7 otters km^{-2}), with

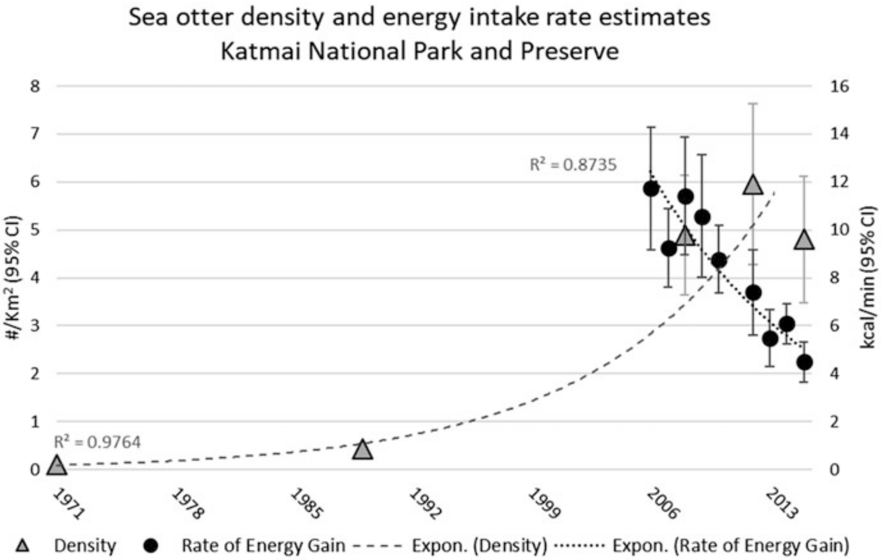

Fig. 8.5 Sea otter population density (individuals km^2; gray triangles) and energy intake rates (kcal min^{-1}; black circles) in Katmai National Park and Preserve (KATM). Available habitat = 1450 km^2. All abundance estimates were based on fixed-wing and helicopter aerial surveys (Prasil 1971; DeGange et al. 1995; Bodkin and Udevitz 1999; Coletti et al. 2016). The gray dashed line shows the exponential growth of the sea otter population ($R^2 = 0.9764$), which has likely reached carrying capacity (Coletti et al. 2016). Error bars represent 95% CI. The black dotted line shows the declining trend (polynomial) in energy intake rates concurrent with the increase in population density ($R^2 = 0.8735$). Error bars represent Monte Carlo simulation-based 95% confidence intervals

no significant change since 2002. The average energy intake rate (~8 kcal min^{-1}) has been stable, which indicates a population that has been at or near carrying capacity for over a decade (Fig. 8.6; Coletti et al. 2016). Unlike the diet for sea otters in KATM, those in KEFJ feed primarily (58% of the diet) on mussels (*Mytilus trossulus*) (Coletti et al. 2016), which are orders of magnitude more abundant than in other regions in the Gulf of Alaska (Bodkin et al. 2018). The high dependence of KEFJ sea otters on mussels is unusual but likely results from the limited clam habitat. However, while the population density and energy intake rates of sea otters have been relatively stable since 2006, the density of mussels has varied (Coletti et al. 2016; Bodkin et al. 2018). In contrast to the top-down effect of sea otters on prey density, variation in abundance of mussels is influenced by bottom-up effects, such as nutrient availability, productivity, and recruitment, which are largely independent of sea otter foraging (Davis et al. 2019). These bottom-up effects may become more significant in structuring prey communities as climate change, ocean acidification, and human development influence the coastal regions.

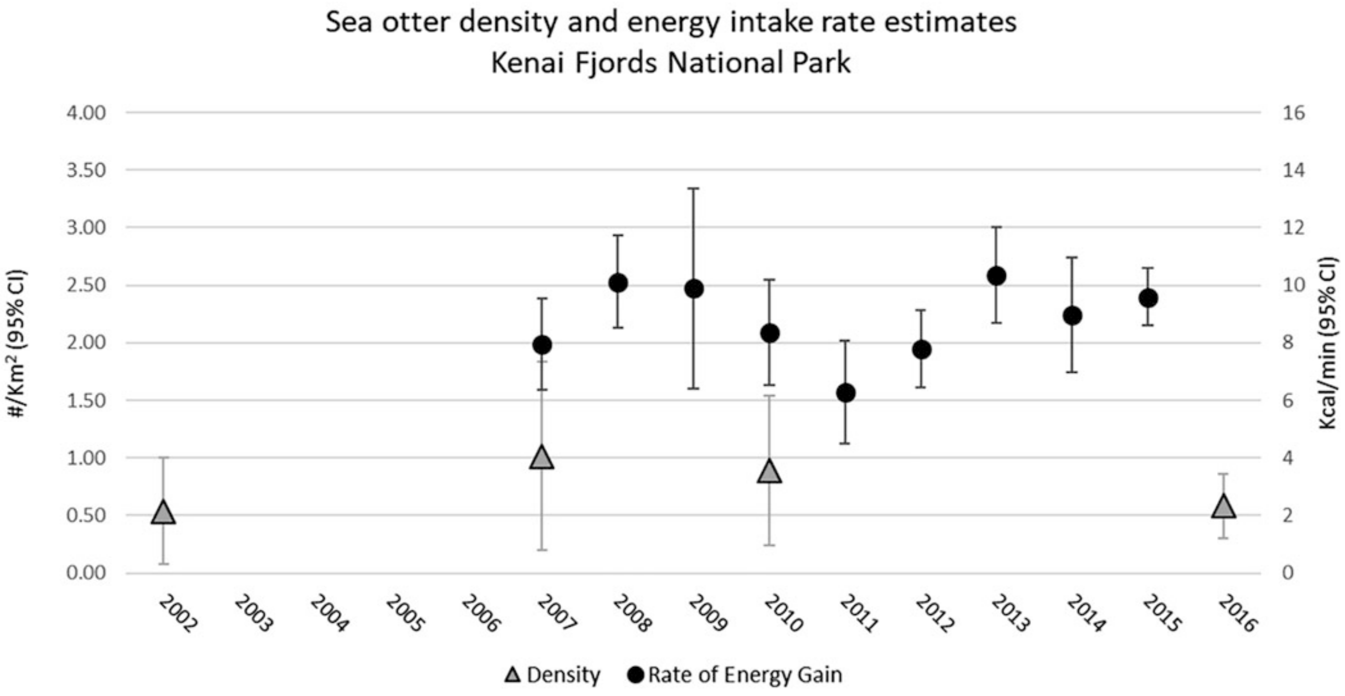

Fig. 8.6 Gray symbols represent the density (estimated abundance relative to suitable habitat) of sea otters living in the Kenai Fjords National Park (KEFJ). Available habitat = 1485 km^2. All abundance estimates are based on fixed-wing aerial surveys (Bodkin and Udevitz 1999; Coletti et al. 2016; Esslinger 2017). Error bars represent 95% CI. Black symbols represent energy intake (consumption) rates (kcal min^{-1}). Error bars represent Monte Carlo simulation-based 95% confidence intervals. Both the density and the energy intake rates indicate a stable population (Coletti et al. 2016)

8.7 Future Directions

The long-term goal of sea otter conservation is full pre-exploitation recovery throughout their historical range and restoration of nearshore ecosystems. This will inevitably result in the demise of some commercial invertebrate (primarily clam, crab, and sea urchin) fisheries and a financial effect on human society. In this section, I focus on three geographic regions on the frontlines of sea otter reoccupation resulting from natural range expansion or proposed translocations. Understanding the spatiotemporal effects of sea otters on littoral invertebrate communities is needed to predict, manage, and mitigate the economic effects (Carswell et al. 2015; Davis et al. 2019).

Located in southcentral Alaska, Cook Inlet flows into the Gulf of Alaska from the north and is bordered by the Kenai Peninsula to the east and the Alaska Peninsula to the west. Sea otters have been recolonizing this area for several decades, likely from a small remnant population in Kamishak Bay, Alaska (Lensink 1960; Garlich-Miller et al. 2018). The Kenai Peninsula has supported a commercial and recreational razor clam (*Siliqua patula*) fishery for over 50 years. Expansion of the local sea otter population north of Kachemak Bay coincided with declining razor clam densities and closure of the commercial and recreational fishery in 2015 (Garlich-Miller et al. 2018; Booz et al. 2019). While sea otter predation may have contributed to the collapse of the fishery, other factors, such as disease, over-harvesting, and environmental changes, also may have contributed (Coletti et al. In prep). A similar pattern of razor clam decline may occur along the west coast of Cook Inlet, which has not experienced the same rate of sea otter reoccupation (NPS unpublished data). Although razor clams in this area are less accessible to humans, they are abundant and support commercial and recreational fisheries (Booz et al. 2019). Razor clams also are prey for coastal bears, which support an ecotourism industry (Smith and Partridge 2004). As the western sea otter population expands, razor clam densities will decline, leading to conflicts with human fisheries, indirect effects on ecotourism, and a shift in the diet of some bears. Cook Inlet provides an opportunity to study the cascading effects of sea otter reoccupation on littoral habitat, food webs, and human fisheries so that management can anticipate, plan, and potentially mitigate the effects of sea otter recolonization.

There have been no sea otters along the Oregon coast for over 100 years (Kenyon 1969). In the early 1970s, 93 sea otters were translocated to the Oregon coast from the Aleutian Islands. However, they disappeared by 1981 for unknown reasons. The Elakha Alliance, a non-profit organization, has advocated for the restoration of sea otters along the Oregon coast through translocations from other areas, which would restore and enhance the nearshore marine ecosystem. The alliance recognizes the potential for fisheries conflicts (primarily sea urchins and crabs), but it also emphasizes that sea otter reoccupation will enhance the natural environment and generate social and economic opportunities, which would not exist otherwise. Regardless of whether there are future translocations, sea otters from the expanding population in Washington State will eventually result in the reoccupation of the Oregon coast.

Indigenous Northeast Asians, such as the Ainu and Kamchadals of Hokkaido (Japan), the Kuril Islands, and Kamchatka (Eastern Russia), hunted sea otters for their fur, similar to Alaskan natives (see Sect. 10.2; Hattori et al. 2005). Prior to the sixteenth century, there was little trade in sea otter pelts, with the earliest record of Japanese exports to China by 1483 (Takahashi 2006). In the eighteenth century, Russians expanded their influence in the Far East and began competing with the Japanese and Ainu for the Chinese fur trade, which resulted in the near extirpation of sea otters in northern Japan. The Maritime Fur Trade in Japan ended in 1911 with the International Fur Seal Treaty, and sea otters from the Kuril Islands moved into northern Hokkaido in the 1970s. Surveys conducted from 2017–2018 observed ~20 sea otters, including three pups, along the northeast coast of Hokkaido, with the largest concentration in the Moyururi and Yururi Islands (Y. Mitani and R. Davis, unpub. obs). Both reproduction and immigration from the Kuril Islands will contribute to the expanding population. The coast of northeast Hokkaido has commercial fisheries for sea urchin (*Strongylocentrotus droebachiensis*), clams (*sachalinensis*), and crabs (*Paralithodes brevipes*). These fisheries have thrived for over 100 years in the absence of sea otters. In addition, the sea urchin fishery is commercially enhanced by captive rearing and release. The abundance of prey and the shallow water habitat will result in rapid growth of the sea otter population in northern Hokkaido. At the moment, the small number of sea otters is tolerated by fishermen and are a tourist attraction. It is illegal to kill sea otters in Japan under the 1911 International Fur Seal Treaty, but fishermen are allowed to harass them until they leave the area. Even with the treaty, fur seals are culled to reduce fisheries conflicts, and this may extend to sea otters if they threaten invertebrate fisheries. The emerging sea otter population in Hokkaido offers an opportunity to study the societal and political response to a marine predator in a country with a long history of traditional fisheries and dependence on seafood.

Many abiotic, biotic, and anthropogenic factors influence littoral habitats around the Pacific Rim, from earthquakes and volcanic eruptions to contamination and climate change (e.g., rising temperatures and decrease in pH) (Baxter 1971; Armstrong et al. 1995; Driskell et al. 1996; Lees et al. 1996; Fukuyama et al. 2000; DeGange et al. 2010; Hoegh-Guldberg and Bruno 2010; Lesser et al. 2010; Gaylord et al. 2011; Walker et al. 2013; Jewett and Drew 2014; Bijma et al. 2013; Zimmermann et al. 2018). The ancestors of sea otters entered the North Pacific 3–1 Mya, so they are an integral part of many littoral communities. Their sudden and catastrophic removal during the Maritime Fur Trade resulted in major changes in invertebrate and vertebrate populations, which are still apparent today (Jamieson 1993). Compared to other upper trophic-level marine predators, the top-down influence of sea otters on littoral community structure is enhanced because of their elevated resting metabolic rate and food consumption for thermoregulation in the marine environment (see Sect. 3.2.4). In some littoral habitats, such as kelp forests, this resulted in their designation as a keystone species because of their widespread influence on community structure. In some cases, the removal of sea otters led to less diverse and productive habitats, and in others it led to an imbalance in the abundance and size of some mega-invertebrates that became commercially valuable to humans.

From a biological and conservation perspective, restoring sea otters to their full pre-exploitation levels throughout their historical range is necessary to help restore nearshore ecosystems. This is true regardless of the negative effects on commercial fisheries. However, there may be ways to mitigate these effects and find a balance between the benefits accrued from restoring nearshore ecosystems and the societal need for human fisheries. That balance will not resemble present-day invertebrate fisheries, but it may be achievable with innovation and technology (Davis et al. 2019). In the short term, we need ways to bridge the inevitable changes to human fisheries, which will result from the restoration of sea otters to littoral habitats of the Pacific Rim.

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Chapter 9
Sea Otter Predator Avoidance Behavior

Daniel H. Monson

Abstract Predators directly affect their prey as a source of mortality, and prey respond by employing antipredator strategies. Sea otters are a keystone predator within the nearshore community, but higher trophic level avian, terrestrial, and pelagic predators (e.g., bald eagles, brown bears, wolves, white sharks, and killer whales) prey on them. Three antipredator strategies used by sea otters are *vigilance* (group or sentinel detection of danger), *avoidance* (seeking a location that is inaccessible to predators), and *crypsis* (the ability to avoid observation or detection). Vigilant behavior allowed sea otters to escape total extinction during the Maritime Fur Trade of the eighteenth and nineteenth centuries. Female otters with pups practice vigilance when they reduce their foraging time and move along meandering paths. Sea otters usually rest at sea, and when they rest on shore, they usually haul out on offshore rocks, reefs, and small islands—possibly a behavioral response to terrestrial predators (brown bears and wolves can kill non-vigilant sea otters on shore). In areas where many sea otters haul out together, group vigilance may be important in detecting an approaching threat. Along the coast of central California, white sharks are a significant source of sea otter mortality, and the only antipredator strategy is avoidance or crypsis by resting in kelp beds. Despite the threat, sea otters still forage in open water, so the perception of risk may be low. In the western Aleutian Islands, killer whale predation is believed to be the cause of a $> 90\%$ decline in sea otters. As a result, sea otters perceive killer whales as a threat and limit their movements to shallow, complex habitats where the risk of attack is low. This behavioral response is so strong in the western Aleutian Islands that it may it limit sea otter dispersal among islands, with implications for the connectivity and genetic health of the small, isolated populations that remain.

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9.1 The Sea Otter Predator-Prey Relationship

Sea otters are a keystone predator within the nearshore community, capable of exerting strong direct and indirect effects on the dynamics, composition, and size structure of their invertebrate prey communities (Paine 1969; Estes and Palmisano 1974; Kvitek and Oliver 1992; Kvitek et al. 1992; Estes and Duggins 1995). Many predators such as sea otters are themselves prey for higher-level predators, which can modify the effects attributed to keystone species. Sea otters are a conspicuous member of the nearshore environment, making the effects of higher trophic level predators clearer. Specifically, odd numbered trophic level cascades encourage primary production by limiting herbivory, which is the classic sea otter-sea urchin-kelp trophic cascade (Estes and Palmisano 1974; Estes and Duggins 1995; Watson and Estes 2011). Adding top-down control on a sea otter population results in an even numbered trophic cascade, which can limit the keystone effects of sea otters if their densities become too low to control the proliferation of herbivorous urchins, subsequently leading to a reduction in kelp biomass (Estes et al. 2004). Historically, humans were one of the most efficient sea otter predators, and the uncontrolled commercial harvest of the eighteenth and nineteenth centuries nearly extirpated sea otters (see Chap. 10; Kenyon 1969; Bodkin 2015). Other predators target sea otters intentionally or unintentionally, including bald eagles (*Haliaeetus leucocephalus*), brown bears (*Ursus arctos*), white sharks (*Carcharodon carcharias*), and killer whales (*Orcinus orca*) (Sherrod et al. 1975; Ames and Morejohn 1980; Monson and DeGange 1995; Estes et al. 1998; Springer et al. 2003; Williams et al. 2004; Tinker et al. 2016; Monson et al. 2021).

Predators directly affect their prey as a source of mortality, and prey respond by employing various antipredator strategies. The analogy for many predator-prey interactions has been that of a coevolutionary “arms race,” in which the players are constantly adapting to each other’s predatory and antipredator strategies (Dawkins and Krebs 1979). However, the appropriateness of this analogy and the stability of the predator-prey relationship depends on many factors, including whether it is symmetrical or asymmetrical in nature (Dawkins and Krebs 1979; Abrams 1986, 2000). The evolution of antipredation strategies is strongly selected considering the major fitness consequences for the prey (Lima 1998). For sea otters, vigilance (group or sentinel detection of danger), avoidance (seeking a location that is inaccessible to predators), and crypsis (the ability to avoid observation or detection) are three antipredator strategies. The success of vigilance is dependent on the ability of sea otters to detect a threat and escape, whereas avoidance and crypsis require a low level of vigilance and responsiveness. However, all these responses require the prey species to perceive predation risk. Clearly, individuals killed by a predator cannot learn from the experience, which is only possible for survivors of predatory interactions. Therefore, the nature of predatory interactions can influence the prey's response to predation risk, including predator detection and avoiding high-risk habitats. In this chapter, I review the antipredator strategies used by sea otters in response to their various predators and the potential consequences of these strategies on sea otter demographics.

9.2 Humans

The Maritime Fur Trade of the eighteenth and nineteenth centuries eliminated sea otters from much of their range (see Chap. 10; Kenyon 1969; Bodkin 2015). By the early twentieth century, less than one percent of the pre-fur trade population survived in 11 widely separated remnant colonies scattered across the north Pacific from Russia to California (Kenyon 1969). What antipredator strategies did sea otters use during this period of this intense hunting pressure? Prior to the Maritime Fur Trade, sea otters did not respond to human presence as a threat. Even today, sea otters inhabiting many areas in California, including Monterey Bay, where viewing-based tourism brings humans and otters in close contact on a daily basis, are so tolerant of humans that tourists must be reminded not to approach too closely.

Sea otters are more vigilant in locations where they have been hunted or harassed by humans, diving in response to humans at much greater distances (100 s of meters) (D. Monson pers. obs.). As a result, adaptive behavior and learning may influence sea otter antipredator behavior. During the eighteenth century, the fur trade relied on hunters using small, traditional kayaks (Fig. 9.1). On the hunting grounds, paddlers fanned out. When a hunter spotted a sea otter, he and his partner paddled to where the animal dove. One man held up a paddle vertically as a silent signal (Fig. 9.2). Other hunters converged to form a circle around the spotters, with a radius a bit wider than a sea otter could swim under water. When it surfaced to breathe, the hunters scared it under again. They tired the animal, forcing it to surface nearer and more frequently until it was exhausted and close enough for one hunter to get a good shot while his paddling partner steadied the kayak. The primary weapons for hunting were specialized darts. Hunters not only thrust them by hand but launched them farther and faster with a throwing board (also called an atlatl; Woodward 1938; Korsun 2012). Early Russian observers estimated that about one in a hundred sea otters escaped the attack (Father Gedeon and Yuri Lisianski, quoted in Korsun 2012, p. 58). By the end of the nineteenth century, as rifle accuracy improved, more hunters became proficient in their use and employed them more often, especially by the shore-based hunters south of Alaska (Scammon 1874).

Considering these observations, it is not surprising that the remnant sea otter populations that survived the Maritime Fur Trade were in locations extremely inhospitable to human hunters: avoidance replaced vigilance as an antipredator strategy (Kenyon 1969). Remnant sea otter populations survived in locations like

Fig. 9.1 In 1794, British explorers led by George Vancouver encountered a muster of Native and Russian sea otter hunters off Alaska's southcentral coast. Hundreds of workers in kayaks were preparing to paddle about 800 km east to hunt at Yakutat. Records about this foray from both English and Russian sources survive. Image from Vancouver (1798), *A Voyage of Discovery to the North Pacific Ocean and Round the World*, via the National Oceanic and Atmospheric Administration

Latex Rocks at the north end of the Kodiak archipelago (Alaska), where tidal currents and hazardous reefs make boating treacherous. Similarly, the Big Sur coast of California is an extremely rugged and exposed, cliff-lined coast where Maritime Fur Trade hunters likely could not hunt effectively much of the year. And in Russia, "The Russian traders rapidly extirpated the sea otters on Behring (Bering) Island, who took refuge on the inhospitable Copper (Medny) Island" (Grebnitsky 1902). In contrast to these coastal settings, a pelagic population persisted north of Unimak Island in the southern Bering Sea in an area characterized by shallow water <50 m deep and extending out to 30 km offshore (Lensink 1960). In this area, most sea otters occurred >5 km offshore. Presumably, they survived here because hunters would have been looking for the proverbial needle in a haystack while working kilometers from shore. These observations suggest that when faced with a predator as formidable as humans, avoidance by sheltering in refugia not easily accessible to hunters is the only strategy.

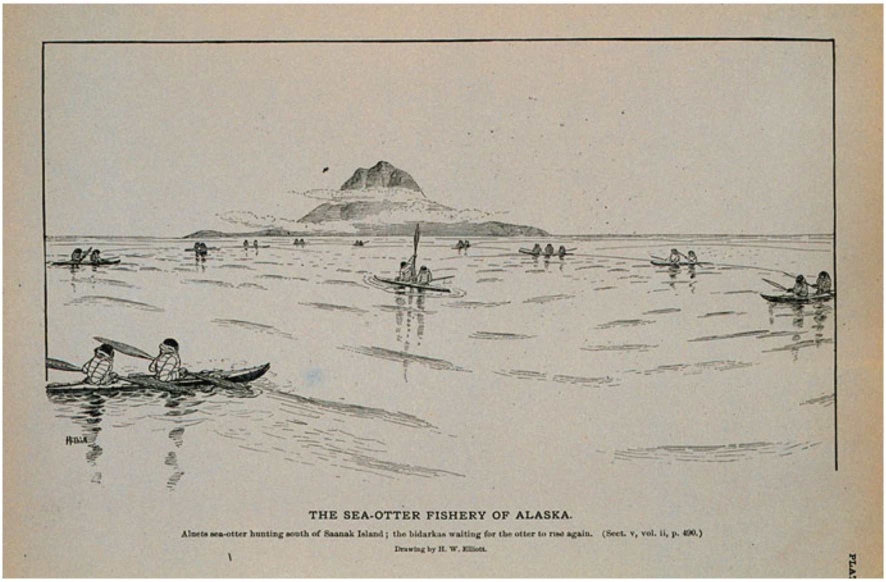

Fig. 9.2 Hunting in the Aleutians in the 1870s, by Unangan traditional methods also used during the Russian period. Drawing by Henry Wood Elliott, plate 234 in *The Fisheries and Fishery Industries of the United States*, GB Goode (ed), 1884, US Bureau of Fisheries, Washington, DC. Public domain image courtesy of the National Oceanic and Atmospheric Administration

9.3 Bald Eagles

Unattended sea otter pups are preyed on by bald eagles (Sherrod et al. 1975; Anthony et al. 2008). The risk of eagle predation on pups appears to have influenced the behavior of female sea otters when accompanied by vulnerable newborns. Specifically, mothers of newborn pups decrease foraging and tend to dive at night, which reduces the amount of time the pup is unattended at the surface and minimizes exposure to eagle predation (Gelatt et al. 2002; Esslinger et al. 2014). Females promptly switch back to diurnal foraging patterns when their pups reach a size greater than an eagle can carry, suggesting this shift in foraging behavior is a true predator avoidance strategy (Gelatt 1996). Females may employ other behaviors indicative of greater vigilance while accompanied by newborns (Cortez et al. 2016). For example, females carrying their newborn pups frequently swim at the surface in long, meandering loops that bring them back to the same location without any apparent reason. We can only speculate about the reason for this behavior, but continuous movement may be related to the threat posed by bald eagles, which decreases after the pup is one month old. These observations indicate that female sea otters perceive predation risk, even when the risk is to the pup, and modify their behavior accordingly.

9.4 Brown Bears

Terrestrial predators can kill sleeping or distracted sea otters on shore. As a result, sea otters often rest at sea away from the shore, and this may be an antipredator behavior (Gilkinson et al. 2011). When sea otters do haul out to rest, most locations are on offshore rocks and small islands that are less accessible to terrestrial predators. While offshore haulouts may reduce predation risk, it does not eliminate it. Brown bears actively prey on sea otters in Russia and Alaska (Fig. 9.3: Bednykh et al. 1986; Koshcheev 1989; Monson and DeGange 1995; Monson et al. in prep). Situations where this occurs are specific to certain locations, and it is unlikely that terrestrial predators pose a significant mortality risk in sea otter populations. However, where it occurs, the prevalence of brown bear predation may be underappreciated because terrestrial predators also scavenge marine mammal carcasses that wash ashore, and it is often assumed that any marine mammals consumed by a terrestrial predator must be the result of scavenging (Monson et al. 2021). While not well documented, there is some evidence that wolves (*Canis lupus*) prey on sea otters where the opportunity arises (Watts et al. 2010; Watts and Newsome 2017).

In areas where many sea otters haul out together, group vigilance may be important in detecting an approaching threat. Sea otters have been observed consistently hauling out on an offshore reef that enabled predatory attacks by brown bears at low tide (Monson et al. 2021). All successful attacks occurred when one or a few animals were hauled out, which reduced group vigilance. In addition, sea otters using this reef were less vigilant to the presence of brown bears than were harbor seals, and thus brown bears were much more successful in capturing sea otters (Monson et al. 2021). However, sea otters have only reoccupied this area for

Fig. 9.3 Brown bear feeding on a sea otter on Shakun Island, Alaska

approximately three decades, and they may increase their vigilance or reduce their use of vulnerable sites over time (Coletti et al. 2016). Alternatively, perceived predation risk may be too low at these sites to elicit a consistent predator avoidance response.

9.5 White Sharks

White sharks have been a known source of sea otter mortality in California for more than 40 years (Ames and Morejohn 1980; Ames et al. 1996; Estes et al. 2003). Recently, shark-related mortality has increased significantly and is preventing further range expansion of the California sea otter population (Tinker et al. 2016; Moxley et al. 2019). However, white sharks do not appear to consume sea otters, suggesting they are victims of investigatory bites, which are still fatal, rather than a prey species (Tinker et al. 2016; Moxley et al. 2019).

Sea otters have no defense against sharks, which attack from below the surface. As a result, vigilance may not be an effective antipredator strategy, so their only alternative is avoidance or crypsis by resting in kelp beds. Species targeted by sharks commonly avoid habitats where the risk of attack is high, even if the habitat contains abundant food, which exemplifies how fear can influence prey behavior and the ecosystems they inhabit (Brown et al. 1999; Frid et al. 2007, 2008; Wirsing et al. 2007, 2008; Ritchie and Johnson 2009; Willems and Hill 2009; De Vos et al. 2015a, b; Atkins et al. 2019; Srinivasan 2019). Nevertheless, sea otters do not avoid open water where many shark attacks occur, suggesting that predation risk has not altered their behavior in California. White sharks tend to target single individuals, and most attacks are fatal even if investigatory in nature (Le Boeuf et al. 1982; Ainley et al. 1985). In this situation, sea otters may never learn that a particular habitat is high-risk. As a result, white shark mortality has prevented northern range expansion of the California sea otter population for decades. Presumably, this barrier is simply caused by the elimination of all individuals that venture north of the current range. However, it is not known if individuals living near the boundary actively avoid this area in response to the risk of a shark attack.

9.6 Killer Whales

Killer whale predation is believed to be the cause of a >90% decline in the Southwest stock of Alaskan sea otters (Estes et al. 1998, 2005, 2009; Doroff et al. 2003; Springer et al. 2003; Laidre et al. 2006). In contrast to white sharks, killer whales target aggregations of marine mammals (e.g., sea otters, seals, and sea lions; Fig. 9.4), where many individuals may survive an attack resulting in the potential for survivors to associate predation risk with specific habitats (Baird and Dill 1995).

Fig. 9.4 Carcass of a killer whale, which was found in Spring 2020 along the coast of northwestern Bering Island in the Commander Islands, Russia. The stomach contained six mostly intact sea otters and one that was partially digested. Three of the sea otters were adults, three were subadults, and one was of indeterminate age. One sea otter carcass, which was lodged between the pharynx and the esophagus, may have dislodged the epiglottis (goosebeak) from the boney nares (i.e., laryngeal displacement), causing asphyxiation. Image courtesy of Sergey Fomin

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 (Lima and Dill 1990; Schmitz et al. 1997; Brown et al. 1999; Srinivasan et al. 2010, Srinivasan 2019).

In the western Aleutian Islands, sea otters have shifted their distribution dramatically since the early 1990s, when a decline attributed to killer whale predation was identified (Estes et al. 2010). Specifically, sea otters in the western Aleutians now occur in places where the risk of attack is low, such as shallow, complex habitats that are very close to shore and inaccessible to killer whales. Evidence indicates this highly altered distribution pattern is the result of the risk of predation by killer whales in open water habitats and not because otters have moved to where prey availability is highest (Peckarsky et al. 2008; Stewart et al. 2015). This change in distribution is likely the only antipredation strategy available to a prey species that are unable to evade or fend off an attack by an overwhelmingly powerful predator in open water. An additional, non-consumptive effect of killer whale predation on the surviving western Aleutian sea otter population may be as a selective force limiting sea otter dispersal, with implications for the connectivity and genetic health of the small, isolated populations that remain (Orrock et al. 2008; Davis et al. 2019).

9.7 Conclusions

When confronted with overpowering predators such as humans, white sharks, and killer whales, sea otters have three antipredator strategies: *vigilance* (group or sentinel detection of danger), *avoidance* (seeking a location that is inaccessible to predators), and *crypsis* (the ability to avoid observation or detection). Sea otters are gregarious but not highly social, so rafting or hauling out on land in large numbers improves group vigilance and alerts conspecifics to the presence of surface predators (see Chap. 5). Avoiding detection by resting in kelp beds may reduce exposure to predation, but white sharks and killer whales are known to pursue prey close to shore, where kelp may be abundant. Avoiding habitats with a high risk of attack is the only other strategy. However, avoiding high-quality feeding habitats comes at a cost and may occur only when predation risk meets some threshold level and/or may only develop when a significant number of individuals survive attacks and thus learn that there is a risk. This may explain why some sea otters occur in areas with white shark or brown bear predation. However, female sea otters exhibit clear predator avoidance behavior in protecting their pup against bald eagle predation.

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Chapter 10
Sea Otters and the Maritime Fur Trade

Shana Loshbaugh

Abstract The Maritime Fur Trade of the eighteenth and nineteenth centuries influenced countries of the North Pacific Rim, including China, Japan, Russia, Canada, Mexico, and the United States. Especially affected was Alaska, which probably would belong to Canada if the fur trade had not inspired Russian adventurers to colonize it in the eighteenth century. That event changed the lives and cultural history of maritime Native people, especially the Aleuts (Unangan and Sugpiaq), who were conscripted (enslaved) to hunt sea otters for Russian traders from the mid-1700s until the United States purchased Alaska in 1867. After Russia withdrew from the territory, American (and, to a lesser extent, British and Japanese) hunters pursued sea otters throughout their original range, often as poachers. Sea otter populations reached the brink of extinction until the signing of the International Fur Seal Treaty in 1911, which included protections for sea otters. In hindsight, the rush for the otters' "soft gold" was a predictable boom and bust cycle, a cautionary example of unsustainable resource use, and a socioeconomic driver of Western—mainly American—involvement in the Pacific region starting in the eighteenth century. The trade's profound effects on the population biology of this important marine predator and the littoral community of the Pacific Rim are still apparent today.

Keywords Alaska · America · California · China · Extinction · Fur trade · Japan · Maritime · Russian America · Sea otter

In a sense, Alaska owes its geopolitical existence to sea otters. Without them, eighteenth century Russians may not have explored and settled along the North Pacific coast of North America. The Russian colonial effort, founded on profits from sea otter pelts, put this region on the world map and influenced the boundaries of Alaska, British Columbia, and the Pacific Northwest. In this chapter, I describe how

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Fig. 10.1 Current and former range of sea otters. Circles indicate locations of remnant sea otter populations after the 1911 International Fur Seal Treaty. From west to east, the remnant colony locations were: Kuril Islands, southeast Kamchatka, Medny Island, Rat Islands, Delarof Islands, False Pass, Sandman Reef, Shumagin Islands, Kodiak Island, Prince William Sound, Haida Gwaii, Monterey coast, and San Benito Islands. Remnant colonies from Kenyon (1969) and Doroff et al. (2011). Base map of ranges by C Azhderian from Larson and Bodkin (2015)

profits from the commercial harvest of sea otters prompted the Russian occupation of Alaska, fueled its first economic boom, and played an important role in the history of the Russian Far East, the United States, Canada, Mexico, and Japan (Fig. 10.1). The demand for pelts pushed sea otters to the brink of extinction, pulled Alaska into the world economy, and shaped the fates of both Natives and foreign settlers in the eighteenth and nineteenth centuries. It is a remarkable story of the tightly intertwined and brutal history of sea otters and the humans who wanted their valuable fur, which they called “soft gold.”

10.1 Native Uses of Sea Otters

When sea otters first appear in historical records, their range in the North Pacific extended from Hokkaido in Japan to the Baja California Peninsula in Mexico. Coastal Natives traditionally hunted them in modest numbers for their fur, which was used for prestige garments and blankets. The remains of sea otters have been found in archaeological sites throughout the region, dating back thousands of years (Simenstad et al. 1978; Jones et al. 2011). Writing in 1925 about San Nicholas Island off the California coast, anthropologist Alfred Kroeber wrote, "Sea otters were to be had in comparative profusion and, to judge from the habits of other tribes, their furs formed the most prized dress and chief export . . ." (Koerper 2011).

The cultural importance of sea otters to Native peoples who inhabited the North Pacific Rim for thousands of years is largely forgotten. Enduring Alaska folklore describes sea otters as transformed human spirits (Crowell and Laktonen 2001). The Ainu of Hokkaido and Kuril Islands preserve a folk epic, "Kutune Shirka," that centers on the capture of a "golden sea otter" (Waley 1951). Museum collections contain otter amulets carved of ivory or bone (Fig. 10.2; Crowell and Laktonen 2001; Korsun 2012). Whether Natives commonly ate otters is a matter of conjecture. Opinions on the edibility of sea otters vary, but it is likely that they were a hardship food when tastier options were not available.

10.2 The Early Asian Sea Otter Trade

Indigenous Northeast Asians, such as the Ainu and Kamchadals of Hokkaido (Japan), the Kuril Islands, and Kamchatka (Eastern Russia), hunted sea otters for their fur as Alaskan natives did. Prior to the sixteenth century, there was little trade in sea otter pelts, with the earliest record of Japanese exports to China by 1483 (Takahashi 2006, p 40). Unlike those in South China, winters in Northeast China (i.e., Manchuria) are cold. As trade expanded and Manchus became powerful and prosperous in the seventeenth century, interest in sea otter pelts grew (Ravalli 2010).

Fig. 10.2 Ivory sea otter amulet from Paramushir Island in the northern Kuril Archipelago, probably from the pre-Ainu Okhotsk culture (ca. seventh century). Image courtesy of M. Toyama of the Nemuro City Museum of History and Nature, Hokkaido, Japan and Y. Mitani

The Japanese began trading sea otter pelts obtained from Ainu hunters in the Kuril Islands (Takahashi 2006), which the Japanese called *Rakkoshima*: the Sea Otter Islands (Ravalli 2010). Wealthy Chinese wore sea otter fur as trim on garments or in the lining of winter coats. In addition, residents of the Far East thought the pelts had healing powers (Ravalli 2010). During the same period, furs became the economic foundation of the growing Russian Empire. After decimating boreal furbearers (e.g., sable, mink, and fox) in European Russia, hunters moved eastward across Asian Siberia beginning in 1582. By 1647, when they established the town of Okhotsk, their first Pacific coast settlement, Russian trappers were aware of sea otters, called them Kamchatkan sea beavers, and obtained pelts from Natives. The ocean east of Kamchatka Peninsula was referred to as the Beaver Sea (Steller 1988). In the eighteenth century, Russians expanded their influence in the Far East and began competing with the Japanese and Ainu in the Chinese fur trade. China became Russia's largest trading partner, and sea otter fur earned the sobriquet "soft gold," replacing dwindling sable (marten: *Martes zibellina*) as one of the most valuable international trade products. Competition for sea otters in the Kuril Islands fueled international conflict between Russia and Japan (Ravalli 2010). Border disputes between them regarding control of the southern Kuril Islands—which Russia has controlled since World War II—continue today.

10.3 Bering's Expedition Discovers Sea Otters

Tsar Peter the Great (1672–1725) strove to consolidate the Russian empire and transform it into a modern European power. His successors, especially Catherine the Great (1729–1796), continued this mission. It was the Age of Enlightenment, and the tsarist court recruited skilled Russian and Western European scientists for ambitious explorations of its frontiers (Jones 2014). One such expedition, led by Danish captain and cartographer Vitus Bering, ventured into the North Pacific (Fig. 10.3a). The expedition's two ships launched from Petropavlovsk in May 1741. Equipped with faulty maps, they sailed into the Gulf of Alaska, where adverse weather permanently separated them (Waxell 1962). Both eventually sighted mainland Alaska, lost men, endured privations, and returned to Russia late in the season. The *St. Paul*, captained by Alexei Chirikov, reached Petropavlovsk in October. Bering's ship, the *St. Peter*, wrecked on an uncharted island in the western Aleutian Archipelago, later named Bering Island (Figs. 10.1 and 10.3b). The feeble castaways, starving and worn out by scurvy, lay in the sand while ravenous arctic foxes (*Vulpes lagopus beringensis*) tried to eat the corpses (Waxell 1962). Bering and 28 others were casualties, and his men buried them on the shore (Fig. 10.3c, d). Led by Danish First Mate Sven Waxell and German physician-naturalist Georg Wilhelm Steller, the survivors hunkered down for a long winter. In addition to foxes, their new neighbors included sea otters, helplessly naïve about humans. The men easily killed many of them onshore and subsisted on their flesh. Opinions of the fare varied. According to Steller's journal, published first in 1743 and a significant source of

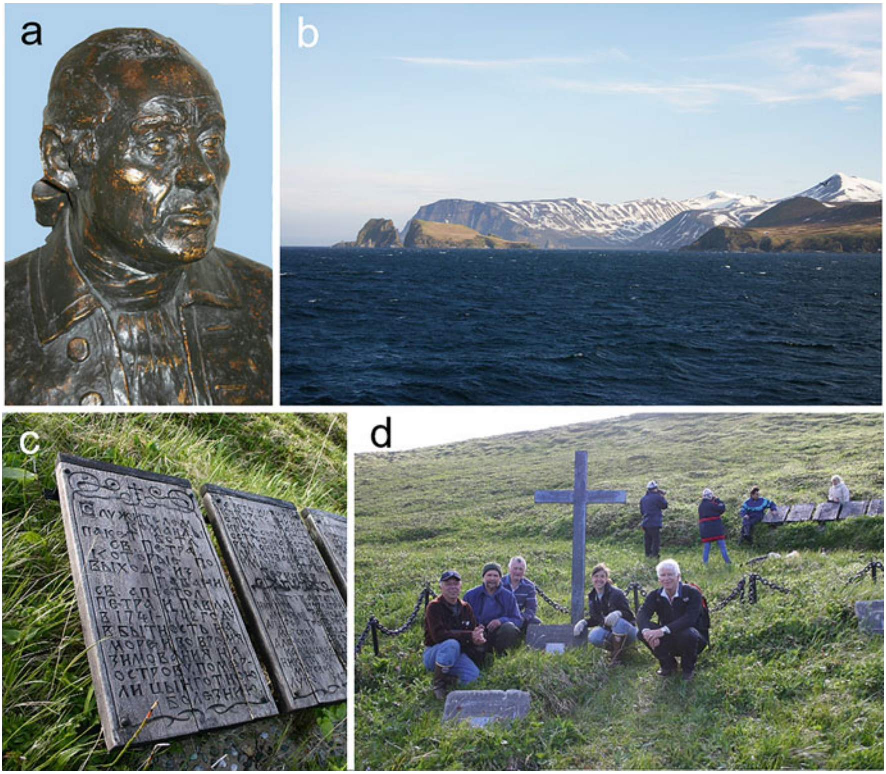

Fig. 10.3 (**a**) Bronze bust of Vitus Bering in the Aleutskiy Krayevedcheskiy Muzey (museum) in the town of Nikolskoye on Bering Island. (**b**) Coastline of Bering Island. (**c**) Commemorative plaque for Vitus Bering and the other 28 men who died on Bering Island during the winter of 1741–42. (**d**) Memorial grave site for Vitus Bering and his men on Bering Island. Images courtesy of R. Davis

information about the expedition (Steller 1988), Bering flatly refused to eat sea otter meat, sticking to ptarmigan for his final meals. Waxell (1962, p 112) later wrote:

> Sea-otter flesh, which until March was our main means of sustenance, we ate at first with great repugnance, for it is very tough and consists mainly of sinews. It is almost like a piece of leather and has to be chewed, chewed and chewed again before it becomes slightly softened and can be downed bit by bit.

However, Steller became a fan and wrote (Steller 1988, p 147):

> The meat is rather good to eat and tasty, but the females are much tenderer and tastier, and they are against the course of nature most fat and delicious shortly before, during, and after giving birth. The nursing otters . . . can be compared at all times with a nursing lamb because of their tenderness, both roasted and boiled.

Months later, the castaways figured out how to kill and haul ashore the huge, strange, and slow-moving beasts that floated in the lagoons: dugongs, later named

Steller's sea cows (*Hydrodamalis gigas*). Those were delicious compared to sea otters and became the preferred food. Feeding on fresh meat and the island's plants, which Steller pressed them to eat, the survivors recovered from scurvy and regained their strength (Steller 1988; Waxell 1962). Steller wrote that after the men stopped eating sea otter meat, they continued killing them even though hunts entailed hiking farther and farther from camp. As otters became wary, the men began attacking at night, trying to find sleeping animals on shore and club them on the head. They killed them for the pelts, which the bored men used as currency as they gambled at cards in their chilly huts. In February, fur seals, as naïve as the otters had been, came ashore and also became prey.

In nearly a year marooned on the island, Steller had ample time to observe sea otters, and he acquired an affection for them. He even suggested taking some to Russia and raising them in captivity (Steller 1988). He wrote (Steller 1988, pp. 147–148):

> In life, it is an extraordinarily beautiful and pleasant animal, as well as amusing and comical in its habits; at the same time, it is a very cajoling and amorous one. When one sees them running, the gloss of their hair excels the blackest velvet. They lie together as families; the male is with its female, the half-grown offspring … and the nursing young. The male caresses its female by stroking, for which he uses the front feet like a dog, and lies on her, but she teasingly often pushes him away from her. Not even the most loving human mother engages in the same kind of playing with her children, and they love their children in such a way that they expose themselves to the obvious danger of death. When the young are taken from them, they cry aloud like a little child and grieve in such a way, as we have discovered several times, that within ten to fourteen days they dry up like a skeleton, become sick and weak, and do not want to leave the land. When fleeing, they take their nursing young in the mouth, but the grown ones they drive ahead of them. If they are lucky enough to escape, they begin, as soon as they are in the sea, to ridicule their pursuers so that one cannot look on without particular amusement. They stand in the sea upright like humans and hop up with the waves, holding the front foot over the eyes and look at one as though the sun were bothering them. They lie on their backs and scratch their noses with their front feet, they throw their children in the water and catch them again. When a sea otter is attacked and cannot see an escape route anywhere, he blows and hisses like an infuriated cat. When he receives a blow, he gets ready to die in this fashion: he lies on his side, pulls his hind feet after him, and covers his eyes with his front feet; and when he is dead, he lies like a dead person since he crosses his front feet on his chest.

The following summer, the remaining mariners left the island in a boat made from salvaged pieces of the *St. Peter*. They rowed west to Kamchatka, sitting on bales of furs gathered during their sojourn. They carried nearly 900 sea otter pelts (Steller 1988). They sold those furs in Asia and became rich men. The word spread that other lands and islands lay east of Kamchatka, teeming with sea otters.

10.4 The Rush for Sea Otter Fur Begins

Suddenly, Russians could access multitudes of sea otters free from Japanese claims. Fur traders went into a frenzy as wealthy Chinese paid high prices for sea otter pelts. In distant cities and the tsarist court, powerful people pondered Steller's detailed descriptions and drawings. The next year, a Siberian trader retraced the route of the shipwreck survivors. He found the island but also wrecked there. He and his 20 men harvested 1200 sea otters in the year it took them to repair and refloat their ship. They named the island after Bering. In 1744, they found another island (Medny) nearby with numerous sea otters (Jones 2014). Today, Bering and Medny Islands, with associated small islets, are known as the Komandorski (Commander) Islands and belong to Russia. This expedition launched momentous changes for the region.

Siberian fur traders were men of the northern forest, not of the high seas. Rather than employing their Russian brethren, the fur traders quickly learned to use Natives, such as the Kamchadals, who were familiar with the region and with sea otter hunting, to catch more animals. Historical archaeologist Aron Crowell (1997, p 13) noted:

> Unlike the sable and other taiga and forest furbearers, which could be trapped by the Russians themselves if not by the Native hunters under their control, the hunting of sea otters was a difficult skill that required the mastery of kayak[1] handling and the use of traditional weapons: the throwing board, dart, bow, and barbed harpoon arrow. The use of rifles was found to frighten sea otters and cause them to abandon areas where they were thus hunted.

After a few years of heavy hunting, sea otter numbers plummeted around the Komandorski Islands. Exploring farther, the fur traders found more islands strung ever eastward toward the vast new world, America, glimpsed by Bering's 1741 expedition. Meanwhile, the helpless sea cows at Bering Island, targeted by nearly every ship sailing past, slipped into extinction within one human generation of Bering's discovery.

10.5 Conquest of the Aleutian Islands

Russians established a pattern along the North Pacific Rim of what is now Alaska. A ship—armed, provisioned, and crewed by Natives and fur-traders from Siberia and the Russian Far East—sailed east for a season hunting among the islands. After a few seasons in one area, these hunters would kill most of the sea otters, and the ship would continue to the next unexploited island (Lensink 1962; Jones 2014). When hunters reached what they called the Near Islands (~475 km east of Bering Island), they encountered the Unangan[2] people of the archipelago. First contact turned into one of the ugliest chapters of Alaska's history. Many encounters deteriorated into violence. At their worst, Russian crews murdered locals, sacked villages, raped women, and stole food. They also brought Eurasian diseases that caused virulent epidemics.

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[1] These boats appear under varied names in the historic records. English-speakers often called them "canoes"; Russians used the word "baidarka" or "bidarka" which remains a popular term in Alaska.

[2] The Russians called the island people they encountered "Aleuts." Although the Russians came to call all coastal Natives from Adak to the Copper River "Aleuts," the overarching name the people of the Aleutian Chain used for themselves was Unangax̂ (plural noun) or Unangan (singular noun or adjective, also used to refer to their language).

Violence was a losing proposition for all. Russians generally overran the Unangax̂, whom they named Aleuts, but could scarcely be called victors. Conflicts with the Natives reduced the workforce, cut into profits, and displeased their rulers in distant St. Petersburg. Unlike European invaders on America's Atlantic coast, Russians did not come to establish a New Russia by displacing or eliminating indigenous people. Instead, they came to collect fur tribute. They needed the Natives alive and compliant (Luehrmann 2008).

Unangax̂ otter hunting skills surpassed those of the Kamchadals. Their small skin boats, now known commonly as kayaks, were technological marvels so fused to their owners that the men seemed amphibious (Fig. 10.4a, b). Ivan Veniaminov, the talented priest who spent many years in the Aleutians, later wrote, "The Aleut baidarka is such an accomplished piece of work of its kind, that a finished mathematician would not be able to add anything to the perfection of its sea-going qualities" (quoted in Woodward 1938, p 121).

By gifts or coercion, Russians conscripted (enslaved) Unangax̂ to hunt for them. According to environmental historian Ryan Tucker Jones in his 2014 book, *Empire of Extinction*, it took the Russians a generation to transit and subdue the Aleutian Islands. As they moved east, they found more people and sea otters. Sea otters were exterminated throughout much of their range not by commercial harvest *per se*, but by serial harvests that extirpated animals from one area to the next (Bodkin 2015). This type of harvest prevented any recovery of the population when the hunters moved on, and it placed sea otters on course for extinction.

10.6 The Russian Invasion of Alaska's Southcentral Coast

In 1784, Irkutsk fur merchant Grigory Shelikhov sailed to Kodiak with cannons and armed men. He envisioned a new approach to the fur trade: to use permanent colonial bases rather than seasonal voyages. He attacked the Koniag and conquered the Kodiak Archipelago by force. This act led to the first enduring Russian settlement in Alaska and incursions into what would later be called Cook Inlet and Prince William Sound. As soon as the Russians established a foothold, they got back to pursuing sea otters.

By then, the Russians had drafted many working-age Unangan men and women, who traveled with Shelikhov and were part of organized marine hunting squads. The Russians found the people on Kodiak and the adjacent mainland different from the Unangax̂, but still skilled at kayaking and hunting marine mammals. Russians also called these people Aleuts, later modified in Native communities as "Alutiiq." But in the twenty-first century, the maritime people of southcentral Alaska increasingly were recognized as Sugpiat, more closely related to Yup'ik Eskimos of the Bering

Fig. 10.4 (**a**) Three-hole baidarka or kayak (638 cm in length, 61.2 cm in width, 37.4 cm in height, and 27.5 kg) fabricated ca. 1875 by Native Aleut from Attu Island, who had been brought to Simushir Island in the Kuril Archipelago by the Russian fur company to work with Ainu sea otter hunters (Oya and Suzawa 2013). (**b**) Sea otter hunters in the Kuril Islands portrayed by the Japanese master woodblock artist Utagawa Hiroshige (1797–1858). Image (**a**) courtesy of the Hakodate City Museum of Northern Peoples, Hokkaido, Japan and Y. Mitani. Image (**b**) courtesy of the Lavenberg Collection of Japanese Prints

Sea than to Unangan people.[3] Shelikhov only stayed in Alaska for one year, but he and his men unleashed socioeconomic forces that brought Alaska and the North

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[3] Like many colonialists, the Russians tended to use names from their own land or third parties rather than indigenous names. In Alaska, modern Natives and scholars who work with them have expended considerable effort pondering the most appropriate names for peoples and places.

Pacific region into a changing world system of colonialism, globalized trade, and mercantile capitalism. Russia moved away from the system of collecting tribute, which Catherine the Great officially banned in 1788 (Crowell 1997).

Other fur-trading companies tried and failed to follow Shelikhov's team into Alaska. After several interim managers, the competent but controversial Aleksandr Baranov arrived in Kodiak in 1791 to direct Shelikhov's Alaskan business interests. In 1799, following the deaths of both Shelikhov and Tsarina Catherine, their heirs signed agreements granting Shelikhov's company monopoly control over the Alaskan fur trade. Modeled on the British Hudson Bay Company and the Dutch East India Company, it became the Russian-American Company. Baranov became *de facto* ruler of a fragile Russian colony on America's northwestern extremity.

10.7 Sea Otter Hunting Techniques

By the late eighteenth century, the Russian mode of operation was to dispatch amphibious hunting parties to scour the coasts for sea otters. Most hunters used the traditional kayaks while others paddled larger open boats.[4] A Russian supervisor traveled with each squad. Hunters spent most of their time at sea but, if beaches were suitable, sometimes camped ashore, turning the larger boats over to make temporary shelters. Over time, hunting parties grew larger and traveled farther. The journal of British explorer George Vancouver described encountering a flotilla at Port Dick (on the outer Kenai Peninsula coast) in 1794 (Vancouver 1798). About 500 boats mustered in lower Cook Inlet off Nanwalek, skirted the peninsula to Resurrection Bay, and picked up supplies there (and perhaps more men) before continuing east to hunt near Yakutat (Fig. 10.5; Purtov and Kulikalov 1794).

On the hunting grounds, paddlers fanned out. When one spotted a sea otter, he and his partner paddled to where the animal dove. One man held up a paddle vertically as a silent signal. Other hunters converged to form a circle around the spotters, with a radius a bit wider than a sea otter could swim underwater. When it

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Many official names have changed in the past few decades, and the literature contains a confusing array of names from past usage. "Sugpiat" is the plural noun, with "Sugpiaq" as the adjective or singular noun. Their homeland extends west to east from the Alaska Peninsula through Prince William Sound. The Sugpiat are subdivided into Koniag (residents of the Alaska Peninsula and Kodiak archipelago) and Chugach (in Prince William Sound and on the lower Kenai Peninsula). To complicate matters further, some on Kodiak want to be known as "Qikertamiut" (people of the island), and some refer to the smaller population along the outer Kenai Peninsula coast as "Unegkuhmiut" (Crowell and Luehrmann 2001).

[4] Russians called a larger boat a *baidara* (equivalent of an umiak) and a smaller one a *baidarka* or *bidarka* (plural *baidarki*). Native boatwrights developed a larger *baidarka*, with three seats rather than the traditional one or two (Fig. 10.4a). Russian officials or other passengers could ride along and not always have to paddle (Crowell and Laktonen 2001). Many Alaskans consider these boat names to be Native, but according to Gregory Weissenberg, a bilingual retired educator who studies Russian names in Alaska, the terms come from the Dnieper River area of Ukraine.

Fig. 10.5 In 1794, British explorers led by George Vancouver encountered a muster of Native and Russian sea otter hunters off Alaska's southcentral coast. Hundreds of workers in kayaks were preparing to paddle about 800 km east to hunt at Yakutat. Records about this foray from both English and Russian sources survive. Image from Vancouver (1798), *A Voyage of Discovery to the North Pacific Ocean and Round the World*, via the National Oceanic and Atmospheric Administration

surfaced to breathe, the hunters scared it under again. They tired the animal, forcing it to surface nearer and more frequently until it was exhausted and close enough for one hunter to get a good shot while his partner steadied the kayak (Father Gedeon and Yuri Lisianski, quoted in Korsun 2012, p. 58; Fig. 10.6). Observer Yuri Lisianski estimated that about one in a hundred sea otters escaped the attack. He wrote, "I heard from expert hunters that sometimes 20 kayaks fight with a single sea otter for half a day. There are also some animals that pull arrows out of themselves with their paws, but for the most part after the lapse of several hours they become the hunter's catch."

The primary weapons for hunting were specialized darts. Hunters thrust them by hand and could also launch them farther and faster with a throwing board (also called an atlatl; Woodward 1938; Korsun 2012)[5]. Fletched like an arrow, each dart had a detachable, notched blade tied to the shaft by a cord or sometimes held by the hunter

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[5] "Atlatl" is a Nahuatl word from Mexico, now widely used, especially by Native Americans, to describe the throwing board tools traditionally used in North and South America.

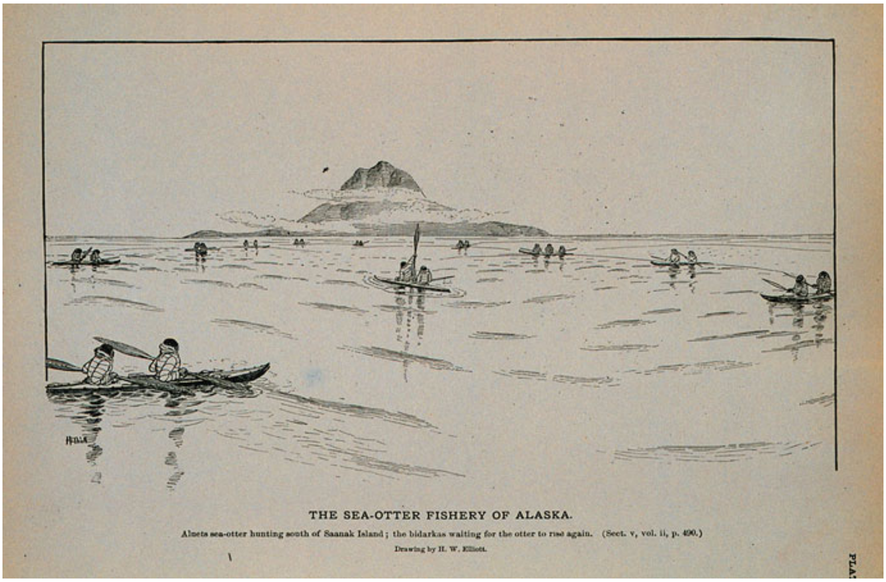

Fig. 10.6 Hunting in the Aleutian Islands in the 1870s using Unangan traditional methods, which also were used during the Russian period. Drawing by Henry Wood Elliott, plate 234 in *The Fisheries and Fishery Industries of the United States*, GB Goode (ed), 1884, US Bureau of Fisheries, Washington DC. Public domain image courtesy of the National Oceanic and Atmospheric Administration

(Woodward 1938; Korsun 2012). If the blade got under an animal's skin, even if the hunter let go, the buoyant shaft and cord encumbered the wounded animal and, once it died, helped hunters retrieve the carcass (Scammon 1874; Crowell and Laktonen 2001). Credit for the kill went to whoever first drew blood, and hunters sought prestige by trying to bag the most animals. In the early colonial phase, hunters tried to kill every sea otter encountered, even breeding females and small pups, whose pelts had little value (Jones 2014). Contemporaneous Western observers such as Fyodor Litke described the Unangan lust for killing sea otters, comparing it to the way cats go after mice (quoted in Gibson 1987a).

When the Russians reached Kodiak and Cook Inlet, they brought Unangan hunters. As they moved into Southeast Alaska and later south to California, the Russians traveled with Unangax̂ and Sugpiat, the two groups considered the best sea otter hunters. Initially, the Russian-American Company focused its activities specifically where sea otters lived. Natives whose sustenance focused on terrestrial resources, such as game animals, forest furbearers, and riverine salmon runs, had less involvement with the Russians. In 1798, Baranov wrote dismissively of the Kenai Athabascans of southcentral Alaska: "Even when there were sea otters there, they were getting but very few, because Kinai natives do not know how to handle baidarkas, have few of them, and are afraid of the sea" (Baranov 1798).

In other areas such as California, methods included netting the animals at sea or entangling them in hooked lines (Woodward 1938). When surprised on land, the animals could be shot or bludgeoned (Steller 1988). Many observers noted that the females' reluctance to abandon their threatened pups made them especially vulnerable (Woodward 1938; Steller 1988). Guns were rarely used in the early years because they frightened away animals, tipped kayaks with their recoil, and were associated with higher loss rates (Woodward 1938). By the end of the nineteenth century, when rifles were better designed and more hunters were proficient in their use, they were used often, especially by shore-based hunters south of Alaska (Scammon 1874).

10.8 The Sea Otter Fur Trade in the Early nineteenth Century

Chinese market demand for sea otter fur increased throughout the eighteenth century. However, by 1800, the availability of sea otters began to wane for the Russians, and the remaining populated areas were beyond their direct control. Sea otters were extirpated along thousands of kilometers from Bering Island to Yakutat, with the few surviving groups too small to harvest profitably. In pursuit of dwindling numbers of sea otters, Russians and their conscripted hunters turned south into the maze of wooded islands and inlets now called Southeast Alaska, where large otter populations still existed. In 1808, Baranov moved the Russian-American Company headquarters from Kodiak to Sitka. He and his men now encountered a more complex situation. Militant indigenous groups—most notably the Tlingit—had ample forewarning about the Russian advance. Rather than colonial conquest, the Russian relationship with Southeast Alaska Natives was an uneasy standoff.

The young United States and Western European powers, especially Britain, were active in the more temperate regions of the northeastern Pacific. They challenged two empires' efforts to assert sovereignty, those of the Russian tsar to the north and the Spanish king to the south. Poachers off the coast had no trouble selling the pelts they gathered in the freewheeling port of Canton in China. Indeed, English sailors on Captain James Cook's 1778 voyage collected sea otter furs from Natives on Vancouver Island and in "Cook's River" (the Alaskan inlet that now bears Cook's name). Not knowing what they had, the sailors traded a few beads for worn furs to use for bedding on the ship. When they reached China at the end of 1779, they were astonished at the prices offered for the used goods. "So great was the rage with which our seamen were possessed to return to Cook's River, and procure another cargo of skins, by which they might be enabled to make their fortunes, that, at one time, they were almost on the point of proceeding to a mutiny," their last captain, James King, wrote (Cook and King 1784, p 246).

At the southeasternmost extreme of the sea otters' range, the Spanish dabbled in the fur trade. Historian Adele Ogden studied the sea otter hunt along the California coast, delving into original Spanish sources and uncovering a complex saga of swashbuckling adventurers and shameful swindlers (Ogden 1941). The oldest reference she found of Spanish involvement in the fur trade was a 1733 note from an itinerant priest. He wrote of sailors near Cedros Island off the Baja Peninsula encountering a colony of animals so plentiful and naïve that the men killed them with sticks, skinned them, and sent the pelts to Mexico (Ogden 1941).

By 1780, Spanish authorities were contracting with coastal Native hunters to bring them sea otter pelts in exchange for beads, iron, knives, clothing and, farther north, abalone shells. One entrepreneur advised the viceroy of New Spain to trade sea otter pelts to China in exchange for mercury to use in Latin American mines. However, the Spaniards lacked the resources or skills to hunt sea otters, while California Natives saw little reason to participate. Catholic missions viewed the hunt as an income opportunity and lobbied to get better trade goods as incentives for their converts. But Spanish corruption and greed led to counterproductive theft from the Natives, and rival colonies in the Philippines blocked their New World compatriots from the profitable Chinese trade. Thus, the Spanish in California cooled to the idea of hunting sea otters (Ogden 1941).

The British also scaled back their Pacific activities after a serious play for claiming Alaska in the days of Captain Cook. This drawdown may have been caused by political disruption from the Napoleonic Wars (Wheeler 1971), London's focus on concentrating resources into the East India Company and Canada (Ogden 1941), or the growing influence of the United States. With low capital reserves and Britain restricting their access to Atlantic ports, Yankee merchants from the new nation were especially keen to ramp up Pacific trade (Gibson 1992). In 1790, Captain Robert Gray became the first United States trader to sell sea otter pelts in Canton and to circumnavigate the world (Wheeler 1971). In the decade that followed, New England Yankees (nicknamed "Boston men,") mostly displaced Englishmen in the North Pacific. Soon they were shipping as many sea otter pelts (10,000–15,000 a year) to Canton as the Russians were able to ship to Siberia (Gibson 1992).

Short on supplies, ships, and a laborforce, the over-extended Russians could not effectively control the territory they claimed south of their new colonial capital, Novo-Arkhangelsk (New Archangel), at present-day Sitka. However, they retained clout through their naval officers, superior Native otter-hunting squads, and international diplomatic acquiescence to St. Petersburg's colonial land claims. The Russian-American Company caught and processed its own sea otter pelts, so it had little need to bargain for pelts with regional Natives or foreign fur merchants (Gibson 1992). Still, Baranov had to deal with the foreign interlopers to get basic food and supplies for his impoverished men in Russian America.

Pacific Northwest Natives were skilled traders with long experience bartering products, such as fish oil, cedar, and dentalium shells (tooth shells or tusk shells [*Antalis pretiosum*] used in indigenous jewelry, adornment, and commerce), to other indigenous groups to the north, south, and inland. Sea otter pelts had not been a significant trade item prior to the White men's interest, but indigenous hunters ramped up harvests in response to the demand. They played the different intruders off against each other and bought weapons from the British and Yankees, which the more cautious Russians banned. Natives were not above cheating now and then, such as blackening pale pelts with charcoal, and if they felt wronged in business transactions, they sometimes resorted to lethal reprisals (Gibson 1992).

Spanish efforts to control their California shores and sea otter resources were no more successful than those of the Russians farther north. The situation was anarchic, with diverse groups passing through to exploit the sea otters and each other (Ogden 1941). One Yankee ruse, first documented near Carmel in 1796, was to pull into a California bay, tell local authorities that the crew was ill and the vessel damaged after the arduous voyage from New England, and anchor for prolonged repairs and provisioning. This story was plausible, but Californians noticed that, while Yankee guests lingered, nearby cattle and sea otters mysteriously vanished at night (Ogden 1941). Spanish hospitality soured, followed by a period of paramilitary skirmishes, arrests, bribery, and (eventually) international diplomatic discussions (Ogden 1941). Reminded of the high value of sea otter pelts, the Spanish collected them opportunistically by seizing them from poachers or trading them in the Pacific Northwest for abalone shells, which Natives there coveted (Ogden 1941).

The influx of international fur traders, starting in the final decades of the eighteenth century, led to the rapid depletion of North American sea otter populations. Historian James Gibson described the frenzy: “The extremely high value of sea otter fur—more than three times as valuable as beaver fur in Canton at the beginning of 1811—caused a fast rush and early peak to the coast trade, as well as a quick slump in prices and a heavy toll on sea otters” (Gibson 1992, p 177). The rush led to a market glut as pelts saturated the previously lucrative Chinese trade, and profits fell. The volatility and high investments required to pursue the coastal fur trade led all parties to diversify their goods. English-speaking traders offered liquor, blankets, sugar, weapons, and cloth. The latter became popular when Natives sold traditional fur clothing off their back. As otters grew scarce, Natives offered foreigners fish, game, slaves, artwork, and (if particularly desperate) their women as prostitutes (Gibson 1992).

The decline in the sea otter trade along the coast between Russian America and New Spain allowed English-speaking traders moving overland to increase their presence on the intervening wedge of the Pacific coast. The United States gained a foothold with the Lewis and Clark Expedition reaching the mouth of the Columbia River in 1805, in an area that eventually became the Oregon Territory. Unlike the British navy, the land-based Hudson Bay Company also was keen to enter the sea otter trade. This formidable British mercantile venture played an outsized role in what would become Western Canada. Using its superior access to food from the interior plains, the Canadian company offered grain and other food to the Russians in Sitka (Gibson 1992). In the long run, this venture outlasted the Russians and Yankees along a stretch of the Pacific coast that eventually became British Columbia.

The “Boston men” established ambivalent relations with Russian America early in their history. A few of them worked for the Russians, and others befriended Baranov, providing him with rum for personal use and food for his hungry employees. Joseph O’Cain, a creative but aggressive Boston mariner, worked up and down the Pacific Coast in the early nineteenth century. In 1803, he showed up in

Kodiak and offered Baranov a deal. The Russians had skilled hunters but lacked ships to exploit distant sea otter populations, whereas the "Boston men" had a large fleet but no hunting expertise. They would hire Alaskan squads, take them to California, and split the resulting take (Ogden 1941; Wheeler 1971). This arrangement lasted for a decade, much to the distress of the California authorities. The tsar's emissary, Nikolai Rezanov, was visiting San Francisco in 1806, forging ties with Commandant José Darío Argüello and congratulating him on repulsing Yankee poachers. Unbeknownst to the two men, that same year, O'Cain's colleagues and Alaskan hunters were setting up base camps on the Channel Islands for clandestine sea otter hunting. In 1807, the joint-venture sent kayak hunting parties into San Francisco Bay under the noses of the Spaniards, who did shoot a few Alaskans. Then the Russian supervisor quarreled with the Yankee skipper, took the Alaska share of the pelts, bought his own ship, and sailed off with his men to the Hawaiian Islands (Ogden 1941). Later joint-ventures went more smoothly, but unreliable wheeling and dealing was the norm. When things went wrong, the Natives (Alaskan or Californian) usually suffered the brunt of the violence.

To make the prolonged voyages from the North Atlantic to Alaska profitable in this competitive environment, maritime trading ships adopted global itineraries with stops in milder Pacific climes. This had a profound effect on Hawaii, where foreign ships began hiring "Kanakas" (Native Hawaiians) as crew members in 1805 and increasingly shaped the economy, landscape, society, and politics of those islands (Gibson 1992). Other regions that saw increased United States activities included California, Latin America, and the Far East.

Baranov felt the Yankees were taking advantage of the Alaskans, so he sent his ship to California under his trusted assistant, Ivan Kuskov. Spanish authorities learned that kayaks were swarming the waters between San Francisco and Bodega Bays. Baranov's informants told him that the Spaniards could not project authority north of San Francisco. In 1809, Kuskov set up a camp at Bodega Bay for the Russian-American Company. To evade the Spanish, Alaskan hunters portaged kayaks more than 50 km across what is now Marin County to northern San Francisco Bay. At summer's end, they took more than 2000 pelts back to Russian America. As New Spain descended into the Mexican Revolution, its grip loosened even further (Ogden 1941). During the chaos, the California sea otter harvest peaked in 1811, with about 9000 animals taken that year (Ogden 1941).

In the spring of 1812, Kuskov and his men established a fort north of Bodega, about 100 km from San Francisco's Presidio. This became Fort Ross, the southernmost point of Russia's reach into America. Its purpose was to provide food to Russians in Alaska, barter with Californians for pelts, and serve as a base for sea otter hunting north of San Francisco Bay (with a few poaching parties farther south). Relations with the locals were complex, with a mix of hostility, accommodation, and negotiation. Spaniards continued to fight hunting parties, while local Natives such as the Pomo ended up working with the Russians. Control of the skilled Alaskan hunters perpetuated Russians' prominence in sea otter hunting far from their homelands. Yankee poachers, deprived of Alaskan hunters and distracted by the War of 1812, backed away from the fur trade for a while. The tsar's government cracked down on the interlopers in 1814, reducing the pilfered peltry to about 3000–4000 pelts annually (Gibson 1976).

10.9 The Sea Otter Fur Trade from 1820–1840

By the 1820s, sea otters were so rare in traditional hunting areas that foreign traders turned their focus elsewhere. It was a decade of turmoil and decline for the global sea otter fur trade. The valuable animals dwindled everywhere, and diverse trading factions fought for the remnants (Ogden 1941). Demand from China slackened but increased in new markets in Europe and Mexico (Ogden 1941). After the war with the British ended in 1815, Yankees flocked to the Pacific. American merchants persisted in the Pacific fur trade because the decline in available sea otters increased prices for the few pelts garnered, and their strategy of agile ships, diverse wares, and flexible itineraries gave them resilience, which the autocratic empires of Russia and Spain lacked (Gibson 1992).

The political situation on the West Coast of North America had changed. Baranov retired in 1818 and died about a year later. The naval officers who replaced him followed new rules that forbade Russian-America to trade with foreigners. Sea captains avoided the prohibition by trading ship-to-ship or by going through Fort Ross (Ogden 1941). Among the indirect beneficiaries were northern Native[6] groups who became intermediaries between interior tribes and the coastal Russian and other foreign trading posts (Gibson 1992; Znamenski 2003). In Southcentral Alaska, Dena'ina Athabaskans used trade hubs such as the Kenai Peninsula to pass beaver, fox, and other inland furs to Russian traders. Even Native communities that traditionally had not been involved in sea otter hunting were drawn into the Maritime Fur Trade. A generation after Baranov dismissed the Dena'ina "Kinai natives" for maritime ineptness, the son of a village leader became a supervisor for sea otter hunting in California, and his descendants continued this pursuit throughout the nineteenth century.[7] Tlingit and other Pacific Northwestern tribes ran out of sea otters and fostered diversified and less profitable trade in items, such as potatoes and carved artwork (Gibson 1992). This commerce strengthened their positions to negotiate with White intruders and fend off foreign control (Gibson 1992). The Russian empire classified indigenous groups as "dependent" or "independent"

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[6] Native American ethnicities divide into several major subgroups, and in the Northwest the main distinctions are made among Unangan, Eskimo peoples (which include the Sugpiat), and "Indians" (which include the far-flung Athabascan peoples and the tribes of Southeast Alaska, the Pacific Northwest, and California).

[7] Qadanalchen, son of the headman at Shk'ituk't (later called Kenai Village), went to Fort Ross to hunt sea otters, which is how the family got its surname. His great-great granddaughter, Kenai elder Mary Nissen, told the 1974 Kenai Area History Conference that her grandfather, Alexsay Kalifornsky, also hunted sea otters, and her brother, prominent Kenaitze culture-bearer Peter Kalifornsky, wrote about this (Kalifornsky 1991).

peoples. In Alaska, it classified the Unangan and Sugpiaq peoples as dependent, the Dena'ina Athabaskans as semi-dependent, and some Natives such as the Tlingit as independent (Golovin 1979).

As the Kingdom of Hawaii became an important global shipping entrepot, it suffered increasing corruption, venereal disease, saturated markets, and ecological damage. It also fell increasingly into the American sphere of influence. Kanakas could not hunt otters as well as Alaskan Natives, but their talents included boating prowess and swimming through the surf to retrieve otters killed by riflemen (Ogden 1941).

Deprivation during the Mexican War of Independence (1808–1821) made isolated California communities more desperate for trade supplies and willing to deal with outsiders. Rebellious *Californios*, losing trust in New Spain's authorities, often were happy to collaborate with American smugglers. Ogden described Yankee involvement with the sea otter trade of that time as "... the great fur game of hide-and-seek at the end of the Spanish period" (Ogden 1941, p 80). Mexico, which then included Alta California, became independent in 1821. The new nation started with a free trade policy (Ogden 1941), and cowhides and tallow replaced much of the former fur trade (Gibson 1992). Other valuable California exports were horses and coinage. Despite becoming a smaller percentage of the trade, sea otter pelts remained coveted, premium items. Traders, even those based in Hawaii, always accepted sea otter pelts (Ogden 1941).

The new acting governor of Mexican California, Luis Antonio Argüello (son of José), ended up contracting with Russians to hunt freely along the coast and split the harvest with the Mexican government. Soon, other Mexicans replaced Argüello, argued among themselves, and suspected the Russians of cheating. In 1830, a new governor banned all foreigners from hunting in California. That fall, Ferdinand von Wrangel, then governor of Russian America, sent an expedition to California specifically requesting that the fur-trade relationship be re-established. The Mexican governor refused, although he did say that Russians were "good people," unlike those from the United States (Ogden 1941, p 105).

Americans flocked to California and found creative new avenues to pursue the sea otter trade. American adventurers, including "mountain men" who trapped beaver across the western territories, migrated overland to the Pacific coast. Deserters from whaling ships also arrived. Mariners from New England saw the advantages of this situation. Seeking opportunities in a time of transition, some stayed and became citizens of Mexico. Starting in the 1820s, certain citizens could obtain permits to hunt sea otters. Interpreting rules loosely, some hired or subcontracted noncitizens, including Alaskan Natives. For a while, individual Mexicans even contracted directly with Fort Ross to hire hunters in exchange for a share of the profits. One distinction between the Mexican rules and those in Alaska was a ban on hunting pups (Ogden 1941). By the 1830s, Californians were displacing foreign workers in the sea otter fur trade. They used rifles more often than spears, which frightened sea otters away from coasts and ships. When Wrangel made another pitch to renew partnerships with Mexican authorities, they again rebuffed him.

Poachers still played a significant role. By the 1830s, they were often independent, cosmopolitan privateers who roamed the Pacific, seizing opportunities.

Captains were often, like many of the naturalized Mexicans they fought, scions of New England shipping families. Known as *contrabandistas*, they found it easier to poach sea otters than negotiate contracts, follow the rules, and share proceeds. These captains described their hunters nebulously as “Indians of the northland” (Ogden 1941, p 120). Apparently, at least some were Haida and Tlingit. Even in the 1830s, enterprising agents found large rafts of naïve sea otters, and the prices paid in Canton peaked in 1831 at $55 per pelt (Ogden 1941).

Contrabandistas enraged legal Mexican hunters. The interlopers took all the sea otters they could kill—including pups—stole other hunters’ supplies, and killed livestock on land. The local response to the long-term threat was to try to wipe out all the sea otters before the competition could. In 1836, a group of *contrabandistas* and a California hunting squad had a gun battle on Santa Rosa Island that left four Northwestern Native men dead (Woodward 1938). Two years later, that same *contrabandista* captain died when his crew of Native hunters mutinied. That era’s violence destroyed the traditional culture of the indigenous people of the Channel Islands, who were forced to evacuate to the mainland in 1835[8] (Woodward 1938). By about 1840, dwindling prey and the poor reputation of big-boat poachers led to the end of this reign of terror (Ogden 1941).

On another front, the Russians sparred with the Hudson Bay Company over control of the transboundary Stikine River in Southeast Alaska. The Tlingit leveraged the situation to increase their control of the area’s fur trade, including the meager remains of the sea otter resources. As part of the diplomatic settlement between the Russians and the British in what became Canada, the Hudson Bay Company agreed to provide foodstuffs to Sitka from the Willamette Valley, which it controlled at the time (Gibson 1992). This alternative supply source, combined with Mexican government hostility and the decline in sea otter numbers, were factors in the Russian decision to shut down Fort Ross in 1841 and abandon claims to American lands south of 55° N latitude (Ogden 1941).

Californians continued pursuing the small groups of surviving sea otters up until the gold rush in 1848 gave them more lucrative adventures. In its late phase, the regional hunt concentrated in southern California between Monterey and Santa Barbara and among the Channel Islands. Another lucrative site was Cedros Island. By the 1840s, hunters located only scattered animals, and the returns became too small for a viable business. Hunts were suspended during the Mexican-American War (1846–1848), but by the end of 1848, with the United States now in control of California, rumors of gold began circulating. Hunters repurposed their boats and camping gear to travel up rivers into the foothills, launching a new boom in mining (Ogden 1941). Ogden makes the case that the sea otter trade lured Americans to California, and thus it was a factor that tipped the region’s control from Spanish to

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[8] One young woman was left behind during the evacuation and lived alone on San Nicholas Island for nearly 18 years before being rediscovered. Her life was fictionalized in an award-winning 1960 novel for young readers, *Island of the Blue Dolphin*, by Scott O’Dell.

English-speaking dominance. Yet by the time the United States annexed California, the sea otter fur trade was essentially over, save an occasional serendipitous kill.

10.10 Purchase of Alaska by the United States and Renewed Sea Otter Hunting

By the mid-nineteenth century, sea otters had vanished from much of their former range, and authorities with the Russian-American Company and its colony knew the resource could no longer cover expenses. Company historian Petr Aleksandrovich Tikhmenev (1978) wrote about the 1830s, although his report was not published until 1861:

> Although there had been no appreciable decline in the export of sea otters from the colonies, because the hunters had moved successively from place to place over a line of outposts along the entire Pacific Coast of the Russian possessions, it could be assumed that the otters would shortly become extinct or at least considerably diminished. The measures of the colonial administration to prevent the natives from destroying these animals indiscriminately, such as refusing to barter for pelts taken too young, and strict sorting of furs, did not always solve the problems. The obvious decrease in the otter catch of the Kurile Islands forced the company to seek new sources of supply (Tikhmenev 1978, p 206)

The Russians strove to diversify the colony's economy. Expeditions inventoried mineral resources such as coal and gold, and they opened new posts to exploit areas without sea otters, such as Bristol Bay at the mouth of the Nushagak River in 1818 and farther north at Russian Mission and Nulato, founded in 1837 and 1838, respectively (Bundtzen 2018).

From the beginning of the Russian hegemony, a few sporadic efforts were made to "rest" individual sea otter stocks. After debate, denial, and the collapse of the California hunt, the Russian-American Company began conservation measures to preserve the remnants of North America's sea otters, ramping up its efforts starting in the 1840s (Jones 2014). It imposed rotating hunting moratoria in depleted areas, banning hunting for four years to allow the animals to repopulate. Soviet historian Svetlana Fedorova described the results as successful, but Jones called the policy a failure caused by poaching, lax enforcement, and rest periods too short to address the animals' slow reproduction rate (Fedorova 1973; Jones 2014). Still, the measures did temper the species' decline.

Combined with the low sea otter numbers, conservation measures further diminished the fur trade profitability. Buyers sought alternatives. Effort shifted from sea otters to fur seals and land-based furbearing animals. Fashion also shifted to beaver hats and coats lined with shearling lamb. Russia finally decided to sell Alaska for many reasons, but the collapse of the sea otter fur trade was a major factor. No other product from Alaska at the time generated the excitement and revenue to match it. When the United States purchased Alaska in 1867, sea otters were listed among its attractive resources. Senator Charles Sumner, who lobbied Congress to approve the purchase, rhapsodized about the animals' "exquisite purple-black fur" and described the previous fur rush as a "fury" (Sumner 1867).

When Russian administrators left Alaska, they took with them any pretense of sea otter conservation. What followed was a free-for-all, as American entrepreneurs hiked up demand for the rare furs. Yankee adventurers, former poachers, and coastal Natives, whose families earlier hunted the animals for the Russian-American Company, set out to find the last sea otters and kill them. Prices increased, and sea otter numbers cratered. In some ways, the sea otter trade in the late nineteenth century resembled the African elephant ivory trade at the end of the twentieth century. Spiraling profits and lack of economic alternatives pushed coastal villagers to continue a hunt against their own long-term interests. Historian Sonya Luehrmann, focusing on Kodiak, noted that for many Sugpiaq men, catching sea otters was their only marketable skill in the growing cash economy:

> . . . [T]he steady decline of the sea otters made it increasingly difficult for hunters to earn their living except by incurring ever greater debts, changing their position from one of skilled, sought-after laborers to dependents of companies that were already looking for alternatives to a business that was doomed to end soon (Luehrmann 2008, p 102).

In British Columbia, Washington, Oregon, and California through the late nineteenth century, the diminished hunt remained a rare pursuit for the dogged few who might be lucky to kill enough valuable animals to justify the effort. Scammon listed California's islands, Oregon's Cape Blanco, Washington's Point Grenville, and Gray's Harbor as the active American sea otter hunting locations of his time (Scammon 1874). He described hunting parties rowing out along the wild coasts with rifles and open boats, mimicking the Alaskan native approach of trying to encircle rafts of otters, and tire the quarry by preventing them from surfacing long enough to breathe between dives. Other riflemen built towers on the shore from which to shoot sea otters in the surf (Scammon 1874; Ravalli 2018). Scammon estimated that only half the animals shot from shore were retrieved.

In the nineteenth century, poachers from Britain and later the United States were active intermittently in the Kuril Islands. After the United States purchased Alaska, international whaling decreased, other sea otter populations declined, and Yankee ships returned to the Kuril Islands (Ravalli 2018). Scattered sea otter populations remained, protected by dense fog and the archipelago's remoteness. Over the years, ships from many nations pursued sea otters there, and catch levels are unknown. Scammon reported that at least 1000 sea otter pelts came from the Kuril Islands in the decade after Alaska was purchased (Scammon 1874). Small-scale, sporadic hunting continued in the Kuril Islands until 1945 (Nichol 2015).

In the 1880s, when United States entrepreneurs opened canneries, mines, and tourist ventures in Alaska, job options diversified. The loss of wild furbearers contributed to the rise of fox farming (Luehrmann 2008). In remote areas such as the roadless islands and coastal villages, job opportunities remained sparse. Natives succumbed to epidemics, abandoned many remote settlements, and congregated in towns such as Dutch Harbor, Kodiak, Kenai, and Sitka. Competition among trading companies led to erratic prices for sea otter pelts. For example, when two posts competed for pelts in Seldovia (a coastal village near the tip of the Kenai Peninsula), they bid up the price to $112 per pelt. When its competitor folded in 1883, the Alaska Commercial Company (ACC) used its monopoly status to cut pay to $35 per pelt (Jacobsen 1977).

Records from the ACC trading post manager and a Russian Orthodox priest working in Seldovia describe the decline. Sea otter furs were a critical source of income for the area's Sugpiaq men. In 1896, the villagers celebrated killing 50 sea otters. In 1897, the manager paid $125 for a single sea otter pelt, when foxes and lynx were worth a dollar each and martens and wolverines $1.50. In 1898, the area's hunters killed six sea otters. The following year they killed none, and in 1900 the rumor of one sea otter spotted at a remote island "… prompted a response of eight bidarkis rushing to the scene, but all for naught" (Springer 1997, p 101). The following year, the priest encountered dejected Seldovia hunters paddling around vainly searching another former hunting area (Znamenski 2003).

Kenyon (1969) reviewed the literature, interviewed coastal hunters, and did his own fieldwork to estimate when sea otters disappeared. He suggested the following dates: Oregon 1906; Washington 1910; Mexico 1919; and British Columbia 1920s. Other evidence suggested that the last verified Canadian sea otter kill of the era was on Vancouver Island in 1931 (Nichol 2015). The pending extinction of sea otters, a valuable asset, raised concerns at a time when the mood in the United States shifted from unrestrained exploitation of resources to conservation and resource management (Nash 2001). Biologists estimate that the world sea otter population decreased to ~2000 animals, hanging on in small, inbred groups hidden in scattered sites, mainly in the Aleutian Islands (Kenyon 1969). Some survived in the Kuril Islands, in Prince William Sound, along a swathe from Kodiak to the outer Kenai coast, in Haida Gwaii (the Canadian archipelago formerly known as the Queen Charlotte Islands), and in California's rugged Big Sur coast. They found refuge on exposed coasts that offered few if any anchorages and where offshore reefs made hunting hazardous (Kenyon 1969).

The turning point came in 1911 with the adoption of the world's first international wildlife conservation treaty. Russia, Japan, Britain, and the United States signed the North Pacific Fur Seal Treaty. The fur seal pelt trade had become a big business, but also a scandal of wasteful mismanagement. Sea otters were so rare as to be economically trivial, but negotiators decided to include them in the treaty (Ravalli 2009). However, as the treaty only applied to international waters (where sea otters do not live), legal hunts continued in several areas, and the end of the hunt had more to do with the lack of animals than the letter of the law (Van Blaricom 2015). In 1913, Congress designated a wildlife sanctuary in the Aleutian Islands, with sea otter preservation a priority (Lensink 1962; Van Blaricom 2015). Eventually, it became part of the Alaska Maritime National Wildlife Refuge.

10.11 Effects on Sea Otter Populations

Natives and Far Eastern merchants (beginning as early as the fifteenth century), harvested sea otters for their fur before the Maritime Fur Trade began to diminish sea otter populations in the mid-eighteenth century (Ravalli 2018). Estimates of the pre-exploitation sea otter population range from 150,000–300,000 animals (Bodkin 2015). Merchant records suggest that the maximum annual take peaked out at 10,000–30,000 from 1784 (the year Shelikhov arrived in Kodiak) to 1811. After the War of 1812 sidelined Yankee poachers, Russian authorities limited hunting in waters under their jurisdiction because declining sea otter populations undermined profits (Ravalli 2015). The sheer number killed during the peak of the fur rush damaged the population, but even more unsustainable was the spatial distribution of the harvest. Because population biology was not understood and because of the practical difficulties of travel to such remote and inhospitable shores, hunters sequentially obliterated localized subpopulations. A hunting squad would camp on an island and spend a season until they killed almost every sea otter. This led to a destructive pattern of serial depletion, making recovery slow or impossible (Jones 2014).

Cosmopolitan naturalists such as Martin Sauer and Carl Heinrich Merck, who accompanied the 1790s Billings expedition, raised concerns even before 1800 that overhunting was decimating both sea otters and Russian-American Company profitability (Jones 2014). But men pursuing the animals and the profits they generated found it convenient to deny the population effects and believed that the crafty animals fled east and south to avoid the hunters (Jones 2014). By the mid-nineteenth century, Russia's colonial authorities were seriously concerned that sea otters would become extinct (Jones 2014). In hindsight, and with enhanced knowledge of population dynamics, modern analysts believe that if the sea otter hunts had been managed to spare breeding females and to spread the pressure widely, the same number of cumulative pelts could have been taken in a sustainable manner (Lensink 1962; Jones 2014).

Sea otter behavior makes them particularly vulnerable to hunting. They had no innate fear of humans, and they would sometimes approach vessels out of curiosity (Steller 1988). When on land, they were slow and ungainly. Living in nearshore waters, they did not cross deep seas to flee attackers or recolonize available habitat (Jones 2014). The animals reproduce slowly, and because hunters killed females and pups as well as males, populations did not recover. Even if hunting parties left a few animals, those remnants still faced local subsistence users, poachers, and non-human predators.

Despite their vulnerabilities, sea otters were not entirely defenseless. Some learned how to evade hunters. Echoing Lisianski's observations, California sources included anecdotes of the animals' efforts to stay alive, as paraphrased by Ogden (1941, p 9):

> The otter is noted for its cunning when being hunted. A favorite trick is that of diving in the opposite direction to that from which it is being chased, thus passing under the hunters' boat

Table 10.1 Estimated sea otter harvest during the Maritime Fur Trade (1742–1911)

	1742–1798 Early Russian	1799–1867 Russian-American Co.	Subtotal: Russian Colonial Era	1868–1911 Early US	Total: 1742–1911
Alaska/Russian America	180,000[a]	124,209[b]	264,800[c]	107,372[c]	359,375[d]
Pacific Northwest		158,070[e]			
California			49,969[f]		
All North America			~700,000[c]	158,070[e]	500,000[d] ~900,000[c]

Original data came from vessel manifests and reports by the Russian-American Company, other colonial authorities (Tikhmenev 1978), and reports of the U.S. Bureau of Fisheries. Gibson (1992) and several works by Adele Ogden listed vessel data in appendices. Lensink (1962) and Kenyon (1969) performed the meta-analyses from available sources. Jones (2014) and Ravalli (2018) reexamined and commented on the extant data

[a] Jones (2014)
[b] Tikhmenev (1978)
[c] Lensink (1962)
[d] Kenyon (1969)
[e] Gibson (1992)
[f] Ravalli (2018)

> and coming up behind. Apparently realizing that boats travel more slowly against the wind, the otter often swims to the windward. Sometimes it will try to find a tide rip or, if near the shore, the animal has been known to make straight for the breakers among jagged rocks. It also hides behind rocks. A very common trick is to make a series of short dives followed by a very long one, when the boats are quite close, which takes the animal completely out of range.

After reviewing historical records, Lensink (1962) concluded that the total commercial harvest during the Russian and United States trade (1742–1911) was nearly one million sea otters (Table 10.1). In contrast, Kenyon (1969) estimated half of that number.

The fur trade damaged the populations of other species. The Maritime Fur Trade caused the extinction of Steller's sea cow and led to an aggressive and wasteful hunt of fur seals. When sea otters became scarce, fur seals became alternative targets, and in 1786 the Russians discovered their last breeding refuge on the Pribilof Islands in the Bering Sea (Jones 2014). Other ripple effects included ecological changes to the nearshore community structure as humans abruptly removed sea otters as predators of sea urchins, which resulted in a trophic cascade affecting nearshore community structure (Kenyon 1969; Estes and Palmisano 1974; Simenstad et al. 1978; Estes and Duggins 1995; Estes 2015).

10.12 Effects on Native Hunters

The major role of epidemic diseases in decimating Alaskans is indirectly linked to the hunt for sea otters, but the fur trade had other direct and damaging effects. As sea otters declined, so did Alaska's Native populations in areas of Russian activity. As mentioned previously, the first Russian invasion of the Aleutian Islands was inexcusably violent. But the later, more peaceful period of organized hunting expeditions also took a heavy toll. Erratic Russian census records estimate that the most severely affected human population was in the Aleutian Islands, which numbered 8000–20,000 at the time of Bering's expedition in 1741. By 1800, it had decreased to about 2000 (Reedy-Maschner 2010). The second-most affected Natives were the Sugpiat in Kodiak, with an estimated population of 57,000 in 1792 but only 1500 in 1834 (Gibson 1987a).

One big problem was the removal of the hunters, who provided essential meat for their extended families, from villages for months and even years during risky hunting expeditions (Black 2004). Starting in 1799, the Russian-American Company conscripted all Aleut men 18–50 years of age to work for the company (Gibson 1987a). They could drown, get sick or injured, encounter aggressive bears, or run out of food and fresh water while hunting. Storms were particularly hazardous (Luehrmann 2008). More unanticipated threats lay in wait. In 1800, more than 100 hunters perished together in Southeast Alaska when Unangan and Sugpiaq men, more than 1000 km from home, gathered mussels on a low tide. They succumbed to paralytic shellfish poisoning. The catastrophe's site became known as Peril Strait (Baranov 1800).

The otter hunters dreaded the Tlingit. Before European intervention, warriors from Southeast Alaska were expanding their influence. Tlingit raiders pressured the Eyak of the Copper River Delta, harried the Chugach of Prince William Sound, and enslaved those they captured. Baranov frequently wrote of trouble with the Tlingit. When they destroyed his first post at Sitka in 1802, many casualties on the Russian side were Sugpiaq and Unangan workers (Black 2004). Long-distance sea otter hunts were so hard on Native men that the Russian-American Company faced workforce shortages (Black 2004). Old census records showed that the loss of men resulted in a preponderance of women in the Aleutian Islands (Reedy-Maschner 2010). Colonial authorities noted the falling population with alarm. In 1795, Baranov wrote:

> Imagine the poor natives making this journey both ways, 2,000 versts[9] in narrow baidarkas without sails—using only paddles. They have to endure hunger on the way and often perish in stormy seas because this coast offers no adequate shelter. In places where the natives are not subjugated, they are always in constant danger of attack by the bloodthirsty inhabitants of these regions. It is under these conditions that they have to hunt sea otters. . . . (Baranov 1795)

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[9] The verst is an old Russian distance measure, equivalent to 1.067 km.

The Russian-American Company started sending sailing ships along with hunting flotillas to assist. Native hunters could stack kayaks on the mother ship and travel in relative safety while traversing long distances with wind power rather than the toil of their own paddling (Luehrmann 2008). But that alleviated only a portion of the trade's hardships.

10.13 Effects on Natives Left Behind

The relentless fur trade harmed other Alaskans who were not hunters, especially in coastal communities. Starvation was always a possibility because able-bodied hunters were no longer available to capture large marine mammals. Women, children, and older men left behind struggled to catch fish, pick herbs and berries, and collect eggs from seabird rookeries in the spring (Black 1988). Forced to give all sea otter pelts to the Russians, some experienced hypothermia during cold weather and resorted to wearing grass garments and bird skins (Merck, cited in Jones 2014).

Native women lived at the mercy of Russian men, facing depredations and temptations in the absence of their menfolk. Nearly all the invaders were working-age males. They turned to Native women to cure their lusts and loneliness and do essential tasks, such as making clothing and preparing food (Gibson 1987a). Another factor breaking up families was the policy of taking Native hostages, often children, to assure compliance of adult men (Liapunova 1987). Sometimes children were sent as far away as Russia, but if they survived, they could attain education in Russian schools and prestige as translators or other professionals (Black 2004).

Native oral histories and early colonial correspondence speak of rape and child abuse.[10] For example, traders from the Lebedev-Lastochkin Company, based at what is now Kenai's Old Town, kidnapped Native women (Kolomin 1791, p 41). When Vancouver visited Kenai in 1794, he referred to small buildings inside the palisades of the Russian fort for Natives, who "... were the companions, or the immediate attendants on the Russians composing the establishment" (Vancouver 1798). Missionaries, who arrived that same year, railed against fornication (Ioasaph 1795). As Russian Orthodox Church influence increased in the colony, many couples asked priests to marry them. As conquest evolved into coexistence, relations between Russian men and Native women ran the gamut from violent exploitation through prostitution to strong marital bonds. By the mid-nineteenth century, families of mixed race and ethnicity were common (Gibson 1987a). Russian dependence on Natives of both sexes and the colony's social and economic situations led to a diaspora. Russians transported women and sea otter hunters to other places leading to the mixing of cultures and bloodlines throughout Alaska and other hunting areas (Black 2004).

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[10] Modern anthropologists such as Sven Haakanson and Alan Boraas have spoken publicly about these unpleasant topics.

10.14 Effects on Colonial Russians

The Russians in Alaska also had a challenging time hunting sea otters. Natives did most of the physical work, but Russian hunters experienced similar dangers and privations. In the early years, they also faced scurvy, Native attacks, and Russian ships with a tendency to sink. Pay was poor, and Alaska's realities dashed their hopes of rapid and profitable returns. Relying on the Russian-American Company for supplies, tools, and housing, many ended up in debt peonage, effectively serfs to the company. Their unhappiness is documented in mutinies and high death rates (Black 2004).

Establishing permanent settlements on the American coast forced the Russians and the Natives they employed to live together and become interdependent. However, the Natives, who vastly outnumbered Russians and were vital to acquiring sea otter pelts, food, women, or a safe night's sleep, were critical for profitability (Gibson 1987a). Because of chronic shortages of supplies from Mother Russia, colonial workers often adopted indigenous lifestyles (Crowell 1997). Nikolai Rezanov, who toured Alaska in 1805 and wrote extensively about it, faulted the burghers of Russia's cities for profiting from the abusive trade:

> Now I will speak of the garrison. The lovers of pelts at Irkutsk will say of course: 'What for? Why such fantasies?' I will answer them that they must be very poor indeed if only the count of sea otters interests them, but not the destinies of the people involved. If somebody would count for them what these sea otters cost in human lives, perhaps then they would push their caps made of these same sea otters lower on their brows to hide their faces in shame (Rezanov 1805, p 161).

10.15 The Economics of the Maritime Sea Otter Trade

The sea otter trade was Alaska's first entry into the globalizing economy, its first boom-bust cycle, and a clear example of unsustainable resource exploitation. Indirectly, the trade also increased the presence of Russia, Britain, and the United States in the Pacific, which went beyond commerce to include political intrigues involving Hawaii, Latin America, the Philippines, China, and Japan. At its peak around 1800, the Russians shipped about 15,000 sea otter pelts per year to China. At the same time, British and American poachers were shipping a roughly equivalent number to Canton from the waters off California, the Pacific Northwest, and Southeast Alaska. Because of fluctuating exchange rates, inadequate records, and changing prices, we cannot put a modern value on the fur trade, but profits garnered global attention and spurred increased Russian investment in Alaska. The primary commodity purchased from China in exchange for sea otter pelts was tea (Fedorova 1973).

Likewise, we cannot tally how many otters were harvested for their fur. Many records hide intentional and accidental misreporting; they omit counts from Japan, the Russian Far East, poachers, ephemeral merchant companies, or trade among Natives. Also missing are counts of abandoned carcasses, stolen goods, spoiled hides, and the cargoes of sunken ships. After reviewing the literature, Lensink (1962) estimated that almost a million animals may have been harvested during the fur-trading era from 1742 to 1911. Others have come up with smaller counts, but the tally was likely in the hundreds of thousands (Table 10.1).

As early as 1793, Baranov observed that sea otters in Cook Inlet were disappearing. He wrote, "The number of sea otters taken in the [inlet] had been decreasing every year," noting that earlier hunting parties took one or two thousand in a season, but after much effort, barely caught 400 that year (Baranov quoted in Tikhmenev 1979). He then took his hunters to Prince William Sound instead, but soon otters there declined as well. By the time the Russian-American Company incorporated in 1799, Baranov knew that he needed to shift operations east to unexploited areas to make it profitable. That was a major reason the Russians reduced efforts in other parts of Alaska and established their capital in Sitka. The drive east put Russian America into increasing contact with other nations but exacerbated problems such as restive Natives and poor agricultural prospects that undermined the colony in the long run.

Despite the move, the sea otter population declines continued. With their primary income source dwindling, the colonial authorities sought to diversify the economy. Other furs, however, faced steep competition from Canada, Europe, and even Russia, while they lost ground to changing fashions. Other products such as ice and coal failed to gain adequate markets. The Russian-American Company became a money-losing operation in the early nineteenth century.

Fur, the economic basis of Russian culture, was the only economy in Russian America. Even Siberia was diversifying into agriculture and mining, but the American colony lacked the access and capital to develop alternatives. Based on records from the 1830s, Gibson (1987b, p 35) noted that about 90% of the Russian men in Alaska worked in the fur business. "Little wonder that when the fur trade ended, so did Russian America. Its monolithic economy was simply too vulnerable," Gibson wrote. Russia's loss was America's gain. The Yankees had stolen profitable sea otter pelts from the Russian territory, and they continued to profit from the animals even as they destroyed the trade and nearly exterminated the species. Lensink (1962) pointed out that when poorly documented poaching is included, the Americans probably harvested more sea otters than the Russians. Between the purchase of Alaska in 1867 and the formal end of the hunt in 1911, the value of pelts harvested from Alaskan waters exceeded the price paid for the territory itself.

10.16 Lessons from the Sea Otter Fur Trade

Sea otters have attracted human interest over thousands of years. Chinese demand for their pelts drew Europeans and Siberians into the uncharted North Pacific Ocean in the eighteenth century. During the following 170-year rush for "soft gold," the combination of indigenous Unangan (Aleut) maritime hunting prowess and the enormous market demand (emanating from China and Europe) proved lethal for most sea otters. Russian and then Yankee fur traders nearly extirpated the animals. Their near extinction by 1900 transformed both indigenous human societies and coastal environments. The socioeconomic impacts of the ephemeral boom influenced economic and geopolitical expansion throughout the North Pacific region, including Japan, Russia, Canada, the United States, and Mexico.

Shifting public attitudes, economic realities, and international cooperation finally gave sea otters enough protection to end the carnage and population decline. The sea otter population has recovered to ~150,000, reoccupied parts of its historical habitat, and restored the nearshore ecosystem, although full re-occupation is decades away (Davis et al. 2019). Sea otters became one of conservation's greatest success stories, yet they were not fated to live in peace with their human neighbors. In peculiar twists of fate, the Cold War (with nuclear bomb tests on Amchitka Island in the Aleutians) and Alaska's subsequent rush for crude oil (e.g., the *Exxon Valdez* oil spill) each proved catastrophic for local sea otter populations, although not on the scale and scope of 170 years of relentless hunting. Despite the epic recovery from the brink of extinction only 100 years ago, the future of sea otters is not assured, and humans remain critical to their survival.

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Part II
Ethology and Behavioral Ecology of Polar Bears

Chapter 11
Polar Bear Taxonomy and Evolution

James A. Cahill

Abstract Polar bears are members of the family Ursidae and are closely related to brown bears. 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 genetic basis of these adaptations remains poorly understood, but several genes have been identified that may have facilitated the dietary transition. Despite their dramatically different ecological niches, hybridization between polar and brown bears is common. However, it has not affected polar bear diversity because gene flow has been exclusively from polar bears into brown bears (i.e., unidirectional introgression). Despite low genetic diversity, polar bear abundance is not at risk from inbreeding depression based on their long history of stable population size. Polar bear subpopulations are divided into management groups that roughly correspond to a combination of ecologic, genetic, and national boundaries, but some biological population structure is present.

Keywords Brown bear · Diversity · DNA · Genetic diversity · Genomics · Hybridization · Polar bear · Taxonomy · Ursidae

Polar bears (*Ursus maritimus* Phipps 1774) have adapted to the Arctic marine environment since they diverged from brown bears (*Ursus arctos*) ~400 Kya (Box 11.1; see Chap. 12). During the past 20 years, and especially since the sequencing of the polar bear genome in 2011, our understanding of polar bear evolution and taxonomy has greatly improved. In this chapter, I provide an overview of polar bear taxonomy and evolution, genetic diversity, historical distribution, population status, and genetic evidence of positive selection for the sea ice habitat and a carnivorous diet.

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Box 11.1: Original Scientific Description Found in great numbers on the main land of Spitsbergen; as also on the islands and ice fields adjacent. We killed several with our musquets (sic), and the seamen ate of their flesh, though exceeding coarse. This animal is much larger than the black bear; the dimensions of one were as follows:

Length from the snout to the tail, 7′ 1"
Length from the snout to the shoulder-bone, 2′ 3"
Height at the shoulder, 4′ 3"
Circumference near the fore legs, 7′ 0"
Circumference of the neck close to the ear, 2′ 1"
Breadth of the fore paw, 0′ 7"
Weight of the carcass without head, skin or entrails, 610 lb.
—Constantine John Phipps (1774)

11.1 Taxonomy

Polar bears (Order Carnivora; Suborder Caniformia) are one of eight extant members of the family Ursidae, which are most closely related to other Arctoid carnivores, such Pinnipedia (seals, sea lions, fur seals, and walruses; Davis 2019) and Canidae (dog-like carnivorans). These three groups diverged relatively quickly, making phylogenetic inference of their branching order a challenge. As a result, phylogenies generated from different genes lead to different conclusions (Bininda-Emonds et al. 1999; Delisle and Strobeck 2005; Flynn et al. 2005; Fulton and Strobeck 2006; Agnarsson et al. 2010; Eizirik et al. 2010; Nyakatura and Bininda-Emonds 2012). However, multiple gene phylogenies have led to a consensus that Ursidae was the first lineage to diverge (Fig. 11.1; Nyakatura and Bininda-Emonds 2012).

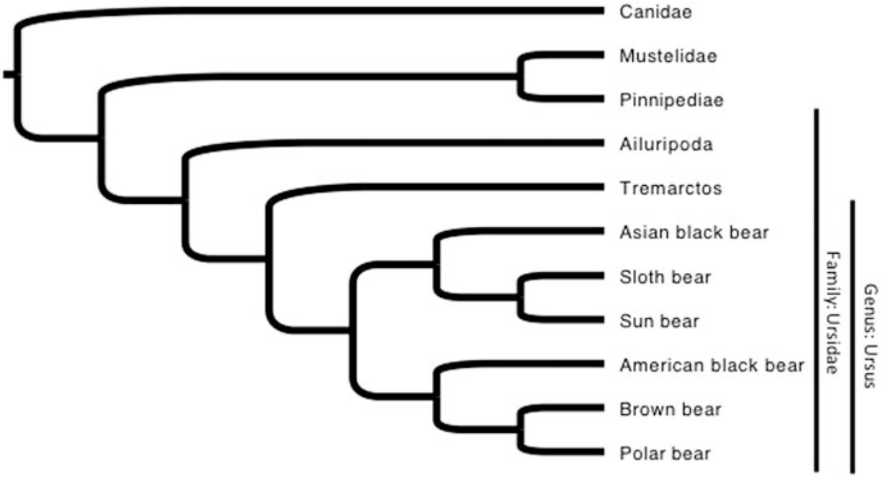

Fig. 11.1 The taxonomic relationship of the polar bear to other carnivorans (Delisle and Strobeck 2005; Nyakatura and Bininda-Emonds 2012; Kumar et al. 2017)

Within the Ursidae there are three extant genera: *Ailuropoda*, *Tremarctos*, and *Ursus.* Six of the species, including polar bears, belong to the genus *Ursus,* while the remaining genera contain one extant species each. The ancestors of giant pandas (*Ailuropoda melanoleuca*) were the first lineage to diverge 24.8–14.4 Mya (Talbot and Shields 1996; Waits et al. 1998; Yu et al. 2004; Fulton and Strobeck 2006; Krause et al. 2008). Lineages leading to the genera *Tremarctos* and *Ursus*, which came from Eurasia across the Bering Land Bridge, diverged 13.0–6.7 Mya (Figueirido and Soibelzon 2010; Kumar et al. 2017). Tremarctine bears (e.g., spectacled bear [*Tremarctos ornatus*]) were the first Ursidae to occur in the Western Hemispheric fossil record, initially in North America and later in South America. It is likely that the divergence of Tremarctine and Ursine bears coincided with the ancestors of Tremarctine bears migrating to South America during the Great American Biotic Interchange (GABI), which followed the joining of North and South America (Figueirido and Soibelzon 2010).

Genomic evidence suggests that all members of the genus *Ursus* shared a common ancestor 6.0–4.5 Mya (Kumar et al. 2017). Interspecies hybridization was common during the early phase of diversification, and this, combined with the relatively rapid diversification of Ursine bears, makes the branching order within *Ursus* difficult to ascertain (Kumar et al. 2017). However, polar bears and brown bears have been identified as close relatives in a range of studies (Goldman et al. 1989; Delisle and Strobeck 2005; Krause et al. 2008; Kumar et al. 2017).

11.2 Polar Bear and Brown Bear Pre-genetic and Genetic Studies

The evolutionary relationship of polar bears and brown bears has been the subject of substantial debate, with various studies leading to differing interpretations. Genetic and genomic data have given us a better understanding of polar bear evolution, which differs from earlier taxonomic studies.

11.2.1 Pre-genetic Studies

In 1968, Bjorn Kurtén produced an early but influential description of polar bear evolution. Kurtén proposed that brown bears were the nearest relatives of polar bears, which originated from a population of brown bear-like ancestors. He hypothesized that these bears became isolated in northern Russia and adapted to the Arctic sea ice habitat (Kurtén 1964). This hypothesis has been validated by genetic and paleontological studies. The specific details of Kurtén's hypothesis, such as the location of the initial sea ice adapted population, are difficult to substantiate, but polar bears and brown bears are closely related genetically. Although both species are found in Eurasia and North America, their migration into North America is more recent than their divergence (Barnes et al. 2002).

11.2.2 Genetic Studies

Early genetic analysis of bears, which was based on allozymes, mitochondrial restriction enzyme fragment length polymorphism, and cytochrome b sequencing, showed that polar bears and brown bears are closely related (Goldman et al. 1989; Shields and Kocher 1991; Wayne et al. 1991). Partial mitochondrial DNA sequencing for each species revealed that polar bear mitochondrial haplotypes fell within the diversity of North American brown bears (Cronin et al. 1991). All polar bears form one mitochondrial clade, but brown bears from Admiralty, Baranof, and Chichagof (ABC) Islands in Alaska possess mitochondrial haplotypes more closely related to polar bears than to other brown bears (Cronin et al. 1991; Talbot and Shields 1996; Waits et al. 1998). Brown bear mitochondrial studies have established a shared nomenclature of numbered clades, and in this widely used system, polar bears and ABC Islands brown bears are classified as members of clade II (Fig. 11.2).

Microsatellite analysis for both species provided additional insight into their biogeography, including identification of separate management units for polar bears (Paetkau et al. 1999). In contrast to the mitochondrial DNA studies, microsatellite studies of brown bears from the ABC Islands were so similar to mainland Alaskan brown bears that they are mitochondrially divergent from polar bears (Paetkau et al. 1998). This may have resulted from male-mediated gene flow between the ABC Islands and the mainland, which caused nuclear/mitochondrial discordance (Paetkau et al. 1998). However, the paraphyly (i.e., grouping species based on the last common ancestor) of brown bears remains prominent. Nuclear genetic studies gave a different picture, indicating a larger divergence between polar bears and brown bears (Yu et al. 2004). However, as these studies sought primarily to establish the species-level phylogeny of all bears, they lacked sufficient sample size to confirm or reject the hypothesis that polar bears fall within the diversity of brown bears.

11.2.3 Ancient DNA

The introduction of ancient DNA into polar bear and brown bear phylogenetics was a milestone because it enabled the study of population variability over time. An early study of mitochondrial DNA from Beringian brown bears (to the limit of radiocarbon dating ~60 Kya) found substantial turnover in mitochondrial haplotypes. Perhaps most relevant to polar bears, these studies identified a now-extinct group of brown bears, which had polar bear-like mitochondrial haplotypes similar to brown bears from the ABC Island (Barnes et al. 2002).

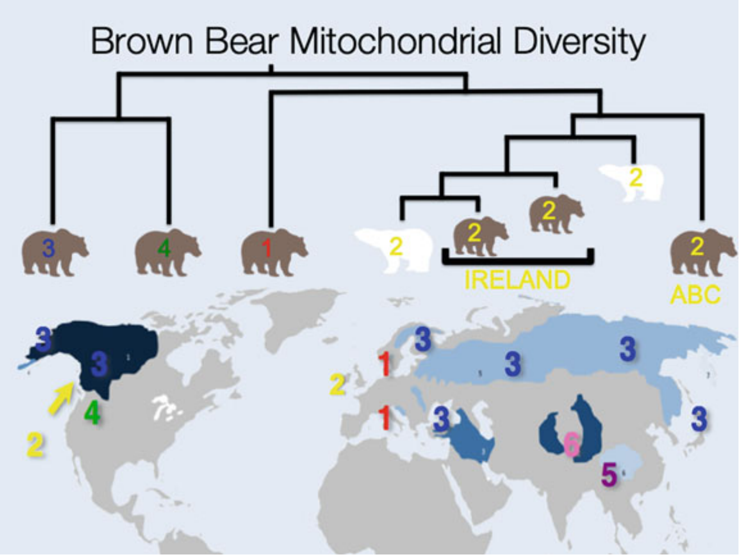

Fig. 11.2 Geographic distribution of brown bear mitochondrial genomes. Polar bears, along with Admiralty, Baranof, and Chichagof (ABC) Islands brown bears and some extinct Irish brown bears, make up clade II

However, in 2010 the full mitochondrial genome was sequenced from the mandible of a polar bear, which had lived 130–110 Kya in Svalbard, Norway (hereafter referred to as the Svalbard mandible) (Lindqvist et al. 2010). This mandible has a derived morphology similar to that in modern polar bears (Ingólfsson and Wiig 2009). Intriguingly, while the Svalbard mandible's mitochondrial DNA was more closely related to that of extant polar bears than to brown bears (including those from ABC Islands), the Svalbard individual was an outgroup to all extant polar bears (Lindqvist et al. 2010), which suggests that the animal had lived very close to the origin of polar bears.

Shortly after the Svalbard mandible's mitochondrial genome was published, another study of ancient brown bears further complicated the mitochondrial story. Analyses of several Irish brown bears from the Pleistocene and early Holocene (55–5 Kya) revealed that some (but not all) Irish brown bears had clade II mitochondrial haplotypes that fell between those of the Svalbard mandible and those of modern polar bears (Edwards et al. 2011). Isotopic analysis confirmed that these bears had a terrestrial diet, meaning that they were not simply misclassified polar bear remains (Edwards et al. 2011). This analysis indicated that polar bears and brown bears were mitochondrially paraphyletic, and it raised the issue of hybridization between the species (Fig. 11.1). It also showed that mitochondrial DNA alone was insufficient to determine when polar bears and brown bears diverged (Fig. 11.2).

11.2.4 Current Hypotheses

The number of genetic samples and their geographic and temporal diversity has gradually increased for polar bears. Prior to 2012, studies remained largely restricted to either a single locus, usually from mitochondrial DNA, or a small number of loci of rapidly evolving microsatellites. An important transitional study from single locus mitochondrial studies to nuclear genomic studies sequenced 14 nuclear loci in polar bears and brown bears in 2012 (Hailer et al. 2012). Contrary to results from the mitochondrial DNA, this and subsequent genomic studies confirm that polar and brown bears form distinct clades, with the most recent common ancestor (TMRCA) dating from 479–343 Kya, most likely in Eurasia (Hailer et al. 2012; Cahill et al. 2013; Liu et al. 2014). Polar bear-like mitochondrial DNA in brown bears appears to be the product of polar bear introgression (i.e., hybridization with repeated backcrossing; Cahill et al. 2013).

11.3 Polar Bear Diversity

Diversity within and among populations can play an important role in species management and long-term viability. Typically, polar bears are divided into 19 subpopulations, or management units, within their entire range (Paetkau et al. 1999; Schliebe et al. 2008; see Chap. 17). Despite relatively large natal dispersal distances (e.g., 93 km for females and 52 km for males in the Barents Sea subpopulation), these subpopulations are genetically distinguishable (Paetkau et al. 1999; Zeyl et al. 2009; Peacock et al. 2015). Clustering analyses using microsatellites from more than 2000 individuals representing 18 of the 19 subpopulations indicate that the management units could be grouped into three major clusters comprising the polar basin (subpopulations directly bordering the Arctic sea), the Canadian Archipelago, and the more southern Canadian subpopulations that include Hudson Bay and Davis Strait (Peacock et al. 2015). Gene flow between subpopulations and larger clusters continues, but recent anthropogenic-driven climate change may be reducing connectivity among some subpopulations (Peacock et al. 2015; Laidre et al. 2018).

The origins and history of these subpopulations are largely uncertain, but it is likely that they originated sometime prior to the Last Glacial Maximum (LGM; 26–19 Kya). All extant polar bears share a matrilineal common ancestor living 93.2–12.9 Kya (median 33.4 Kya) (Edwards et al. 2011), a date which roughly coincides with the LGM. Hybridization with brown bears suggests that polar bears inhabited both the North Atlantic and Pacific Oceanic regions during the LGM (Cahill et al. 2013, 2018). However, the polar bear mitochondrial DNA haplotype that introgressed into Pacific coast brown bear populations is more divergent, sharing a common ancestor with extant polar bears more than 120 Kya (Lindqvist et al. 2010). This suggests that all extant polar bears are matrilineally descended from the North Atlantic population, but it is unclear whether the Pacific population contributed to extant polar bears.

While the geographic range of polar bears has shifted substantially over time, their population size has been relatively stable for ~300,000 years (Miller et al. 2012; Cahill et al. 2013; Liu et al. 2014). Overall, polar bear genetic diversity is quite low and consistent with an effective population size of less than 4000 and an average DNA sequence difference among individuals at ~2 sites per 10,000 (Cahill et al. 2013). This low and stable population size is interesting, but the ultimate biological consequences are unclear. Small population sizes are associated with relaxation of purifying selection and the accumulation of deleterious alleles, which is frequently cited as a management concern (Harris and Nielsen 2016; Benazzo et al. 2017). However, their long history and small population sizes suggest that low genetic diversity in polar bears may not be a cause for concern. Nevertheless, low genetic diversity in their major histocompatibility complex (MHC) loci, which is an important component of the vertebrate immune system, suggests that polar bears may have low resistance to new pathogens resulting from climate change (Weber et al. 2013).

11.4 Polar Bear Hybridization with Brown Bears

Although polar bears are a distinct species and not nested within brown bear diversity, their close genetic relationship allows viable hybrid offspring. Healthy and reproductively viable polar-brown bear hybrids have been observed in captivity and in the wild (Preuß et al. 2009; Stirling 2011; Pongracz et al. 2017). Whole-genome studies have found extensive evidence of admixture (Cahill et al. 2013, 2015, 2018; Liu et al. 2014; Kumar et al. 2017). All North American brown bears studied to date have polar bear ancestry, as do some Eurasian populations (Cahill et al. 2013, 2015, 2018; Liu et al. 2014). In extant brown bears, polar bear ancestry is greatest in the Kuril Islands between Japan and Russia and the ABC Islands of southeast Alaska (Cahill et al. 2015, 2018). However, ancient DNA has revealed that during the late Pleistocene to early Holocene period (129–82 Kya) in Ireland, polar bear ancestry in brown bears represented at least 24% of the genome (Cahill et al. 2018).

Collectively, hybridization studies of polar bears and brown bears indicate that gene flow between the species was widespread geographically among multiple populations, including at least one instance of hybridization on the east and west coasts of the Atlantic and Pacific Oceans (Cahill et al. 2018). However, none of these studies has shown evidence of gene flow from brown bears into polar bears (Cahill et al. 2013; Liu et al. 2014; Peacock et al. 2015; Barlow et al. 2018). This raises the question: if hybridization is so common, what is preventing the introgression of brown bear ancestry into polar bears? There are three hypotheses.

1. *Genetic incompatibilities control backcrossing success.* At present, we lack sufficient evidence to refute this hypothesis, but it is possible that certain combinations of alleles are incompatible and prevent backcrossing into polar bears.

However, there is no evidence to support this hypothesis, and the prevalence of gene flow into brown bears indicates no robust incompatibilities.

2. *The demographic characteristics of the admixture events are responsible for the direction of gene flow*. Species that are expanding their range tend to be recipients of gene flow and hybridization (Currat et al. 2008). For example, when anatomically modern humans expanded into the Neanderthal's range, they were the principal recipients of gene flow (Green et al. 2010). Most documented hybridization events between polar bears and brown bears may have occurred after the LGM, when brown bears expanded into what had previously been polar bear habitat. However, DNA from pre-LGM polar bears that were expanding into brown bear range has revealed their gene flow into brown bears, so demography seems unlikely to be the sole force at work (Cahill et al. 2018).
3. *Behavioral or ecological factors control backcrossing success.* First generation hybrids are genetically intermediate between the parent species, but they are not necessarily equally suited to both ecological niches. Polar-brown bear hybrids may be less successful at surviving in the specialized arctic sea ice niche than the generalist terrestrial omnivore niche, and it has been proposed that the non-white pelage of F1 hybrids may reduce seal hunting success (Cahill et al. 2018). However, learned behaviors are unlikely to underlie the biased gene flow because the introgression of polar bear mitochondria is widespread (Cronin et al. 1991; Edwards et al. 2011).

Ultimately, all of these hypotheses may contribute to the genomic isolation of polar bears. However, the important insight for polar bear evolution is that through some combination of these effects, polar bears have become a closed gene pool without detectable introgression from related species (Cahill et al. 2013; Liu et al. 2014; Peacock et al. 2015; Barlow et al. 2018).

11.5 Natural Selection

One of the most fascinating aspects of polar bear evolution is their rapid specialization from a temperate terrestrial omnivore to an Arctic marine carnivore. Paleontological evidence is limited because of a paucity of skeletal remains, which might reveal the pattern of morphological development. However, the Svalbard mandible discussed earlier provides some intriguing clues. Polar bears and brown bears have substantially differing dentition, and the Svalbard mandible is clearly from a polar bear (Ingólfsson and Wiig 2009). Further isotopic analysis of the mandible revealed that this individual consumed a marine diet rather than a terrestrial one (Ingólfsson and Wiig 2009). These findings suggest that many of the major adaptations to the polar environment arose during the divergence between polar bears and brown bears 479–343 Kya, well before the Svalbard mandible (~124 Kya).

The genetic basis of polar bears' rapid adaptation to their new ecological niche remains incompletely understood. However, recent molecular studies have identified candidate genes underlying their adaptation. Tests for positive selection of protein coding genes revealed signatures of selection for a range of genes, including the enrichment of those involved in adipose tissue development, heart development, blood coagulation, and sarcomere formation (Liu et al. 2014). The apolipoprotein B (APOB) gene for a blood glycoprotein is one in which polar bears exhibit nine fixed missense mutations since their divergence with brown bears (Liu et al. 2014). APOB plays an important role in the regulation and processing of low-density lipoprotein (LDL) cholesterol in mammals, so the genetic changes in polar bears may enhance their adaptation to a high-fat diet (Whitfield et al. 2004; Liu et al. 2014). Two candidate genes (LYST and AIM1) may be responsible for the polar bear's white coat (Trent et al. 1990; Gutiérrez-Gil et al. 2007; Liu et al. 2014).

An emerging avenue of research into natural selection in polar bears is gene duplication or loss. A recent study identified a range of differences between polar bears and brown bears. Comparing these changes using whole-genomic data from 17 polar bears, nine brown bears, and two outgroup American black bears revealed a high rate of gene loss in polar bears since their divergence from brown bears (Rinker et al. 2019). As with the mutational analysis, copy number variation revealed significant enrichment for changes related to fatty acid metabolism associated with a carnivorous diet (Liu et al. 2014; Rinker et al. 2019). Taken together, these findings suggest that adaptations for a high-fat diet (i.e., seal blubber; see Chap. 12) were among the most impactful genomic changes in polar bear evolution.

11.6 Future Directions

Our understanding of polar bear taxonomy, evolution, and population dynamics has increased dramatically in recent years. This is an exciting time for polar bear research, with many opportunities to further our knowledge. New genetic information will be vital for polar bear conservation and management, and there remains much to be learned about the genetic changes that enabled polar bears to occupy the sea ice environment and feed primarily on seals. Although our knowledge about polar bears has increased, meaningful application of that knowledge for conservation and management is just beginning.

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Chapter 12
Polar Bear Behavior: Morphologic and Physiologic Adaptations

John P. Whiteman

Abstract Polar bears possess morphologic and physiologic characteristics that reflect their terrestrial lineage as members of the bear family (Ursidae) as well as adaptations to the Arctic marine environment. Among marine mammals, they are the least adapted for aquatic life. They exhibit substantial seasonality in body mass, body condition, and many physiological functions, reflecting the annual cycle of both their Arctic sea ice habitat and the availability of their main prey, ringed seals. This hypercarnivorous diet has likely influenced the polar bear's craniodental morphology and nutritional physiology. Similar to other marine mammal predators, polar bears exhibit a relatively high resting metabolic rate (RMR) and field metabolic rate (FMR). The polar bear skeleton is well adapted for walking, rather than tree-climbing, and to a lesser degree, for swimming. The large feet provide secure traction on sea ice (aided by sharp claws) and propulsion in the water. Their reproduction, winter hibernation (by pregnant females), and sensory systems resemble those of other bears. Future research should focus on nutrient recycling during fasting, adaptation to a high-fat diet, susceptibility to pathogens, and assessment of the fitness consequences of ongoing sea ice loss and chemical contamination of their habitat.

Keywords Climate change · Contaminants · Craniodental · Creatinine · Disease · Fasting · Fat · Hibernation · Metabolism · Morphology · Nutrition · Physiology · Polar bear · Sea ice · Sensory · Thermoregulation · Urea

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12.1 Introduction

At first glance, polar bears (*Ursus maritimus*) stand out as unique among marine mammals because of their strong resemblance to the other seven extant bear species (family Ursidae), all of which are terrestrial. However, polar bears have rapidly evolved to occupy a novel niche as apex predators hunting from the surface of the Arctic sea ice. Indeed, they are powerful swimmers and can make short, shallow dives when pursuing prey (see Chap. 16). The entirety of polar bear natural history unfolds on the sea ice and in adjacent coastal ecosystems, but their fossil record is sparse because most die at sea and their remains sink into the ocean (Ingolfsson and Wiig 2009). The features that distinguish polar bears since they diverged from brown bears (*Ursus arctos*) reflect their adaptation to the sea ice habitat and to a hypercarnivorous diet of marine mammal prey (see Chap. 11; Hailer et al. 2012; Liu et al. 2014).

In this chapter, I discuss the most prominent organismal characteristics of polar bears, often in comparison with other bear and marine mammal species. Because there is a close association between the form and function of an animal and the abiotic and biotic components of its environment, these discussions will be interwoven with references to polar bear behavior and ecology. In addition, because this chapter is written in the early twenty-first century—a period of swift and dramatic change in the Arctic from global warming, pollution, and other anthropogenic effects—I also consider how sea ice loss and environmental change are affecting polar bear morphology, physiology, and behavior.

12.2 Morphology

12.2.1 *Temporal and Spatial Variation in Morphometrics*

The global population of polar bears occupies the Arctic and sub-Arctic and is divided into 19 subpopulations primarily based on movements, although there are varying degrees of restricted gene flow across subpopulation boundaries (see Chap. 11; Paetkau et al. 1999; Peacock et al. 2015; Malenfant et al. 2016). Growth rates, body sizes, and the relationship between body mass and length vary among subpopulations (Durner and Amstrup 1996; Cattet et al. 1997; Derocher and Stirling 1998; Derocher and Wiig 2002). This variation is related to regional ecosystem productivity and diet, but genetic differences, density-dependent effects, and pollution exposure also may be important.

At birth, male and female cubs do not differ in body mass and length, but males become significantly larger during the first year of life. By the time bears reach 20 years of age, roughly the end of their prime adult years, males are approximately twice as massive as females (Derocher and Wiig 2002; Derocher et al. 2005). This dimorphism is among the largest among mammals, perhaps second only to the differences between males and females of some Pinnipedia (e.g., elephant seals [*Mirounga* spp.]) (Derocher et al. 2005). Polar bears reach 97% of their asymptotic (i.e., adult) body length between 4–6 years of age, with females usually reaching this length earlier than males (Derocher and Stirling 1998; Rode et al. 2010). Adult body length is approximately 150–250 cm for females and 200–300 cm for males (Derocher and Wiig 2002; Amstrup 2003).

Polar bears are the largest extant species of Ursidae, rivaled in body mass only by some subpopulations of brown bears (Hilderbrand et al. 1999; Swenson et al. 2007). Adult body mass generally ranges from 150–350 kg for females and 350–650 kg for males, but mass varies substantially throughout their annual cycle (Derocher and Stirling 1995; Stirling 1999; Derocher and Wiig 2002; Amstrup 2003). In general, polar bears gain mass during spring when seals (predominantly ringed seals, *Pusa hispida*) are most vulnerable to predation (because of pupping and molting) and lose or maintain mass during the remainder of the year. During summer and autumn, polar bears in some subpopulations lack access to marine mammal prey because of seasonal reductions in sea ice. These individuals tend to lose body mass as they fast or consume lower-energy terrestrial food, such as vegetation and bird eggs (Rode et al. 2015). In Western Hudson Bay (WHB), summer mass loss rates are ~0.9 kg day^{-1} for adults, ~1.1 kg day^{-1} for subadults, ~0.6 kg day^{-1} for yearlings, and ~0.3 kg day^{-1} for cubs (Derocher and Stirling 1995; Atkinson et al. 1996). These rates of mass loss, which occur when polar bears are likely consuming terrestrial food items, are nearly identical to the rates of mass loss of polar bears fasting in temporary captivity after human-wildlife conflict (Derocher and Stirling 1995; Atkinson et al. 1996; Pilfold et al. 2016). This similarity suggests that terrestrial feeding does little to offset the loss of stored energy. An important exception can occur when polar bears turn to an alternative food source that resembles their typical diet of marine mammals. For example, some polar bears remaining on land during the summer ice melt season in the Southern Beaufort Sea (SBS) maintain their body mass by scavenging carcasses of bowhead whales (*Balaena mysticetus*) deposited after human subsistence harvest (Whiteman et al. 2018).

There are no body mass data for polar bears during winter because of the difficulty of captures in the Arctic during this season, although low masses in spring suggest that polar bears reach an annual minimum in late winter (Durner and Amstrup 1996; Stirling et al. 2008). Indeed, the lipid content of adipose tissue (which is a proxy for body condition; see Sect. 12.2.4) in hunter-harvested polar bears reached an annual minimum during April–May in five subpopulations; importantly, this dataset included lipid content measurements throughout the winter (Galicia et al. 2019). Changes in body mass also depend on reproductive status. Pregnant females accrue extraordinary fat deposits and additional lean tissue before winter hibernation (see Sect. 12.5) to provide the stored energy and organic material required for gestation and lactation (Atkinson and Ramsay 1995; Atkinson et al. 1996).

Polar bear body condition is often quantified by assessing body mass relative to length, an approach that has been validated with complementary data, such as the mass of dissected skeletal muscle and lipid tissue of individual carcasses (Cattet et al. 2002). However, morphometric body condition indices depend on the consistency and accuracy of the underlying anatomical measurements and can fail to reflect subtle variation among individuals (Cattet et al. 1997; Pagano et al. 2017). Body condition has recently declined for some subpopulations of polar bears. In Southern Hudson Bay (SHB), body condition (residuals from a regression of mass versus length) of all age and sex classes declined during 1984–2009 (Obbard et al. 2016). In WHB, declines have occurred during two time periods. First, body condition (mass × length^{-2}) declined during 1981–1997 for males and for females $\geq$4 years of age (Stirling et al. 1999). Second, body condition (defined as MJ of stored energy calculated from mass and length) declined during 2004–2013 for all age and sex classes (Molnár et al. 2009; Sciullo et al. 2016). In Davis Strait (DS), body condition (chest girth as a proxy for body mass) declined during 1978–1994 for males and females $\geq$2 years of age, and this decline continued to 2007 for females but not for males (Rode et al. 2012). In Baffin Bay (BB), body condition (chest girth) declined from 1992–2010 for males and females $\geq$2 years of age (Rode et al. 2012). In the SBS, the body length of individuals >3 years of age declined from 1982–2006 (Rode et al. 2010). Changes in body mass over that period in the SBS were complex, including decreases for some polar bears (e.g., females of age 3–4 years or >8 years) and increases for others (females of age 5–8 years). In contrast to the long-term declines in body condition in some subpopulations, polar bears in the Chukchi Sea (CS) showed either no change between 1986–1994 and 2008–2011 or increases in mass (yearlings of both sexes, adult females) and length (adult females; Rode et al. 2014). Sea ice availability is a primary influence on polar bear body mass, length, and body condition, and some of these declines in body size are attributable to sea ice loss (Rode et al. 2010, 2012; Obbard et al. 2016). Other variables such as population density and local prey availability are also influential (Rode et al. 2012, 2014).

12.2.2 Craniodental Morphology and Feeding

Polar bears are the only Ursidae species that almost exclusively consume vertebrate prey, and this hypercarnivory likely has been an important selection pressure in the evolution of their skull morphology (Christiansen 2007; Figueirido et al. 2009). In comparison to the other seven extant bear species, polar bears have the unique combination of a large and convex mandible with a deep symphysis, a flattened cranium, a deep rostrum, and upwardly-positioned eye orbits (Figueirido et al. 2009). When compared to their closest relative, the brown bear, the flattened appearance of the polar bear cranium may be the most obvious distinction (Fig. 12.1). Likely as a consequence of this flattening, polar bear masticatory muscles exhibit a different morphology than those in brown bears, and the stresses from biting are more unevenly dispersed throughout the polar bear skull, creating greater potential for cranial strain and deformation (Sasaki et al. 2000; Slater et al. 2010). This suggests that as polar bears have diverged from brown bears, changes in

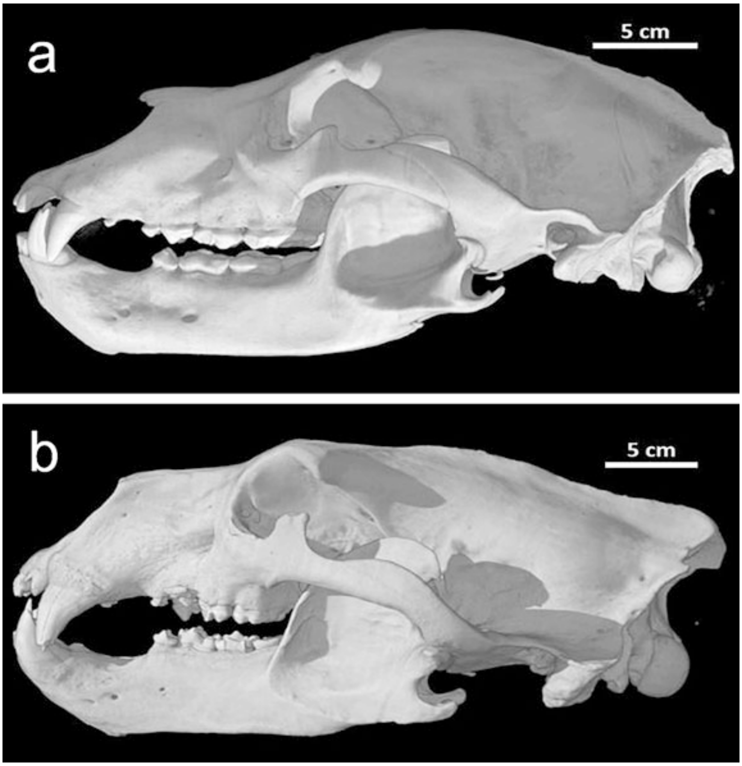

Fig. 12.1 Skulls of (**a**) brown bear (sex unknown; Texas Memorial Museum TMM M-2749), and (**b**) polar bear (bottom; male; Illinois State Museum H 001-05). Images courtesy of Digital Morphology at the University of Texas at Austin

their skull morphology have left them poorly suited for increased masticatory demands, such as chewing vegetation (Slater et al. 2010). Polar bear turbinates, the delicate frameworks of bone in the nasal cavity, are also unique. In comparison to those of black bears (*Ursus americanus*), brown bears, and other caniform terrestrial carnivores, polar bear turbinates have a greater relative surface area associated with olfaction, possibly reflecting selection pressure for detecting widely-dispersed prey on the sea ice (Green et al. 2012).

In some subpopulations, polar bear skull morphology is changing. In the SBS, the width of the zygomatic bones of polar bears sampled during the spring decreased from 1982–2006 for all age and sex classes, except males ≥12 years of age (Rode et al. 2010). Interestingly, bears sampled in autumn showed little change during the same period, although zygomatic width increased for females <8 years (Rode et al. 2010). In East Greenland (EG), the condylobasal skull length of male polar bears declined between 1920–1936 and 1999–2010, and the overall shape of the skull changed between 1892–1939 and 1961–2002 (Pertoldi et al. 2009; Sonne et al. 2013). Like body mass and length, skull size is correlated with the availability of sea ice as well factors such as exposure to pollutants (Pertoldi et al. 2009; Rode et al. 2010; Sonne et al. 2013). The effect of these changes on foraging behavior is uncertain.

Dental morphology is similar among extant bear species, unlike the marked differentiation observed in other Carnivoran families, such as Felidae (Christiansen 2008). All members of Ursidae share the dental formula I 3/3, C 1/1, P 4/4, M 2/3, although the number of premolars may vary from 2–4, and sloth bears (*Melursus ursinus*) lose one pair of incisors as adults (Fig. 12.2). The reduced number of premolars creates a diastema between the canines and molars. This characteristic is generally associated with a herbivorous diet even though it is retained in carnivorous polar bears (Figs. 12.1 and 12.2). However, among Ursidae, polar bears exhibit the smallest molar surface area (i.e., occlusal face) other than sloth bears, likely because of the reduced need for mastication because of their diet (Sacco and Van Valkenburgh 2004; Figueirido et al. 2009). Surprisingly, polar bear carnassial teeth are relatively small and not modified for shearing like other hypercarnivores (Sacco and Van Valkenburgh 2004; Figueirido et al. 2009). Polar bears have the largest upper canines of all Ursidae species other than sun bears (*Helarctos malayanus*), although their large canines are proportional to their body mass (Christiansen 2008). Like those of many other mammals, polar bear teeth exhibit cementum annuli (layers of annual growth) which can be counted in a sectioned and stained tooth for aging (Calvert and Ramsay 1998).

Despite their diet of marine mammals, polar bears do not have specialized teeth for capturing and killing prey like some hypercarnivorous species (e.g., tigers, *Panthera tigris*; Christiansen 2008). This is consistent with the poor performance of the polar bear skull in dissipating bite force stress (Slater et al. 2010). A plausible explanation is that specialized dental weaponry is not required to kill most polar bear prey. For example, ringed seals, which are the primary prey of polar bears in much of the Arctic, are: (1) relatively small, especially pups, (2) easily killed without the need for powerful or prolonged bites, and (3) killed with paw swipes to the head in addition to biting (see Chap. 13; Sacco and Van Valkenburgh 2004). Dental pathologies are common among polar bears. A survey of the teeth and mandibles of 317 polar bear skulls collected from 1906–2011 found that (1) 21% had dental fractures, usually of a canine tooth (2) 13% had bone necrosis indicative of periodontitis and (3) 9% exhibited lesions indicative of temporomandibular joint osteoarthritis (Winer et al. 2016). The effect of these pathologies on hunting success and longevity is uncertain.

12.2.3 Axial and Appendicular Skeletal Morphology

The postcranial morphology of polar bears is typical of Ursidae and their plantigrade, quadrupedal mode of terrestrial locomotion (Pagano et al. 2018a). However, the limb bones may have a greater bone density than those in brown bears, which could reduce buoyancy and benefit swimming, similar to other semi-aquatic

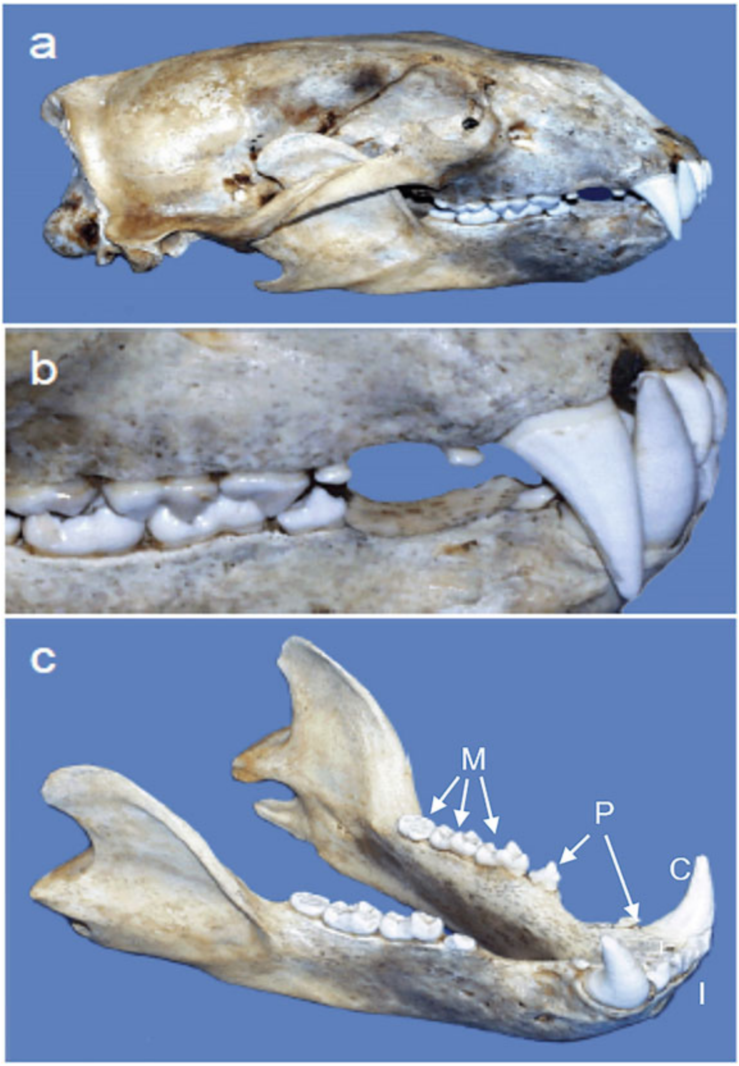

Fig. 12.2 (**a**) Polar bear skull. (**b**) Polar bear dentition showing a diastema in the upper and lower jaws. (**c**) Polar bear mandible showing molars (M), premolars (P; only two are visible on this specimen), canines (C), and incisors (I)

mammals (Wall 1983; Fish and Stein 1991). In comparison to giant pandas (*Ailuropoda melanoleuca*; arboreal as cubs) and sun bears (arboreal as cubs and adults), the tibia in polar bears provides less support for dorsiflexion and supination. These movements are important for tree climbing but are less critical for traversing sea ice (Sasaki et al. 2005). Lastly, pregnant polar bears, which are the only demographic group of this species that reliably hibernate in winter (see Sect. 12.5), appear to increase bone synthesis prior to hibernation (Lennox and Goodship

Fig. 12.3 Ventral view of the foot of a male polar bear captured along the coastline of the Southern Beaufort Sea (SBS), Alaska. For scale, a 10 cm pocketknife is visible in the lower left corner of the image

2008). This may offset bone loss that typically occurs in mammals experiencing months of inactivity. It is unclear whether this increased synthesis occurs in other bear species (McGee-Lawrence et al. 2008).

Polar bear feet are large, possibly for enhanced thrust production during swimming and for distributing body mass over a large area when traversing thin sea ice (Fig. 12.3; Stirling 1999). The footpads are covered with papillae (~1 mm in diameter), creating a rough surface, which enhances traction on sea ice (Manning et al. 1985). The claws are shorter and more curved than those of brown bears, perhaps for grasping prey and for maintaining traction (Amstrup 2003).

12.2.4 Body Composition

Polar bear body composition is highly dynamic. In the SBS, five polar bears sampled at intervals of 8–11 days exhibited mass changes of −10–16%, with changes in lean mass of −7–4% and in fat mass of −9–12% (Pagano et al. 2018b). Nevertheless, their body composition exhibits seasonal trends that reflect their ecology (Arnould and Ramsay 1994; Atkinson and Ramsay 1995; Atkinson et al. 1996; Thiemann et al. 2006; Whiteman et al. 2018). The percent body fat reaches an annual minimum of ~15–25% in spring, before the extensive hunting opportunities of the seal pupping season. Body fat then peaks during summer (~30–40%), after spring hunting has concluded and before the extensive fasting during autumn and winter. The highest percent body fat (~50%) occurs in pregnant females prior to entering winter hibernation (Atkinson and Ramsay 1995; Atkinson et al. 1996).

Polar bears also exhibit variability in the anatomical properties of their lean and fat mass. In spring, their skeletal muscle reaches an annual minimum protein content and maximum water content, consistent with the poor body condition of this season (Whiteman et al. 2017). However, muscle functional characteristics such as fiber type and cross-sectional area do not change seasonally and instead reflect recent activity levels (Whiteman et al. 2017). The lipid content of polar bear adipose tissue is lowest in spring, also correlating with the low overall body condition during this period (Thiemann et al. 2006; McKinney et al. 2014).

Polar bear fat accumulation is primarily subcutaneous, mainly occurring in the rump, although they can possess substantial intra-abdominal and muscular lipid stores (Pond et al. 1992). The subcutaneous adipose tissue of polar bears can be very thick; however, it is not considered blubber as in seals and whales. Indeed, among marine mammals, polar bears and sea otters (*Enhydra lutris*) are notable for their reliance on fur, rather than blubber, for insulation (Liwanag et al. 2012b). Blubber is more homogenous in its anatomical distribution, whereas polar bear subcutaneous fat is accreted in discrete depots with unique anatomical and biochemical properties (Pond et al. 1992; Davis 2019). Also, unlike blubber, in polar bears the distribution of fatty acids (as defined by chain length and saturation) and the thickness of superficial fat are not optimized for insulation (Pond et al. 1992; Grahl-Nielsen et al. 2003; Thiemann et al. 2006).

As with other marine mammals, high concentrations of vitamin A occur in polar bear liver, which can be toxic if consumed (Lewis and Lentfer 1967). Vitamin A precursors are produced by marine algae and can bio-accumulate in apex predators like polar bears (Senoo et al. 2012; Galasso et al. 2017). Accordingly, marine seals feeding at lower trophic levels exhibit lower concentrations of liver vitamin A than polar bears (Lewis and Lentfer 1967). Like nearly all marine mammals (except for the dugong, *Dugong dugon*), polar bears possess multireniculate kidneys (Makita et al. 1998; Williams 2006; Bechshøft et al. 2011a). The origins of this trait remain unclear, although it may be an adaptation for the high dietary salt load, which occurs in the marine environment. Terrestrial bear species also exhibit multireniculate kidneys, possibly indicating a coastal or marine-adapted ancestor for Ursidae (Williams 2006).

12.3 Senses

Vision, audition, and olfaction are important senses for detecting and capturing seals (Owen and Bowles 2011; Green et al. 2012). Polar bear retinas possess the proteins for dichromatic color vision, and behavioral tests of a captive polar bear indicate color perception (Ronald and Lee 1981; Peichl et al. 2005; Levenson et al. 2006). This differs from Cetacea and Pinnipedia, which have monochromatic vision (Davis 2019). Polar bear hearing shows a rapid decline in sensitivity at frequencies of 14–20 kHz, consistent with expectations based on body size (Owen and Bowles 2011). Female polar bears may use odorants to indicate their reproductive status to males during the breeding season. The skin on the bottom of the feet of female polar bears has prominent apocrine glands in association with large hair follicles, and these glands may deposit a scent on the sea ice when they walk (Owen et al. 2015). This would be advantageous because their sea ice habitat lacks stationary, vertical surfaces, such as trees, which are used by other species for scent marking (Owen et al. 2015). Captive male polar bears can distinguish the sex and reproductive status of other individuals based on pedal scent. In addition, both males and females are more interested in pedal scent during the breeding season, demonstrating that scent trails may contribute to seeking and assessing mates (Owen et al. 2015).

12.4 Metabolism

Resting metabolic rate (RMR) is the energy required for basic physiological processes and for heat production to maintain a constant core body temperature. Multiple studies have used respirometry to measure the RMR of captive polar bears at rest, yielding a mean RMR of 0.23 ml O_2 g^{-1} hr^{-1} (0.02 SE) or 1.3 W kg^{-1} for six individuals on a mixed diet of protein and fat (Hurst 1981; Watts et al. 1991; Pagano et al. 2018a). This RMR is approximately twice the predicted value based on body size alone, which is consistent with trends of elevated metabolism for marine mammals and consumers of vertebrate prey (McNab 1988; Williams et al. 2001; Muñoz-Garcia and Williams 2005; Davis 2019). Field metabolic rate (FMR) represents the total energy expenditure by free-ranging individuals exhibiting natural behaviors. Using the doubly-labeled water method, the mean FMR for nine polar bears (mean body mass 176 kg) in the SBS during April was 0.45 ml CO_2 g^{-1} hr^{-1} (0.04 SE). This FMR is equivalent to 52 MJ day^{-1} (assuming an energy equivalence of 26.3 J ml $CO_2{}^{-1}$) or 3.3 W kg^{-1}, which is 2.6-fold greater than the estimated RMR and could be supported by consuming one adult ringed seal every ~11 days (Pagano et al. 2018b).

Locomotion is an important energetic cost for polar bears, and movement rate (km hr^{-1}) is a useful predictor of FMR (Pagano et al. 2018b). Previous studies of polar bears walking on treadmills showed a much higher energetic cost than expected based on body mass, leading to the conclusion that polar bears are inefficient at walking (Best et al. 1981; Best 1982; Hurst et al. 1982). However, these unusually high costs occurred at walking speeds >5.8 km hr.$^{-1}$, and subsequent studies found that free-ranging polar bears rarely walk that fast (Whiteman et al. 2015). At lower, routine speeds, the cost of terrestrial locomotion is similar to other quadrupeds (Pagano et al. 2018a). Polar bears are powerful, long-distance swimmers and this locomotory cost can contribute to seasonal FMR (Durner et al. 2011; Pagano et al. 2012; Lone et al. 2018). Similar to other semiaquatic mammals (e.g., American mink, *Neovison vison*), the mass-specific energetic cost of swimming for polar bears appears to be higher than for walking, although this difference is not as dramatic as it is in humans (Griffen 2018; Pagano et al. 2019).

For several decades it was thought that all polar bears could facultatively enter "walking hibernation" when food-deprived, including during the summer sea ice melt season (Nelson et al. 1983; Stirling 1999; Dyck et al. 2007; Dyck and Kebreab 2009). This physiological state was hypothesized to include a short-term reduction in metabolism as an energy-conserving adaptation, although this supposition has been revised. In other bears, the decline in metabolic rate during winter hibernation is typically associated with a well-defined decrease in core body temperature (T_b) of 2–5 °C to a new setpoint (Tøien et al. 2011; Friebe et al. 2014). However, during the summer, polar bears in the SBS exhibit a gradual decline in T_b of ~0.7 °C, suggesting a slight and continuous decrease in metabolic rate, which is a typical mammalian response to a long-term reduction in food intake (Whiteman et al. 2015). Similarly, rates of mass loss in polar bears fasting in captivity during summer in WHB (during detention after removal from human conflict) suggest a metabolic rate lower than expected when active but higher than expected during hibernation (Pilfold et al. 2016).

12.5 Thermoregulation

The thermoneutral zone of adult polar bears at rest is not well defined, although it ranges from −30–5 °C (Best 1982). Their upper critical temperature (T_{UC}) is unknown, although a polar bear running on a treadmill at 2.2 m s^{-1} (7.9 km h^{-1}) experienced uncontrolled hyperthermia at a surprisingly low ambient temperature of −25 °C (Best 1982). This suggests that polar bears have a limited capacity to dissipate heat and a low T_{UC}. The lower critical temperature (T_{LC}) of polar bears also is unknown. Similar to many animals, polar bears adjust their resting posture as the ambient temperature declines, curling up to reduce their surface area and retain heat (Øritsland 1970).

The primary defense of polar bears against cold temperatures is their thick fur, which in winter provides a thermal insulation of ~0.8 m^2 °C W^{-1}, which is similar to that in other Arctic mammals such as grey wolves (*Canis lupus*) and caribou (*Rangifer tarandus*) but is less than that of the Arctic fox (*Vulpes lagopus*) and Dall sheep (*Ovis dalli*; Scholander et al. 1950; Hart 1956). Polar bear skin is black, and their fur appears white, although individual hairs are translucent and partially hollow (Wang et al. 2015). Despite speculation that polar bear hair absorbs solar radiation for warmth, this hypothesis is not supported (Koon 1998). The fur is composed of long guard hairs and shorter underhairs, and the morphology of individual hairs is more similar to that of terrestrial mammals, such as Felidae, than aquatic mammals, such as Phocidae (Liwanag et al. 2012a). Foreleg guard hair is substantially longer in males than in females (Derocher et al. 2005). Hair cortisol concentration in polar bears has been used as a proxy for blood cortisol during the period of hair growth, and it has been linked to body condition and annual variation in climate indices (Bechshøft et al. 2011b, 2013; Macbeth et al. 2012). Polar bear fur is replaced annually during a gradual molt, which appears to occur between May and August, although the exact timing and pattern of replacement are unknown (Kolenosky 1987). During this summer molt, the density of the underfur declines substantially, which increases thermal conductance (Frisch et al. 1974).

In water, conductive heat loss through polar bear fur increases by up to 50-fold because the fur does not trap an air layer next to the skin (Scholander et al. 1950; Frisch et al. 1974; Davis 2019). In some marine mammals, such as sea otters, unique hair morphology allows "felting," a process of condensing and pressing fibers together through repeated agitation so that they become tightly interlocked and trap air (Kooyman et al. 1977; Williams et al. 1988). In contrast, air is displaced from polar bear fur upon immersion, and the skin comes into contact with water. The intra-abdominal T_b of polar bears can fall quickly (i.e., $-5\ ^{\circ}\mathrm{C\ hr}^{-1}$) to as low as 22 °C when they swim, suggesting that they reduce blood flow to the skin and some visceral organs to minimize heat loss (Whiteman et al. 2015). Such an adaptation would be similar to the intra-abdominal cooling exhibited by diving king penguins (*Aptenodytes patagonicus*) and emperor penguins (*A. forsteri*; Handrich et al. 1997; Ponganis et al. 2003). Hypothermia in cold water is a particular risk for small polar bears, which likely contributes to the behavior of cubs riding on the back of the mother while she swims (Aars and Plumb 2010; Griffen 2018).

12.6 Reproduction and Hibernation

Reproduction in polar bears is similar to that in other Ursidae (see Chap. 14). From March-June, female polar bears enter estrus, and males exhibit peak testicular function (i.e., spermatogenesis; Spady et al. 2007). The timing of hormonal fluctuations, changes in reproductive tissue morphology, and breeding behavior varies among individuals and subpopulations (Rosing-Asvid et al. 2002; Spady et al. 2007; Gustavson et al. 2015b). During courtship, copulation likely induces ovulation (Stirling et al. 2016). Fertilization is followed by embryonic diapause (i.e., cessation of development) for several months until blastocyst implantation occurs between October- November (Spady et al. 2007). This delayed implantation is similar to that in most Pinnipedia (Pomeroy 2011).

Gestation in polar bears is approximately two months, which is surprisingly short for such a large-bodied mammal, and parturition occurs during hibernation. Among Ursidae, short gestation may be an adaptation to protect the health of the fasting,

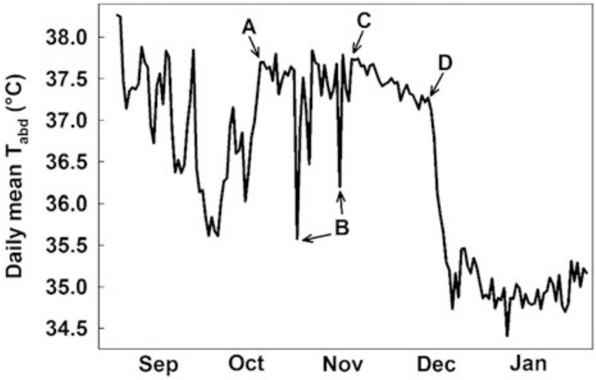

Fig. 12.4 Intra-abdominal body temperature (T_{abd}) of a pregnant polar bear in the Southern Beaufort Sea (SBS) in 2009. During August and September, summer food deprivation likely caused a gradual decline in T_{abd}. (A) An abrupt T_{abd} increase was likely associated with blastocyst implantation, initiating gestation. The bear then began traveling towards its eventual maternal den site, and (B) brief bouts of low T_{abd} likely occurred during swimming events. After entering the den (C), T_{abd} steadily declined, probably to maintain an appropriate temperature gradient for thermoregulation of the rapidly-developing fetus. (D) Parturition likely occurred in early December, immediately followed by a steep decline in T_{abd} to a typical hibernation setpoint. Reproduced from the Supplementary Materials in Whiteman et al. (2015) under the Grant of License to J. P. Whiteman

hibernating mother. Altricial birth favors the depletion of maternal fat stores (during lactation) rather than protein stores (during gestation; Ramsay and Dunbrack 1986). Pregnant females are the only demographic group of polar bears that reliably hibernates in winter, entering maternal dens dug in the snow or earth for up to 200 days (Messier et al. 1994; Ferguson et al. 2000). Other bears (e.g., non-pregnant females with dependent young) may use "shelter dens" for shorter periods (e.g., 50–70 days) during the winter, presumably to avoid inclement weather and poor hunting conditions (Messier et al. 1994; Ferguson et al. 2000). Although the energetics of hibernating polar bears have not been measured directly, respirometry of captive individuals in simulated dens indicates that they reduce their RMR to ~70% based on body mass (Watts and Hansen 1987; Watts et al. 1987). Similar to brown bears, the T_b of female polar bears decreases to a typical hibernation setpoint after parturition (Friebe et al. 2014; Fig. 12.4).

12.7 Feeding and Fasting

Polar bear blood chemistry is an indicator of nutritional status, physiological status, and health (Lee et al. 1977; Tryland et al. 2002; Kirk et al. 2010a; Gabrielsen et al. 2015). Winter is a time of fasting and hibernating for pregnant females and of reduced food intake for other demographic groups. In spring, all polar bears increase their consumption of ringed seals and other marine mammals. In summer and autumn, the nutritional physiology of polar bears is complex. The concept of walking hibernation was thought to include unique nutritional adaptations for fasting in addition to a reduction in metabolic rate (Nelson et al. 1983; Stirling 1999; Dyck et al. 2007; Dyck and Kebreab 2009). To assess these potential adaptations, a study in the SBS examined the nutritional physiology of polar bears during the summer, when this subpopulation temporarily divides into two groups: one on the sea ice and one on shore (Table 12.1; Whiteman et al. 2018). Most variables suggested that during the weeks or months leading up to October, polar bears on the sea ice were in a typical mammalian fast (i.e., they were food-deprived but not catabolizing endogenous protein). This food deprivation likely indicates that the sea ice had retreated to deep water and beyond the distribution of ringed seals on the continental shelf (Harwood and Stirling 1992; Harwood et al. 2012). In contrast, polar bears on shore maintained their lipid and protein stores during the same period by feeding on bowhead whale carcasses left after the human subsistence harvest (Whiteman et al. 2017, 2018).

Although polar bears on the sea ice did not exhibit hibernation-like nutritional adaptations during summer fasting (Table 12.1), they did have low ratios of blood urea-to-creatinine (U:C). This ratio is a key nutritional indicator, with unique relevance for Ursidae (Nelson et al. 1984). Urea is the primary nitrogenous waste product in bears and other mammals. When bears fast during winter hibernation, they stop eating, reduce the catabolism of endogenous protein (i.e., lean tissue), and recycle urea nitrogen in a microbially-mediated process. Accordingly, their blood urea concentration declines substantially (Nelson et al. 1983, 1984; Barboza et al. 1997; Singer 2003; Lohuis et al. 2005; Stenvinkel et al. 2013). This reduces urination and causes creatinine to accumulate (Nelson et al. 1973). As a result, U:C ratios, which are ~20–100 in active, feeding bears, typically fall to $\leq$10 during hibernation (Nelson et al. 1984; Lohuis et al. 2005; Stenvinkel et al. 2013).

Initial observations of low, hibernation-like U:C ratios in active polar bears during summer prompted the walking hibernation hypothesis (Nelson et al. 1983; Ramsay et al. 1991). However, a presumed key benefit of low U:C ratios (i.e., low protein catabolism) was not extensive in the fasting polar bears on the sea ice in the SBS (Table 12.1; Whiteman et al. 2017, 2018). It is possible that the relatively high metabolic rate and activity level of polar bears during summer, as compared to black and brown bears in winter hibernation, creates such a demand for amino acid catabolism that substantial protein degradation continues, despite recycling of urea nitrogen (Whiteman et al. 2018). Further research using isotope tracers could directly test this hypothesis (Barboza et al. 1997).

Although questions remain regarding the underlying biochemical mechanisms, food deprivation clearly causes U:C ratios to decline in polar bears. In captivity, 13 polar bears had mean U:C ratios of ~30–60 the day after feeding. As the bears fasted, these values declined ~30% after three days and ~50% after seven days (Derocher et al. 1990). Fasting for 36–44 days resulted in a mean U:C ratio of 11–16. Declines in U:C ratios also were observed in free-ranging polar bears that had little or no hunting success over ~10 days of monitoring in the SBS (Pagano et al. 2018b).

Table 12.1 Relative values of blood biochemical variables related to nutrition in polar bears (Whiteman et al. 2018)

		Expected values based on physiological state			Observed values in SBS polar bears in October	
Variable	Description	Feeding	Typical fasting	Hibernation fasting	On sea ice	On shore
NEFA[a,b] (non-esterified fatty acids)	Metabolite released when stored fat is used	Low	High	High	High	Low[c]
ALP[d] (alkaline phosphatase)	Digestive enzyme, falls during fasting	High	Low	Low	Low	High[c]
Albumin[e,f]	Protein, correlates with body protein	High	Low	High	Low	High
Glucose[f,g]	Metabolic fuel	High	Low	High	Low	High[c]
ALT[f] (alanine aminotransferase)	Enzyme for protein catabolism	High	High	Low	High[c]	High[c]
Ghrelin[h,i]	Hormone, stimulates foraging	Low	High	Low	Low[c]	Low[c]
Insulin[g,j]	Hormone, regulates glucose storage	High	Low	High	High[c]	High[c]
Cortisol[k]	Hormone for stress response and use of stored fat	Low	High	High	Low[c]	Low[c]
Creatinine[f,l]	Metabolite, rises when urination declines	Low	Low	High	High	Low
Urea[f,l]	Byproduct of protein catabolism	High	High	Low	Low	High
U:C ratio[f,l] (urea: creatinine)	~10 equated with protein conservation and adaptive fasting	20–100	20–100	10	21 ± 11[m]	10 ± 1[m]

[a] Iqbal and Hussain (2009)

[b] LeBlanc et al. (2001)

[c] Specifically, these values did not differ from individuals sampled during April–May during good hunting conditions on the sea ice

[d] Thompson et al. (1989)

[e] Ballantyne et al. (1973)

[f] Lohuis et al. (2005)

[g] Habold et al. (2005)

[h] Kojima and Kangawa (2010)

[i] Gardi et al. (2011)

[j] Herminghuysen et al. (1995)

[k] Harlow et al. (1990)

[l] Stenvinkel et al. (2013)

[m] Mean ± 95% CI

Overall, a U:C ratio $\leq$ 10–13 indicates that a polar bear has fasted for at least seven days (Cherry et al. 2009; Rode et al. 2018). Such low U:C ratios became increasingly common from the 1980s to early 2000s in polar bears sampled from March–May in the SBS and in the Northern Beaufort Sea (NBS; Cherry et al. 2009; Rode et al. 2018). Most notably in the SBS, the percentage of males exhibiting fasting U:C ratios in the spring rose from 44% (1983–99) to 66% (2000–16), likely related to reduced prey availability and reduced body condition of prey (Cherry et al. 2009; Rode et al. 2018). In the CS, which is adjacent to the SBS and NBS, fewer polar bears exhibited fasting U:C ratios. Furthermore, between the same two time periods (1983–99 and 2000–16), the percentage of females with fasting U:C ratios declined from 53% to 10%. This decrease in spring fasting in the CS likely reflects an increase in spring primary productivity, as this region is one of the most productive areas of the Arctic Ocean (Rode et al. 2018).

Polar bears have a strong preference for dietary fat. Captive polar bears allowed to regulate their own food intake selected for 80–100% blubber and 0–20% meat (Best 1985; Folk et al. 1994). Free-ranging individuals have been observed consuming blubber first from freshly-killed seals and occasionally abandoning carcasses despite substantial meat remaining (Stirling 1974; Stirling and Archibald 1977). This preference appears to allow polar bears to maximize energy intake after a kill, based on the higher energy density of lipids (Stirling and Mcewan 1975; Amstrup 2003).

Likely as a result of high lipid intake, polar bears exhibit high concentrations of total cholesterol ($\geq$300 mg/dL) and triacylglycerol ($\geq$250 mg/dL), which are 25% greater than the levels recommended to humans for avoiding cardiovascular disease (Cleeman et al. 2001). Such high values occur in both captive and free-ranging polar bears (Lee et al. 1977; Kaduce et al. 1981; Folk et al. 1994; Kaduce and Folk 2002; Crissey et al. 2004; Whiteman et al. 2013). However, cardiovascular disease is not a concern for polar bear health, similar to brown bears (Bourne et al. 2010; Arinell et al. 2012; Patyk et al. 2015). Although the protective physiological mechanisms are unknown, polar bears exhibit strong positive selection for genetic traits associated with lipoprotein clearance, vascular morphogenesis, and reduced cardiomyopathy, implying an important reorganization of the cardiovascular system in association with a high-fat diet (Liu et al. 2014). In addition, both wild and captive polar bears have the highest concentration of high-density lipoproteins (HDL) reported for Ursidae (Hissa et al. 1994; Crissey et al. 2004; Frank et al. 2006; Arinell et al. 2012; Whiteman et al. 2013). Their levels of this beneficial cholesterol are 2 to 4-fold higher than the minimum threshold (60 mg/dL^{-1}), which is associated with reduced cardiovascular disease in humans (Cleeman et al. 2001; Schaefer and Asztalos 2007; Tall 2009).

In captive polar bears, seal skin and blubber had a gut transit time of 38 hr compared to 12 hr for herring (Best 1985). The apparent digestibility of seal skin and blubber was 93%, consistent with digestibility of 92–97% for crude protein, 94–100% for crude fat, and 48–57% for crude fiber (Best 1985; Jansen et al. 2003; Dyck and Morin 2011). Fecal microbiota of free-ranging polar bears in the Barents Sea (BS) were dominated by the phylum Firmicutes, especially the genus

Clostridium (Glad et al. 2010). However, captive individuals exhibited more diverse fecal microbiota, likely reflecting differences in diet (Schwab and Ganzle 2011).

12.8 Disease and Immune Function

Morbilliviruses infect polar bears in the wild, with canine distemper virus (CDV) being more common than phocine, dolphin, or porpoise varieties (Garner et al. 2000; Cattet et al. 2004; Kirk et al. 2010b). Antibodies to the parasite *Toxoplasma gondii* have also been detected in polar bears (Kirk et al. 2010b). In the SBS, antibodies for CDV were most common in younger polar bears (79% of individuals sampled; 5–7 years of age), whereas *T. gondii* antibody prevalence did not vary with age (Kirk et al. 2010b). In general, the immune system of polar bears may recognize relatively few pathogens and parasites given the surprisingly low diversity in their major histocompatibility complex (Weber et al. 2013). During summer in the SBS, polar bears on shore exhibit greater immune system activity than individuals on the sea ice, including higher counts of neutrophils and monocytes (Whiteman et al. 2019). These elevated counts may result from exposure to terrestrial pathogens, which polar bears on the sea ice do not encounter. SBS polar bears have different antibody profiles on shore (more *T. gondii*, less *Brucella* spp.) than they do on the sea ice, although the fitness effects of these differences are unclear (Atwood et al. 2017).

In general, most infectious diseases for polar bears are unknown (Fagre et al. 2015). For example, periodic outbreaks of alopecia associated with reduced body condition have been observed in the SBS, but the pathogen, thought to be a virus, has yet to be identified (Bowen et al. 2015). Parasites and diseases represent an important research area for polar bears, especially because these factors were ranked seventh in importance out of 24 potential influences on polar bear population dynamics (Fagre et al. 2015; Atwood et al. 2016).

12.9 Physiological Effects of Environmental Contaminants

Similar to most other marine mammals, polar bears are at risk of accumulating high tissue burdens of pollutants because they feed at a high trophic level, are long-lived, and possess substantial lipid stores, which can absorb lipophilic toxins (Desforges et al. 2016). Despite inhabiting regions of low human population, polar bears are exposed to a variety of pollutants that are transported to the Arctic by wind and ocean currents. Because of prevailing currents, the concentration of contaminants, such as organohalogens or polychlorinated biphenyls (PCBs), in polar bear tissues are generally lowest in subpopulations near Alaska and highest in those near Greenland (Bentzen et al. 2008; Dietz et al. 2015). In addition, some contaminants are less common in terrestrial than marine environments, reducing exposure for individuals using shore habitats (Atwood et al. 2017).

Trends in pollutant exposure vary temporally (Letcher et al. 2018). The composition of contaminants in BS polar bears changed between 1967 and 1993–94, most notably a nine-fold increase in one PCB (Derocher et al. 2003). A class of perfluorochemicals recently declined in East Greenland (EG) polar bears, likely because of reduced industrial production in the United States and Europe (Rigét et al. 2013). Contaminant exposure also can be associated with climate change and sea ice loss. Organohalogen and mercury accumulation is higher for polar bears in food webs that have greater primary productivity from open-water phytoplankton than from benthic organisms or ice-associated algae. Such a shift in production has occurred in some regions after sea ice loss (Cardona-Marek et al. 2009; McKinney et al. 2009; Horton et al. 2009; McKinney et al. 2010). Many of the pollutants that polar bears absorb accumulate in their tissues. Lipophilic organochlorines are stored in adipose tissue and are transferred to cubs during nursing (Polischuk et al. 2002). Contaminants that bind to proteins rather than lipids increase in the blood during fasting, possibly because of the catabolism and recycling of endogenous proteins (Tartu et al. 2017).

Chemical contaminants have varying physiological effects on polar bears. Organochlorines are correlated with reduced immunoglobulin concentrations and reduced production of antibodies to influenza and reovirus (Bernhoft et al. 2000; Lie et al. 2004). In polar bear brain tissue, mercury levels well below the expected threshold for negative effects show a surprising correlation with a marker of potential neurological damage (Basu et al. 2009). There is particular concern over contaminants that disrupt endocrine functions in polar bears. Concentrations of some PCBs positively correlate with blood progesterone and negatively correlate with thyroid hormones, pregnenolone, and androstenedione (Haave et al. 2003; Gabrielsen et al. 2015; Gustavson et al. 2015a). The net effect of chemical contamination at the organismal and population scale is difficult to predict because of the complex ecology of this species. Nevertheless, contaminants may be responsible for pseudohermaphroditism in BS polar bears (Wiig et al. 1998). Studies of model organisms such as rats suggest that contaminant levels in free-ranging polar bears are high enough to hinder reproduction, affect fitness, and influence population vital rates (Dietz et al. 2015, 2018).

12.10 Future Research

Many research questions remain about the organismal biology of polar bears. Despite extended fasting being an inherent part of their annual cycle, it is unclear whether they retain and recycle urea nitrogen as occurs during hibernation in other bear species (Whiteman et al. 2018). Although their preference for dietary fat is well documented, there is only indirect evidence for genetic alterations of lipid metabolism (Liu et al. 2014; Rinker et al. 2019). Pathogens, which may affect fitness, are largely unidentified, and the population-scale effects of contaminants have yet to be conclusively assessed (Fagre et al. 2015). Importantly, polar bears should be studied in the context of environmental change and ongoing sea ice loss. Overall, population modeling indicates that the global abundance of polar bears has a 71% probability of declining >30% during the next ~40 years (Regehr et al. 2016). Physiological responses to environmental change will be crucial for their survival. Our current knowledge indicates the dependence of polar bears on the sea ice environment and the prey that it provides, a connection that links the alteration and loss of this habitat to the fates of individual animals and to the future of the species.

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Chapter 13
Polar Bear Foraging Behavior

Anthony M. Pagano

Abstract Polar bears forage in the marine environment, primarily on the sea ice over the shallow waters of the continental shelf. They are solitary, ambush hunters that catch ringed and bearded seals when they surface to breathe in ice holes or haul out on the ice to rest and molt. In most parts of their range, polar bears experience dramatic seasonal variability in their ability to catch seals, with foraging success peaking in late spring and early summer when seal pups are weaned. During this time, the body mass of polar bears can nearly double, especially in pregnant females, such that body composition may reach 49% body fat. The accumulation of body fat is vital for these bears to survive through the autumn and winter when seals are less accessible or when pregnant adult female bears enter dens and fast. When the sea ice retreats in summer, some bears exhibit a temporary switch to omnivory, feeding on a variety of terrestrial food. However, the energetic benefit of most terrestrial food is small relative to their marine mammal prey and, in some regions, increased land use has been associated with declines in body condition. Reduced accessibility of seal prey to polar bears as a result of global climate change threatens the long-term sustainability of this Arctic predator.

Keywords Diet · Diversity · Forage · Fasting · Fat · Hypercarnivore · Hunting behavior · Marine · Prey · Polar bear · Seal · Sea ice · Seasonal · Terrestrial

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13.1 Introduction

Polar bears (*Ursus maritimus*) forage in the marine environment like other marine mammals. They evolved from brown bears (*Ursus arctos*) (Kurtén 1964) to become upper trophic-level predators on the Arctic sea ice where they hunt seals, a niche not exploited by a terrestrial carnivore in Antarctica (Stirling 1977). Unlike other bear species, which are herbivorous or omnivorous, polar bears are hypercarnivores (>70% of their diet is meat), feeding on energy-dense pagophilic (ice-dependent) seals as their primary prey (Fig. 13.1; Stirling and Derocher 1990). They are the least aquatic of the marine mammals and the most recently evolved, lacking many of the physiological adaptations that occur in Cetacea (whales and dolphins), Sirenia (dugongs and manatees), and Pinnipedia (seals, sea lions, and walruses) (see Chap. 11; Berta 2017; Davis 2019).

Like sea otters, polar bears are in the taxonomic Order Carnivora (Suborder Fissipedia), with a morphology typical of a terrestrial carnivore (see Chap. 12). Nevertheless, they are powerful swimmers and exhibit behavioral and physiological adaptations that distinguish them from other Ursidae (see Chap. 12; DeMaster and Stirling 1981; Wall 1983; Slater et al. 2010; Pagano et al. 2012, 2018). Polar bears are solitary hunters on the sea ice. Throughout their range, their primary prey is ringed seals (*Pusa hispida*), accounting for up to 83% of the diet (Thiemann et al. 2008; Rode et al. 2014; McKinney et al. 2017; Sciullo et al. 2017). Polar bears also prey on bearded seals (*Erignathus barbatus*), harp seals (*Pagophilus groenlandicus*), harbor seals (*Phoca vitulina*), hooded seals (*Cystophora cristata*),

Fig. 13.1 Image from a global positioning system (GPS)-equipped video camera collar on an adult female polar bear while eating a ringed seal on the sea ice of the Beaufort Sea (Pagano et al. 2018)

walruses (*Odobenus rosmarus*), beluga whales (*Delphinapterus leucas*), and narwhals (*Monodon monoceros*) (Freeman 1973; Stirling 1974; Calvert and Stirling 1990; Smith and Sjare 1990; Derocher et al. 2002; Thiemann et al. 2008; Mckinney et al. 2013).

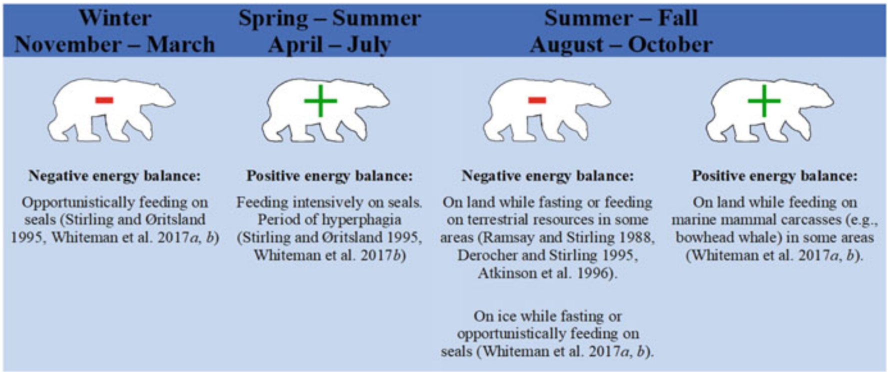
Ringed seals are the smallest (up to 100 kg prior to breeding) and most abundant seal in the Arctic (Hammill 2009). Their small size may have resulted from predation pressure and their reliance on subnivean lairs to hide neonatal pups from polar bears (Stirling 1977). Larger Pinnipedia, such as bearded seals (up to 425 kg), are unable to build subnivean lairs and give birth on the sea ice, making their pups more vulnerable to predation (Stirling 1977; Kovacs 2009). Bearded seals are less abundant than ringed seals, and their larger size makes them difficult to subdue. As a result, bearded seals are more prominent in the diet of adult male polar bears, which are often twice the size of adult females (Derocher and Wiig 2002; Derocher et al. 2010; Thiemann et al. 2008, 2011). For example, the diet of adult male polar bears in western Hudson Bay consisted of 33% bearded seals, while it was only 12% for adult females and 8% for subadults (Thiemann et al. 2011). However, in Baffin Bay, adult female polar bears consume more bearded seals than adult males and subadults, possibly because they kill younger individuals (Galicia et al. 2015).

Ringed and bearded seals use different sea ice habitats (Kingsley and Stirling 1991). Ringed seals primarily use shore-fast ice (ice that is attached to the coastline) for breeding, whereas bearded seals occur in pack ice (drift ice), with areas of open water (Smith and Stirling 1975; Burns and Frost 1979; Finley et al. 1983; Wiig et al. 1999; Pilfold et al. 2014a). The sea ice habitats for both species are located over shallow waters (i.e., depth < 200 m) of continental shelves, and this is the primary foraging habitat for polar bears (Stirling et al. 1977; Burns and Frost 1979; Kingsley et al. 1985; Kingsley 1990; Gjertz et al. 2000; Frost et al. 2004; Durner et al. 2009). Polar bears prefer to hunt in pack ice and along the edge of shore-fast ice, where seals are more abundant and vulnerable to predation (Stirling and Smith 1977; Stirling et al. 1993; Pilfold et al. 2014b, 2015).

13.2 Seasonal Foraging Patterns

Polar bears travel long distances on the sea ice in search of seals and in response to sea ice conditions. As a result, their home ranges are often larger than those of most terrestrial mammals (see Chap. 14; Ferguson et al. 1999; Tucker et al. 2014). Polar bear foraging success varies considerably among seasons (Table 13.1). Little is known about foraging during the winter, but polar bears typically reach their lowest body mass around late March (Ramsay and Stirling 1988; Stirling and Øritsland 1995; Stirling 1997; Galicia et al. 2020). This suggests that activity and foraging success while on the sea ice are lowest during the winter, when darkness prevails across the Arctic and many polynyas are frozen (Messier et al. 1992; Stirling 1997; Ware et al. 2017; Pagano et al. 2020). Polar bears are estimated to consume only one seal per month during the winter, but this increases to three seals per month starting

Table 13.1 Timeline of the seasonal energy balance of non-denning polar bears while on the sea ice or on land



Winter November – March	Spring – Summer April – July	Summer – Fall August – October	
−	+	−	+
Negative energy balance: Opportunistically feeding on seals (Stirling and Øritsland 1995, Whiteman et al. 2017*a*, *b*)	**Positive energy balance:** Feeding intensively on seals. Period of hyperphagia (Stirling and Øritsland 1995, Whiteman et al. 2017*b*)	**Negative energy balance:** On land while fasting or feeding on terrestrial resources in some areas (Ramsay and Stirling 1988, Derocher and Stirling 1995, Atkinson et al. 1996). On ice while fasting or opportunistically feeding on seals (Whiteman et al. 2017*a*, *b*).	**Positive energy balance:** On land while feeding on marine mammal carcasses (e.g., bowhead whale) in some areas (Whiteman et al. 2017*a*, *b*).

in March (Stirling and Øritsland 1995). They acquire the majority of their body fat during the late spring and early summer, when recently weaned seal pups are most vulnerable (Stirling et al. 1977, 1999; Stirling and Øritsland 1995). This is also when most polar bear foraging behavior on the sea ice has been observed (Stirling 1974; Stirling and Latour 1978; Smith 1980; Stirling et al. 2016; Pagano et al. 2018). From April–July, polar bears consume 2–17 adult or subadult ringed seals per month (Stirling 1974; Stirling and Latour 1978; Stirling and Øritsland 1995; Pagano et al. 2018). An exception is breeding adult males, which reduce or forego feeding during the spring breeding season (March–June) to search for estrous females and breed (see Chap. 14; Ramsay et al. 1991; Cherry et al. 2009; Rode et al. 2014, 2018). For adult females, activity rates peak during this period of increased foraging success from May-July (Messier et al. 1992; Ware et al. 2017; Pagano et al. 2020).

Polar bear reproductive success and subadult survival rates are correlated with ringed seal pupping success (Stirling and Lunn 1997; Stirling 2002). In the eastern Beaufort Sea during years of low ringed seal productivity, polar bears exhibit low reproductive success (Stirling and Lunn 1997; Stirling 2002). This highlights the importance of recently weaned ringed seal pups in the spring diet of polar bears (Stirling and Øritsland 1995; Stirling and Lunn 1997). Fluctuations in ringed seal productivity are associated with decadal oscillations in sea ice conditions. Hence, environmental fluctuations that influence seal reproductive success and accessibility can affect polar bear body condition and survival. However, the Beaufort Sea has low biological productivity and a smaller prey base for polar bears relative to most other regions of the Arctic (Stirling 2002). In areas where polar bears have access to more diverse prey, the effect of low ringed seal productivity on polar bear reproductive success may be mitigated (Stirling and Lunn 1997; Stirling 2002). Additionally, polar bears appear to increase their predation of older ringed seals in years of low pup production (Reimer et al. 2019).

In some areas of the Arctic, polar bears move ashore as early as July and may remain on land until November or December (Cherry et al. 2013). During this time, they either fast, switch to an omnivorous diet, or feed on the carcasses of beach-cast marine mammals (Laidre et al. 2018). When freeze-up occurs in the autumn and winter, non-denning bears return to the sea ice to hunt seals. There are few data on the foraging success of polar bears in late autumn, but one estimate was two seals per month in October and November (Stirling and Øritsland 1995).

13.3 Hunting Behavior

Polar bears live in remote areas of the Arctic where direct observation of hunting behavior is challenging or impossible. Insight into polar bear hunting and feeding behavior on the sea ice is based primarily on research conducted in Lancaster Sound and on traditional knowledge from indigenous residents (Nelson 1966; Stirling 1974; Stirling and Latour 1978; Kalxdorff 1997; Voorhees et al. 2014; Stirling et al. 2016; Laforest et al. 2018). In recent years, video from global positioning system (GPS)-equipped video camera collars has further documented polar bear hunting and feeding behavior (Pagano et al. 2018). On the sea ice, polar bears are primarily ambush, sit-and-wait hunters (Stirling 1974; Pagano et al. 2018). In spring (April–June), adult bears hunt 4–25% of the day, while in summer (June–August), this increases to 35–53% of the day (Stirling and Latour 1978). Although polar bears are strong swimmers, seals are faster and more maneuverable in water, so observations of bears catching seals in open water are rare (Furnell and Oolooyuk 1980). Instead, polar bears often wait for seals to return to breathing holes in the ice. Ringed seals maintain 3–4 breathing holes, which typically are more than 200 m apart (Smith and Stirling 1975; Stirling 1988). In winter and early spring, seals maintain these holes using the claws on their fore flippers in ice up to 2 m thick (Smith and Stirling 1975). Polar bears use olfaction to locate seal breathing holes and lairs (Stirling 1988; Derocher 2012; Togunov et al. 2017). Once they locate a hole, the primary method to catch a seal is still-hunting (Stirling 1974; Pagano et al. 2018). This energy-efficient strategy consists of a bear lying, standing, or sitting near a breathing hole (Fig. 13.2). Bears wait for minutes to hours (average 55 min) in anticipation of a seal coming up to breathe (Stirling 1974). Based on indigenous knowledge, a seal may first sniff the air to detect danger when it emerges from a breathing hole (Nelson 1966). As it does so, the surface water undulates, alerting the bear of a returning seal (Derocher 2012).

Video from collar cameras on adult female polar bears in the Beaufort Sea documented two methods that polar bears used to catch seals at their breathing holes (Pagano et al. 2018). For both methods, the bear waits near the breathing hole until it detects a seal surfacing to breathe. The bear may then either (1) stand on its hind legs and pounce with its forepaws, thereby breaking through the ice, stunning the seal with its forepaws, and killing it with bites to the neck and head, or (2) lunge and grab the seal with its teeth as it surfaces for air (Stirling 1988; Sacco and Van

Fig. 13.2 An adult male polar bear still-hunting at the breathing hole of a ringed seal. Image courtesy of Michael Lockhart (U.S. Geological Survey)

Valkenburgh 2004; Derocher 2012; Pagano et al. 2018). If successful, the bear will pull the seal out of the water by the head or neck, after which it may drag the seal to a new location before eating it. Bears preferentially feed on seal blubber. Video from collar cameras also showed some bears feeding on the abdominal organs of ringed seals (USGS, unpublished data). A bear may spend an hour or more feeding on a seal before moving on. On rare occasions, polar bears may cache the remains (Stirling 1974; Eley 1977; Aars et al. 2015; Stirling et al. 2020). More often, the remains are scavenged by other polar bears and Arctic foxes (*Vulpes lagopus*) (Stirling and McEwan 1975; Stirling et al. 2020).

Video from collar cameras on adult female polar bears has also recorded novel hunting methods (Pagano et al. 2018). For example, bears were observed digging holes in the ice—presumably to attract seals—and subsequently still-hunting at these locations. However, no successful seal captures were recorded using this method (USGS, unpublished data). Polar bears have previously been observed digging holes in the ice for catching seals and as a way to weaken the ice around the breathing hole before a seal returns (Nelson 1966). Polar bears also have been documented digging holes through rafted sea ice to access seal lairs, potentially in response to unusual sea ice conditions and nutritional stress (Stirling et al. 2008). Finally, polar bears may use blocks of ice as projectiles to frighten, stun, or kill seals before diving into the water in pursuit (Harington 1962; Pagano et al. 2018 with online video). Throwing rocks or ice to stun walrus also has been observed (Hall 1865; Harington 1962; Mulvaney 2011).

In addition to still-hunting, polar bears stalk seals during 10–25% of their hunts (Stirling 1974; Pagano et al. 2018). In March and April, ringed seals often haul out in subnivean lairs and on the sea ice in the evening and early morning (Kelly and

Quakenbush 1990). In May and June, ringed seals often haul out more on the sea ice mid-day, presumably to warm their skin in the sun, which enhances new hair growth during their annual molt (Finley 1979; Kelly and Quakenbush 1990; Carlens et al. 2006; Davis 2019). With the exception of summer, polar bears may hunt more frequently at night when seals are more active and surface to breathe more frequently (Stirling 1988). In the Beaufort Sea, adult females polar bears are more active at night in April and September and more active during the day in June (Pagano et al. 2020; USGS, unpublished data). Bearded seals haul out more frequently in spring and summer and molt in June (Kovacs 2009). Ringed seals haul out near breathing holes or near narrow cracks in the ice, while bearded seals tend to haul out on the edge of wide leads or ice floes (Kingsley and Stirling 1991). This difference in haul-out behavior may be associated with the greater predation pressure on ringed seals, which are easier to catch along the edge of a lead in the ice than bearded seals (Kingsley and Stirling 1991). Both ringed and bearded seals primarily face down-wind when hauled out, a behavior thought to enhance their ability to hear and smell polar bears, which use olfaction to detect seals at distances of 2–3 km and hunt by walking cross-wind (Kolenosky 1987; Kingsley and Stirling 1991; Togunov et al. 2017). High winds appear to reduce polar bear hunting success of adult ringed seals in the spring, and cross-wind hunting increases in light wind, which would enhance the detection of seals (Pilfold et al. 2015; Togunov et al. 2017).

Polar bears use a variety of methods when stalking seals on the sea ice. One method involves an aquatic stalk in which bears approach seals from the water (Stirling 1974; Smith and Stirling 2019). In some cases, this consists of a bear getting as close as possible before climbing out of the water and running towards a seal while it is hauled out on the ice. In other cases, bears will swim into a seal's breathing hole to catch it (Stirling 1974). Bears also swim along the edge of ice floes and catch resting bearded seal pups (Derocher 2012). Polar bears also may stalk seals, using pressure ridges and other cover to sneak up on their prey (Derocher 2012). Once the bear gets within 15–30 m from a seal, it sprints to overtake and subdue it before the seal can escape into the water (Stirling 1988).

Ringed seals give birth in subnivean lairs from mid-March to early April, and pups are weaned after 6 weeks (Smith and Stirling 1975). Lairs require a minimum snow depth of 20 cm and typically are built near pressure ridges and hummocks near snow drifts (Smith and Stirling 1975). Polar bears detect females and pups in subnivean lairs primarily using olfaction (Smith 1980; Stirling 1988). If a polar bear senses a seal pup within a lair underneath the snow, it quickly pounces on the snow above the lair, trapping the pup before it can escape into the water (Fig. 13.3). The bear then digs through the snow and wedges its head and neck into the lair to extract the pup. Although young pups are an easier catch, they offer a fraction of the energy relative to adult seals. For example, a ringed seal pup <1 month of age provides 5% of the energy obtained from the blubber of an adult ringed seal (Fig. 13.4; Stirling and McEwan 1975; Pagano et al. 2018). Dependent seal pups are still an important component of the spring diet of polar bears and may be especially important for female bears that have recently emerged from dens with first-year cubs (Fig. 13.5; Stirling and Archibald 1977; Hammill and Smith 1991;

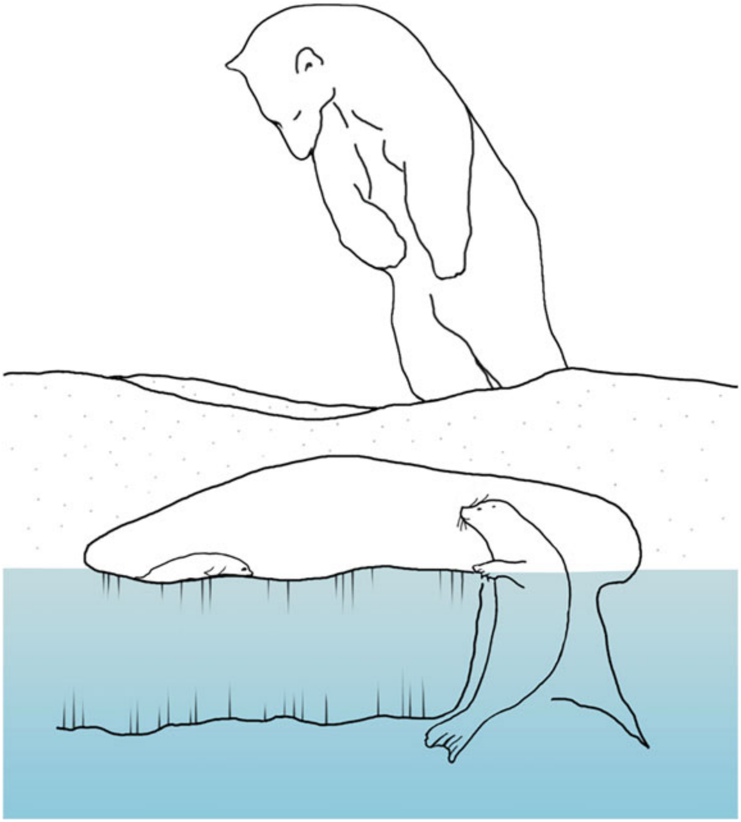


Fig. 13.3 Polar bear preparing to break into the subnivean lair of a female ringed seal with pup

Derocher et al. 2002; Pilfold et al. 2012). Adult female ringed seals are occasionally caught within their lair while caring for their young (Stirling and McEwan 1975). In the eastern Beaufort Sea in spring, adults accounted for 44% of the ringed seal kills observed from 1985-2011 (Pilfold et al. 2012). Predation success of adult seals improves in late spring and early summer as ringed seals begin using breathing holes in areas of new ice with less snow cover and haul out more frequently (Pilfold et al. 2012, 2015). Nevertheless, subadults and recently weaned seal pups account for the greatest percentage of polar bear kills in spring and early summer, likely because they are less experienced at avoiding polar bears (Stirling and McEwan 1975; Stirling and Archibald 1977; Hammill and Smith 1991; Reimer et al. 2019). At the time of weaning, the body composition of ringed seal pups is 45% fat (Stirling and McEwan 1975). Polar bears actively feed (hyperphagia) on adult and newly weaned ringed seals in the spring and summer and may acquire up to two-thirds of their annual energy requirements during this time (Stirling and Archibald 1977; Stirling and Øritsland 1995; Stirling et al. 1999; Pilfold et al. 2012).

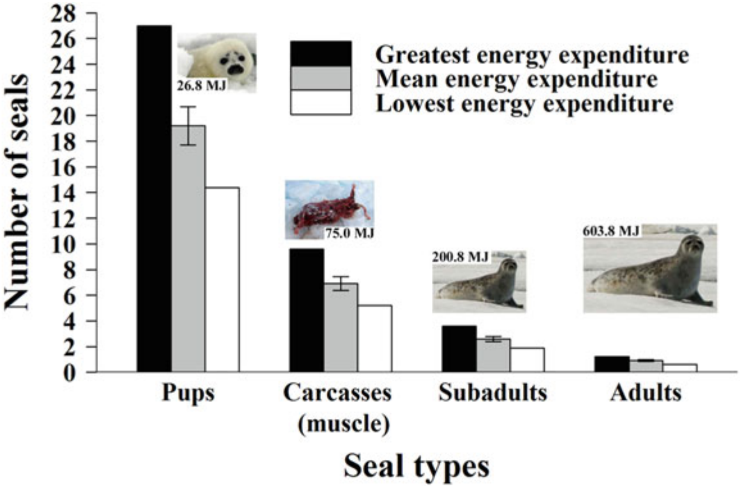


Fig. 13.4 Number of ringed seals (±SE) required for a female polar bear to meet its energy requirements over 10–12 days on the spring sea ice of the Beaufort Sea based on the estimated maximum (black), mean (grey) and minimum (white) field metabolic rates from nine polar bears using the doubly-labeled water method (Pagano et al. 2018). The energy equivalents for fat and protein were estimated for: (1) pups <1 month of age, (2) carcasses, and (3) subadults and adults (Stirling and McEwan 1975; Best 1985; Pagano et al. 2018). Images courtesy of NOAA

Fig. 13.5 Image from a GPS-equipped video camera collar on an adult female polar bear while eating a ringed seal pup on the sea ice of the Beaufort Sea

As a result of hyperphagia, polar bear body mass typically reaches a maximum in early summer (Ramsay and Stirling 1988; Galicia et al. 2020). The body mass of solitary adult females may nearly double, primarily from an accumulation of fat, which may account for as much as 49% of the overall body mass (Ramsay and Stirling 1988; Atkinson and Ramsay 1995). In the Southern Beaufort Sea in 2009, eleven adult females gained 58 kg on average, increasing their body mass by 28% between April–May and August–October (USGS, unpublished data). Similarly, in Western Hudson Bay, the estimated body mass of solitary adult females increased by 50 kg (25%) between February–March and July–August (Ramsay and Stirling 1988). The adipose tissue lipid content in polar bears of five subpopulations increased by 9.7% from spring to autumn (Galicia et al. 2020).

13.4 Learning to Hunt

Polar bear cubs typically stay with their mothers for 2.5 years (see Chaps. 14 and 15). Foraging behavior appears to be learned through observation and mimicking of the mother's behavior (Stirling 1988). Both yearlings and dependent 2-year-old cubs have been observed hunting independently and catching seals (Stirling 1974). During summer, yearlings hunt approximately 4% of the day, and 2-year-old cubs hunt 7% of the day (Stirling and Latour 1978). Yearlings will hunt up to 0.5 km from their mothers, while 2-year-old cubs may extend this distance up to 2 km (Stirling 1974). In summer in the Canadian Arctic, yearlings were observed catching seals at a rate of one seal every 22 days, while the success rate was four-fold greater (one seal every 5 days) for 2-year-old cubs (Stirling and Latour 1978). Still-hunting is the primary hunting method used by cubs (Stirling and Latour 1978). In addition to hunting behavior, mother-offspring social learning influences habitat preferences (Derocher and Stirling 1990; Taylor et al. 2001; Zeyl et al. 2009; Lillie et al. 2018).

13.5 Terrestrial Foraging

Following the period of hyperphagia in early summer, polar bears in some parts of their range move ashore where they either fast, feed on terrestrial-based resources, or feed on beach-cast marine mammal carcasses (Fig. 13.6; Harrington 1965; Russell 1975; Knudsen 1978; Derocher et al. 1993; Kalxdorff 1997; Rockwell and Gormezano 2009; Lemelin et al. 2010; Laforest et al. 2018; Laidre et al. 2018). In many of these areas, terrestrial resources, including fish, birds, eggs, and grass, have been documented as a long-term component of the diet for some individual bears (see Chaps. 12 and 14; Koettlitz 1898; Loughrey 1956). Other terrestrial food includes voles (*Microtus pennsylvanicus*), muskrats (*Ondatra zibethicus*), lemmings (*Lemmus trimucronatus*), Arctic hares (*Lepus arcticus*), caribou (*Rangifer tarandus*), muskoxen (*Ovibos moschatus*), European herring gulls (*Larus

Fig. 13.6 Image from a GPS-equipped video camera collar on a subadult adult female polar bear while eating berries on land on Akimiski Island, Nunavut

argentatus), Canada geese (*Branta canadensis*), seabirds, seabird eggs, mussels (*Mytilus edulis*), sea urchins (*Strongylocentrotus droebachiensis*), crowberries (*Empetrum nigrum*), bilberries (*Vaccinium uliginosum*), cranberries (*Viburnum edule*), mushrooms, mosses, lichens, marine algae, and leaves (Harrington 1965; Knudsen 1973, 1978; Russell 1975). In Western Hudson Bay, 34% of female and 26% of male polar bears fed on plants, including bilberries, crowberries, mosses, grasses, and sedges (Derocher et al. 1993).

With declines in Arctic sea ice resulting from climate change, the energy available from terrestrial food to compensate for declines in marine-based foraging has generated research interest (Fig. 13.7; Dyck and Kebreab 2009; Rockwell and Gormezano 2009; Rode et al. 2010, 2015; Gormezano and Rockwell 2013, 2015). Although there is evidence of increased use of terrestrial resources by polar bears in some areas, terrestrial diets may provide less energy than marine mammal prey, which is supported by the declines in body mass of polar bears summering on land in Western Hudson Bay (see Chap. 12; Ramsay and Hobson 1991; Atkinson et al. 1996; Hobson and Stirling 1997; Hobson et al. 2009; Gormezano and Rockwell 2013; Iverson et al. 2014; Rode et al. 2010, 2015; Robbins et al. 2012; Prop et al. 2015; Pilfold et al. 2016; Dey et al. 2017). Additionally, increased time on land during the summer is associated with declines in body condition in other regions,

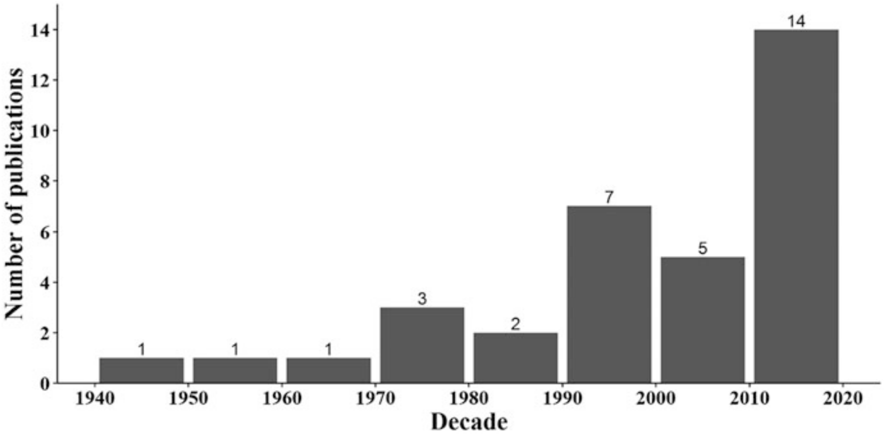


Fig. 13.7 Number of publications per decade that have documented observations of terrestrial foraging by polar bears as of March 22, 2019. Literature search was conducted using the keywords foraging, diet, or food in conjunction with terrestrial, land, or autumn and polar bear. Additional publications were found by scanning the reference lists in the literature

which likely reflects the limited energetic-benefit of terrestrial food for polar bears (Stirling et al. 1999; Obbard et al. 2016). Nevertheless, some research has suggested that terrestrial food could mitigate reduced foraging opportunities on the sea ice (Dyck and Kebreab 2009; Rockwell and Gormezano 2009; Gormezano et al. 2016).

Polar bears on land also feed on carcasses of marine mammals, especially bowhead whales (*Balaena mysticetus*), which wash ashore (Laidre et al. 2018). These carcasses can attract up to 65 polar bears and represent a substantial source of energy (Taylor et al. 1985; Miller et al. 2006; Bentzen et al. 2007; Derocher 2012; Laidre et al. 2018). The carcasses of humpback, bowhead, and blue whales are energetically equivalent to 700, 1300, and 3300 ringed seals, respectively (Laidre et al. 2018). On the northern coast of Alaska, many polar bears scavenge the remains of subsistence-harvested bowhead whales (Miller et al. 2006, 2015; Bentzen et al. 2007; Herreman and Peacock 2013; Rogers et al. 2015). From 2008–10, bowhead whales accounted for ~50% of the autumn diet of polar bears on shore in Alaska (Rogers et al. 2015). Hence, these carcasses serve as an energetically-dense supplemental food during a period when seal accessibility is reduced and bears on the sea ice in this region appear to be fasting (Whiteman et al. 2017a, b). For example, an adult female polar bear in the Southern Beaufort Sea gained 114 kg over 50 days between late August and mid-October, increasing her body mass by 52% as a result of feeding on subsistence-harvested bowhead whale remains (USGS, unpublished data).

13.6 Future Research

Much remains unknown regarding polar bear foraging ecology. For example, we have little information on the number of seals polar bears catch throughout much of the year. Virtually no information exists regarding foraging rates either in late fall when polar bears that spend the summer on land move back to the sea ice, or in winter when subadults, adult males, and adult females with cubs hunt on the sea ice. Additionally, little is known about the environmental factors that enable spring hyperphagia or result in its cessation (e.g., loss of suitable sea ice for hunting or temporal changes in seal vulnerability) and the extent to which foraging success varies with ice conditions or depth. Polar bears may have limited access to seals in deep-water habitats away from the continental shelf (Whiteman et al. 2017a, b). Additional research on the potential foraging opportunities of bears in these habitats would aid our understanding of the consequences of future increases in use of these habitats during the summer (Ware et al. 2017; Lone et al. 2018; Pagano et al. 2020).

13.7 Conclusions

Although they can tolerate an omnivorous diet, polar bears are primarily hypercarnivores that rely on the sea ice to capture seals and other pagophilic prey. They preferentially feed on blubber, which provides a high-caloric diet to sustain their high-energy demands (see Chap. 12; Fig. 13.8; Stirling and McEwan 1975; Pagano et al. 2018). Climate change will reduce the accessibility of seals as the sea ice retreats earlier in the spring and reforms later in the fall (Stern and Laidre 2016). In some regions, more polar bears now fast in the spring than occurred historically (Cherry et al. 2009; Rode et al. 2018). This suggests that foraging success is not simply a function of sea ice availability but also sea ice composition, marine productivity, and changes in the prey base (Stirling et al. 2008; Cherry et al. 2009; Nguyen et al. 2017; Rode et al. 2018). Polar bears in winter have diets containing 86% sympagic (sea-ice associated) carbon, which highlights that sea ice not only functions as an important foraging platform but also supports marine productivity within the Arctic ecosystem (Brown et al. 2018). In some areas, polar bears may be able to mitigate the effects of declining sea ice by switching to alternative marine mammal prey, such as harbor seals, harp seals, or white-beaked dolphins (*Lagenorhynchus albirostris*) (see Chap. 16; Aars et al. 2015; Johnson et al. 2019; Smith and Stirling 2019). Nevertheless, their specialized diet will place them at an increased risk due to environmental change (Van Valkenburgh 1999; Van Valkenburgh et al. 2004). Current models of sea ice decline indicate that polar bear survival will be challenged in an increasingly fragmented and ice-free environment (Amstrup et al. 2008; Atwood et al. 2016; Regehr et al. 2016; Molnár et al. 2020).

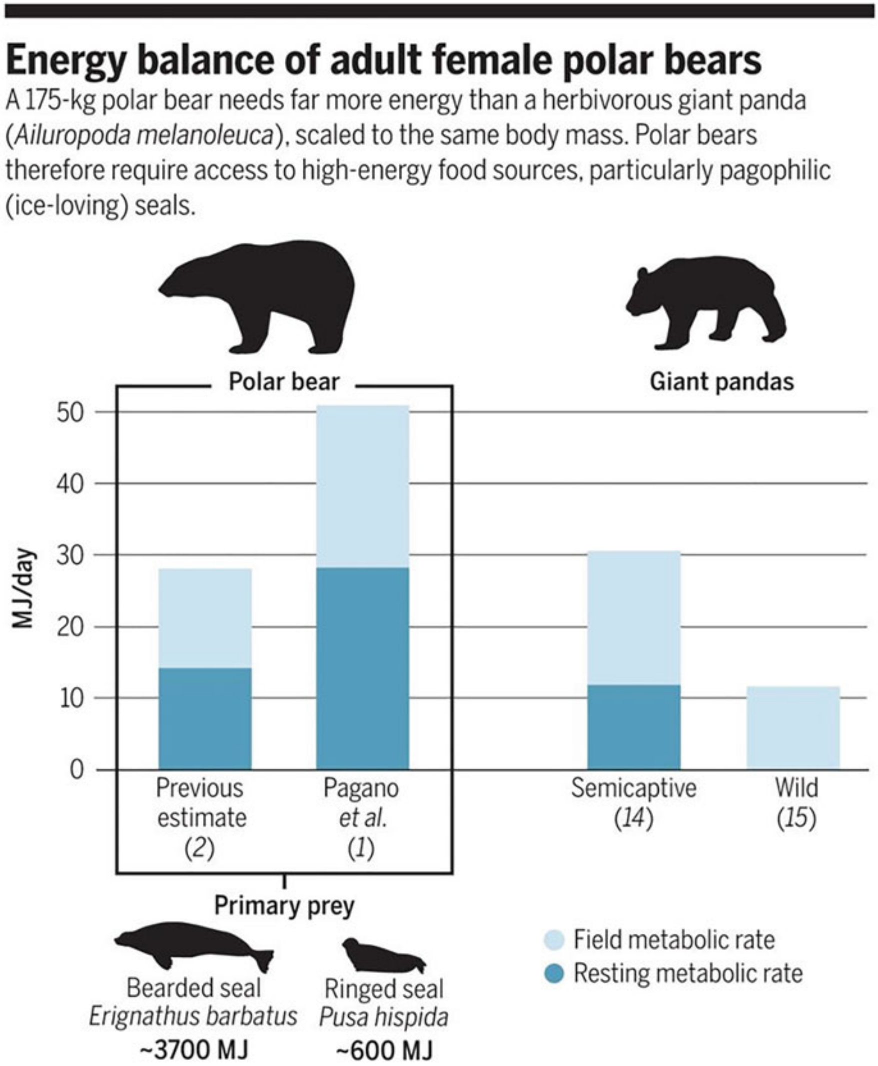


Fig. 13.8 Comparison of estimated Field Metabolic Rate (FMR) of female polar bears on the sea ice of the Beaufort Sea using the doubly-labeled water method and captive resting metabolic rate (Pagano et al. 2018) vs. previously assumed FMR and resting metabolic rate for polar bears (Stirling and Øritsland 1995). The FMR and resting metabolic rate for the herbivorous Giant panda are shown for comparison (Nie et al. 2015; Fei et al. 2016). Graphic: N. Cary/Science (Whiteman 2018)

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Chapter 14
Polar Bear Reproductive and Denning Behavior

Tom S. Smith

Abstract Polar bears are the largest bear species and a top marine predator in the Arctic. They share many reproductive characteristics with other bears but have significant adaptations that enable them to reproduce and thrive in the Arctic. Sexual dimorphism and the ever-changing sea ice habitat influence polar bear reproductive behavior. Without static home ranges, male polar bears search widely for estrous females, often using olfactory cues. The mating system is polygynous, with males competing for mating opportunities in the spring. Delayed implantation allows females to acquire adequate fat reserves for fetal development and lactation prior to denning. Denning is facultative except in pregnant females, which may remain in dens for up to seven months. During the winter, they give birth and nurse altricial cubs, then emerge from the den in the spring. Cubs are weaned at 2.3 years of age. The prolonged pre-weaning period and a cub mortality rate of 20–96% result in a low reproductive rate compared with other terrestrial mammals. If the sea ice continues its current trajectory of decline because of climate change, up to two-thirds of existing polar bear populations may disappear by the middle of the twenty-first century

Keywords Altricial · Climate · Cub · Disturbance · Den · Implantation · Lactation · Mating · Olfactory · Polar bear · Polygynous · Reproduction · Sea ice

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14.1 Introduction

The eight extant species of bears share many traits, including morphology, reproduction, social behavior, and longevity (Stirling and Derocher 1990). However, the habitats they occupy vary widely, ranging from tropical to polar and terrestrial to marine. These differences have influenced their behavior and diet, which ranges from herbivory to carnivory with variations in between. The subgroup of Holarctic bears includes the American black bear (*Ursus americanus*), brown bear (*U. arctos*), and polar bear (*U. maritimus*). Males and females only associate to mate, and males play no role in raising offspring (Stirling and Derocher 1990; Stirling 2011). This subgroup also shares similarities in their reproductive biology, including (1) extended estrus for several months, (2) breeding in spring, (3) delayed implantation of the blastocyst, (4) hibernation for 3–7 months, and (5) birth of altricial young in a den during the winter (Folk et al. 1980; Ramsay and Dunbrack 1986; Ramsay and Stirling 1988; Amstrup 2003). In this chapter, I discuss both the reproductive and denning ecology of the polar bear.

14.2 Reproduction

This discussion of polar bear reproduction includes the (1) mating system, (2) reproductive cycle, (3) reproductive roles of adult males, females, and cubs, and (4) potential effects of climate change on reproductive behavior.

14.2.1 The Mating System

The mating system of polar bears has been influenced by their sexual dimorphism and extensive sea ice habitat (Fig. 14.1). Unlike terrestrial black and brown bears, polar bears generally live on sea ice, which varies in time, spatial extent, and quality (Ferguson et al. 2000a; Durner et al. 2004). Polar bears select areas of sea ice that optimize seal hunting, except when seeking females for breeding (see Chap. 15; Ramsay and Stirling 1986). However, variability in sea ice makes feeding and breeding more complicated than it is for land-based bears (Ramsay and Stirling 1986; Stirling 2011; Stern and Laidre 2016). For example, the distribution of seals is influenced by the timing of sea ice formation and retreat, which results in unpredictable spatiotemporal prey availability (Smith 1980). As a result, polar bears wander widely in search of food and mates, resulting in multiannual home ranges that are much larger than those of most terrestrial mammals (Fig. 14.2; Amstrup et al. 2000; Amstrup 2003).

Females hunt seals to support their daily metabolic requirements and to acquire energy reserves (i.e., fat) in advance of reproduction. Estrous females have pedal

Fig. 14.1 Sexual dimorphism in polar bears as apparent from facial profiles, body size, foreleg guard hairs, ear locations, and scarring (male on right), Western Hudson Bay, Canada. Photo Credit: © D. Guravich/polarbearsinternational.org

Fig. 14.2 Polar bear in search of seals on the sea ice of the Southern Beaufort Sea, Alaska. Photo credit: © S. Amstrup/polarbearsinternational.org

glands, which passively deposit a scent while walking, enabling males to track them (Molnár et al. 2008; Owen et al. 2014; Sergiel et al. 2017). In one case, a male polar bear tracked an estrous female for more than 145 km (Derocher 2012). This sensory adaptation enables potential mates to unite in the vastness of their Arctic and sub-Arctic habitat.

Fig. 14.3 Sexual dimorphism in polar bears: Adult male heads are blockier, ears set farther apart than females, facial scars evident. Photo credit: © T. Smith/byu.edu

Polar bears exhibit sexual dimorphism in body mass, skull size, dentition, and the length of fur on their front legs (Figs. 14.1, 14.3, and 14.4; Ramsay and Stirling 1986; Stirling 2011). Generally, adult males are twice the size of females, with the largest males approaching a body mass of 700 kg (Kolenosky et al. 1992; Derocher et al. 2010). As cubs, both sexes are morphologically similar at den emergence and remain so until their second year, at which time males become larger in body mass, length, and head size (Derocher et al. 2005). Females reach asymptotic body mass by the age of seven years, but males do so at 13–20 years of age (Derocher and Wiig 2002). The shape of the skull is distinctive; with males having a longer skull with a more pronounced sagittal crest (Derocher 2012). Similarly, there are sex-related differences in dentition, with males having significantly longer molars than females (Larsen 1971). Guard hair length is significantly longer in adult males, a secondary sexual characteristic, which may convey fitness to prospective mates (Hamilton and Zuk 1982; Derocher et al. 2005). Both sexual dimorphism and differing reproductive strategies have led to sexual segregation among bears, including polar bears (Clark and Stirling 1998; Rode et al. 2006; Laidre et al. 2013).

The sex ratio for male and female polar bears is close to unity (Stirling 2011). However, females breed every three years on average, so there are three adult males for every estrous female annually (Ramsay and Stirling 1986). Because of this sexual asymmetry, the mating system has been described as polygynous, polyandrous, female defense polygynous, and serial monogamous (Ramsay and Stirling 1986; Berta and Sumich 1999; Derocher et al. 2010). Given the frequency of broken teeth, wounding, and facial scarring among competing males, it also has been described as

Fig. 14.4 Sexual dimorphism in polar bears: Adult female facial characteristics are smooth, more dog-like, ears closer, and little to no scarring. Photo credit: © T. Smith/byu.edu

scramble-competition polygyny (Fig. 14.5a; Ramsay and Stirling 1986; Schwagmeyer 1988; Derocher et al. 2010). The consensus at this time is that the polar bear has a polygynous mating system, driven largely by the disparity between available estrous females and males competing for mating opportunities (Derocher et al. 2010).

14.2.2 *The Reproductive Cycle*

Polar bears have large home ranges, low population densities, and are constantly on the move because of seasonal changes in the sea ice (Ferguson et al. 2000a; Mauritzen et al. 2003). Consequently, it has been difficult to study their reproductive cycle in detail (Derocher et al. 2010). Polar bears mate on the sea ice in the spring (March–May), although there is latitudinal temporal variation (Wiig et al. 2008). During the breeding season, females with dependent young avoid areas where polar bears congregate, primarily the highly productive sea ice edge where ringed (*Pusa hispida*) and bearded (*Erignathus barbatus*) seals raise their pups (Fig. 14.5b; Smith 1980; Taylor et al. 1985). Males seek out estrous females at this time of year, but females with dependent young are anoestrus while lactating because of elevated serum prolactin, which inhibits ovulation (Ramsay and Stirling 1986). In the first year postpartum, the female's milk is 32–36% fat (Fig. 14.6; Cook et al. 1970; Derocher et al. 1993). The fat content of milk does not appear to decline in females

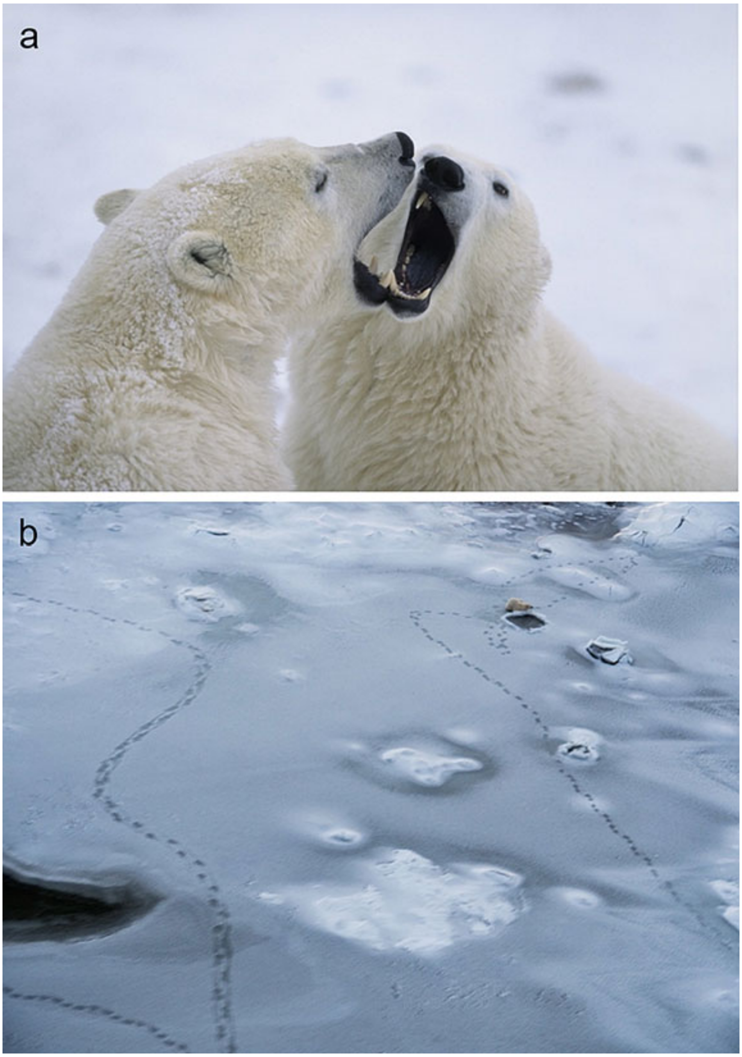

Fig. 14.5 (**a**) Polar bears spar with teeth and claws to establish dominance. (**b**) Polar bear waiting by a seal breathing hole. Images courtesy of (**a**) © Daniel J. Cox/Arctic Documentary Project and (**b**) © M. Stevens / polarbearsinternational.org

nursing older offspring on the sea ice, but the percentage declines by nearly half (18%) in the second year on land in the summer (Derocher et al. 1993; Arnould and Ramsay 1994). The amount of time cubs spend nursing also declines as they increasingly feed on seals captured by the female. As milk production decreases, females enter estrus, which attracts males and initiates weaning (Ramsay and Stirling 1986). Only in rare instances do cubs remain with the impregnated mother, although the occurrence of mixed-age litters has been reported.

Fig. 14.6 Mother nursing twin cubs, Wapusk National Park, Western Hudson Bay, Canada. Photo credit: © Daniel J. Cox/Arctic Documentary Project

In the spring, lone females seek highly productive hunting areas to gain body fat prior to breeding. The stored energy must sustain them through 3–5 months of denning, birth, and lactation. In the autumn, pregnant females seek denning areas where they will give birth to cubs in midwinter. Cubs can remain with their mother for up to 3.5 years (Ramsay and Stirling 1988; Derocher and Stirling 1992), although most are weaned at 2.3 years of age (Amstrup 2003). By comparison, American black bears typically wean after 1.3 years, and brown bears wean after 2.3 years, similar to polar bears (Pelton 2003; Schwartz et al. 2003). The prolonged association of cubs with their mothers influences polar bear reproductive rates, which are among the lowest measured in terrestrial mammals (Derocher and Stirling 1996).

14.2.3 The Role of Adult Males in the Reproductive Cycle

The ever-changing sea ice habitat means that static home ranges do not exist, and the location of sexually receptive females is unpredictable (Ramsay and Stirling 1986). Once a female is located, males will ‘herd’ her for days to remote areas to minimize the likelihood of encountering other males (Fig. 14.7; Stirling et al. 2016). If other males do appear, competition for breeding rights will occur. In this sexually dimorphic species, size is an advantage, and the largest males control access to females. Nevertheless, contests over females occur, as evidenced by scars, wounds, and broken canine teeth (Ramsay and Stirling 1986). The winner may court the female for days until copulation. Observations of actual breeding are rare (Wiig et al. 1992; Amstrup 2003; Stirling et al. 2016). However, males have been observed mounting the same females periodically for more than a week, with copulations lasting from 51–150 min (Stirling 2011; Stirling et al. 2016). Once a sexually receptive female is located by a male, successful breeding may require >2 weeks to complete (Stirling et al. 2016).

Fig. 14.7 A male polar bear pursues a female during the reproductive period in Western Hudson Bay, Canada. Photo credit: © D. Guravich / polarbearsinternational.org

14.2.4 The Role of Adult Females in the Reproductive Cycle

Female polar bear reproduction is similar to that of other Holarctic Ursidae: they breed in the spring, experience delayed implantation, fast through a lengthy denning period, give birth to cubs in midwinter, and emerge from the den in the spring (Amstrup 2003). Because breeding occurs in early spring, before a female has sufficient body fat reserves to carry a fetus through to birth, delayed implantation functions as a safeguard (Amstrup 2003). Females experience a prolonged estrus from March–June, depending on their location (Ramsay and Stirling 1986; Wiig et al. 2008). Implantation of the blastocyst is delayed until autumn, with a gestation period of 195–265 days (Amstrup 2003). First parturition occurs at 4–5 years of age, and females continue to produce litters until an age ~20 years, after which fertility decreases (Taylor et al. 1987; Ramsay and Stirling 1988). At least 40% of adult females in Western Hudson Bay (WHB) display 2-year inter-birth intervals with 55% of cubs successfully weaned (Ramsay and Sterling 1988). In the Southern Beaufort Sea (SBS), the average inter-birth interval was ~3.5 years in the late 1980s (Amstrup and Durner 1995).

The average litter size throughout the Arctic is two cubs (Amstrup 2003), although it varies by location. The average litter size in the SBS is 1.6, whereas in WHB it is 1.9 (Fig. 14.8; Stirling et al. 1977; Amstrup et al. 1986; Ramsay and Stirling 1988; Oftedal and Gittleman 1989; Derocher and Stirling 1992). Milk consumption decreases as cubs age, with yearlings consuming one-fifth as much milk as those in their first year (Arnould and Ramsay 1994). Survival of the cubs depends on prey availability and female hunting success (Amstrup 2003). Female lifetime reproductive success will depend on their longevity, access to mates and

Fig. 14.8 A mother and yearling cross a frozen lake in Western Hudson Bay, Canada. Photo credit: © T. Smith / byu.edu

dens, and cub survival (Taylor et al. 1987). Perturbations that negatively affect these variables reduce fitness and, ultimately, species survival.

14.2.5 The Role of Polar Bear Cubs in the Reproductive Cycle.

Polar bear population dynamics are affected by pre-and post-weaning cub survival. Cubs are born in midwinter (December–January) and gain body mass rapidly (Kenny and Bickel 2005; Robinson et al. 2012). Newborns weigh <1 kg at birth (Blix and Lentfer 1979; Kenny and Bickel 2005), but this increases to 13–22 kg when they emerge from the den in March or early April (Fig. 14.9; Amstrup 2003). Cub survival is correlated with neonatal and maternal body mass and, to a lesser extent, with maternal age, cub sex, and litter size (Ramsay and Stirling 1988; Taylor et al. 1987).

Cub mortality following den emergence ranges from 20–96% among populations (Ramsay and Stirling 1988; Amstrup and Durner 1995; Bromaghin et al. 2015). Causes of mortality include disease, starvation, intra/interspecific predation, and accidents (Blix and Lentfer 1979; Clarkson and Irish 1991; Kenny and Bickel 2005; Amstrup et al. 2006; Richardson and Andriashek 2006). In WHB, cubs have a mean multi-year survival of 53%, and the most important variables are spring and autumn body mass. Cub body mass is correlated with prey availability and, when inadequate, with cub mortality (Derocher and Stirling 1996). Among polar bear populations, litters with three cubs experience higher mortality rates than those with one or two cubs (Robinson et al. 2012; Bromaghin et al. 2015).

14.3 Denning

Polar bear denning is unique among bears in that it is facultative unless the female is pregnant, and maternity denning is unparalleled in its duration. In this section, I discuss the origins and types of denning, the role of maternity denning, and the anticipated impacts of climate change on denning.

14.3.1 Denning Ecology

Many families in the order Carnivora use dens as a part of their lifecycle. The family Ursidae is no exception, with a wide variety of denning strategies among the eight extant species. Specifically, polar bears use dens for a variety of reasons, including

Fig. 14.9 A cub of the year near its den in Western Hudson Bay, Canada. Photo credit: © Daniel J. Cox/Arctic Documentary Project

(1) thermoregulating during extreme weather, (2) resting after feeding, (3) escaping insects during the summer, and (4) avoiding predators (Harington 1968; Ramsay and Stirling 1990; Amstrup and Gardner 1994; Messier et al. 1994; Ferguson et al. 1997, 2001). All polar bears use snow shelters for up to four months, during which time they fast when food is unavailable (Harington 1968; Ferguson et al. 2000b). Unlike

other Holarctic Ursidae, only pregnant polar bears den throughout the winter. Other age and sex cohorts remain active year-round, except when using temporary snow shelters during extreme weather or resting after feeding (Harington 1968; Ramsay and Stirling 1990; Amstrup and Gardner 1994). In early winter, pregnant polar bears excavate dens on the sea ice and onshore (Harington 1968; Lentfer and Hensel 1980; Ramsay and Stirling 1990; Amstrup and Gardner 1994). During this time, they enter a metabolically dormant state of fasting, which continues until late winter when the mother emerges from her den with her cubs (Nelson 1980).

14.3.2 Distribution of Denning Sites

There are three types of polar bear dens: maternity, temporary, and natural (Harington 1968). Maternity dens are occupied by pregnant females for up to seven months and are used for birth, neonatal nursing, and protection from the weather (Uspenski and Kistchinski 1972; Durner et al. 2003). Temporary dens are used to escape harsh weather or to rest after hunting or feeding. Natural shelters include jumbled ice blocks, snow bridges, or caves (Harington 1968). Here I will focus on maternity dens.

The 19 subpopulations of polar bears are widely distributed throughout the Arctic, but high concentrations of maternal dens occur in only a few locations: Kong Karls Land in Svalbard, WHB in Canada, and Wrangel and Herald Islands in Russia (Amstrup and Gardner 1994; Amstrup 2003; Obbard et al. 2010). For example, den concentrations on Russia’s Wrangel and Herald Islands and Svalbard’s Kongsøya Island are >12 dens km^{-2}, with some spaced as close as 15 m (Uspenski and Kistchinski 1972; Hansson and Thomassen 1983; Ovsyanikov 1998). These preferred denning locations provide rugged, mountainous terrain immediately adjacent to productive seal hunting areas. In northern Alaska, the mean distance of dens from the coast is 1.7 ± 4.5 km, with a few dens as far inland as 61 km from the Beaufort Sea (Amstrup and Gardner 1994; Durner et al. 2003). In this area, dens are widely separated by many kilometers (Smith et al. 2007).

Maternal dens in snowdrifts on sea ice are rare, except in the SBS population, where 53% of dens occurred on the sea ice from 1981–91 (Amstrup and Gardner 1994). In other areas, such as the Canadian High Arctic, Svalbard, Greenland, the Russian Arctic, and the Chukchi Sea, dens usually occur in snowdrifts on land (Fig. 14.10; Harington 1968; Uspenski and Kistchinski 1972; Ramsay and Stirling 1990; Wiig 1995; Born et al. 1997; Rode et al. 2015). However, sea ice denning likely occurs to some extent in most populations based on anecdotal observations of females with young cubs leaving tracks on sea ice far from shore in early spring, suggesting that these cubs were not born on land (Larsen et al. 1983; Amstrup 2003).

Sea ice dens are less stable than those on land because of shifting ice conditions. Polar bears that enter a den on the sea ice in late autumn may emerge with cubs as far as 1000 km from the point of origin (Amstrup and Gardner 1994). In spite of the perils associated with sea ice denning (e.g., collision with other ice floes, ice turning

Fig. 14.10 A polar bear den in Western Hudson Bay, Canada. Photo credit: © Daniel J. Cox/Arctic Documentary Project

over, thawing), it is a successful reproductive strategy in the SBS (Amstrup 2003). However, females occupying land dens, where snowfall is greater, have higher reproductive success than those on the sea ice (Rode et al. 2018).

Regardless of location, successful denning requires the accumulation of snow, which allows a pregnant female to excavate a den in early winter (Amstrup 2003). Dens occur most often in snowbanks of suitable depth and density, which form on the leeward slopes of elevated terrain (Harington 1968). Dens in northern Alaska are associated with landscape features such as coastal bluffs, riverbanks, lakeshores, and occasionally gravel pads in oil fields (Durner et al. 2003). These topographic features, even with a small (~1.5 m) rise, accumulate snow early in winter and are suitable den sites (Durner et al. 2001). In WHB, pregnant females initially select dens excavated in peat banks along the edges of creeks, rivers, and lakes adjacent to open lichen tundra (Richardson et al. 2005). This occurs in late summer following sea ice break-up in Hudson Bay and prior to autumn snowfall. These den sites range from 7–150 km from the coast, presumably to avoid other bears summering on land (Stirling et al. 1977). In other areas of Canada, such as the Northwest Territories, Viscount Melville Sound, Baffin Bay, and Nunavut, polar bears seek rugged terrain where snow accumulates in early winter close (8–20 km) to the coast (Harington 1968; Messier et al. 1994; Ferguson et al. 2000b; Van de Velde et al. 2003).

14.3.3 Den Structure

Although denning location varies, den structure is similar (Durner et al. 2003). In northern Alaska, dens begin as small, single chambers with a short entrance tunnel, which eventually drifts closed (Fig. 14.11). As winter progresses, the overlaying snowpack may deepen considerably (as much as 4 m month^{-1}) (Robinson et al. 2014). Snow depths above the chamber in late winter range from 0.1–4.0 m (Durner et al. 2003). Chamber heights range from 0.5–1.0 m (Harington 1968; Uspenski and Kistchinski 1972; Lentfer and Hensel 1980; Larsen 1985). Multiple chambers within a den are rare (i.e., ~18–30%) (Lentfer and Hensel 1980; Durner et al. 2003). Some dens have ventilation holes, although they are not essential for air exchange because of the porous nature of snow (Harington 1968; Lentfer and Hensel 1980; Durner et al. 2003). The inner walls of den chambers eventually become icy (<3 cm), but females claw through this, presumably to enhance gas exchange (Fig. 14.12; Lentfer and Hensel 1980).

14.3.4 Den Site Fidelity

Concentrations of maternal dens in some areas (e.g., Wrangel Island, WHB, etc.) suggest site fidelity (Uspenski and Kistchinski 1972; Amstrup 2003). In northern Alaska, polar bears use barrier islands, riverbanks, and other topography where snow-drifts form early in the winter (i.e., November) (Smith et al. 2007, 2013). As a result, some areas in Alaska (e.g., Pingok, Cottle, Howe, and Flaxman Islands) consistently have winter maternity dens (Smith et al. 2013). However, radio-tracking

Fig. 14.11 View out of the chamber and entrance tunnel of a polar bear den in Western Hudson Bay, Canada. Photo credit: © Daniel J. Cox/Arctic Documentary Project

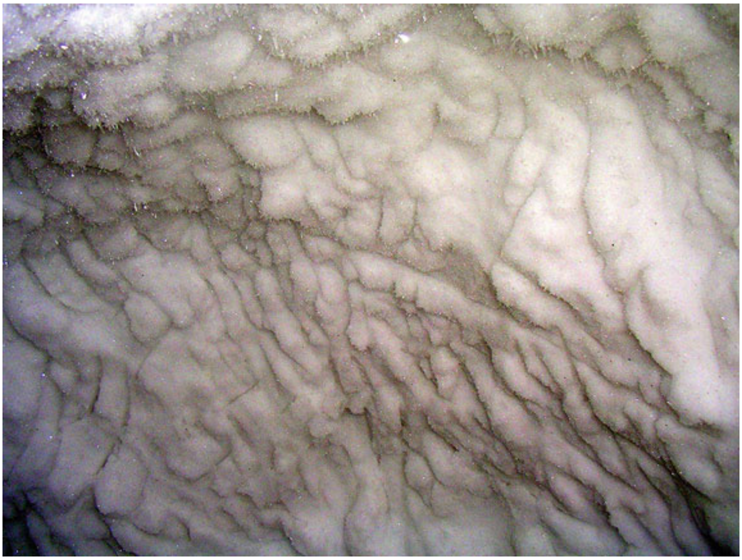

Fig. 14.12 Claw marks on maternity den walls, Southern Beaufort Sea, Alaska. Photo credit: © T. Smith/byu.edu

data from female polar bears in the SBS found that successive maternity dens were separated by ~300 km, indicating a lack of specific site fidelity among individuals (Amstrup and Gardner 1994). Likely determinants of the denning site location include weather and ice conditions, which will vary annually (Amstrup 2003).

In the SBS, females that den on the sea ice in one year tend to do so in subsequent years, although there is a trend for denning on land (Amstrup 2003; Fischbach et al. 2007; Olson et al. 2017). From 1985–94, 62% of SBS polar bears denned on the sea ice, but from 1998–2004, that number had declined to 37%, while denning on land steadily increased from 34–55% from 1985–2013 (Fischbach et al. 2007; Olson et al. 2017). A reduction in sea ice appeared to be the cause of this increasing frequency of denning on land. A shift in denning was not observed in the Chukchi Sea, but the majority (92%) of bears were denning on land when research began in 1986, and the percentage (84%) had not significantly changed by 2013 (Rode et al. 2015).

In WHB, Wapusk National Park has hundreds of maternity dens in peat beneath black spruce trees (*Picea mariana*) in late summer (Derocher et al. 1992; Scott and Stirling 2002). Births occur in these earthen dens between mid-November and mid-December, often before significant snow accumulation (Derocher et al. 1992). These dens expand as snowdrifts accumulate throughout the winter (Richardson et al. 2005). Polar bears have used this area for maternity denning for several hundred years or longer (Scott and Stirling 2002). However, a study of 67 maternity dens in this area found that no individual polar bear used the same den twice

(Ramsay and Stirling 1990). On average, bears selected den sites 27 km (4–52 km) apart between years (Ramsay and Stirling 1990). The distribution of land dens in Wapusk National Park has shifted markedly over a 20-year period (Ramsay and Stirling 1990). As the climate warms and permafrost-peak banks melt under black spruce, the long-term effect on denning behavior in this area is unknown (Derocher et al. 2004).

14.3.5 Denning Chronology

Den construction occurs on both the sea ice and on land when sufficient snow has accumulated to allow excavation. For bears that den on the sea ice or move from the sea ice to land, the timing of sea ice consolidation can alter the onset of denning (Amstrup 2003). In the SBS, polar bears come ashore to den from late October to early November, whereas bears in Svalbard enter dens in November and December (Lønø 1970; Lentfer and Hensel 1980). For SBS and Chukchi Sea polar bears, the mean date for denning (den entry) is mid-November (Amstrup and Gardner 1994; Rode et al. 2018). In the 1990s, the mean date for the start of denning (den entry) in Baffin Bay was 7 September, but this date shifted to 5 October by the 2000s (Escajeda et al. 2018). Mean denning date from 1989–97 in the Canadian High Arctic, including Baffin Bay and Davis Strait, was mid-September (Messier et al. 1994; Ferguson et al. 2000b). Although polar bear use of sea ice habitats near east Greenland changed markedly from 1979–2012, den entry date did not (Laidre et al. 2015). Arctic warming will have significant spatiotemporal effects on polar bears, but how they manifest for maternity denning on the sea ice is unknown.

Polar bears in the SBS had a mean emergence date of 1 Mar ± 2.1 days from 1985–2013 (Rode et al. 2018). In northern Alaska from 2002–03, family groups emerged from dens slightly earlier (18 Mar ± 2.4 days) than the mean emergence date (25 Mar ± 1.5 days) for polar bears on Herald Island, Russia (Ovsyanikov 1998; Smith et al. 2007). By contrast, den emergence was nearly a month earlier (25 February) for WHB polar bears in the vicinity of Churchill, Manitoba (Lunn et al. 2004). The behavior of females and cubs during den emergence varies (Hansson and Thomassen 1983; Smith et al. 2007). After emergence, females and cubs in northern Alaska and Hudson Bay remained near the den for 2–18 days (Lunn et al. 2004; Smith et al. 2007). On the North Slope of Alaska, maternal groups did not range farther than 100 m from dens prior to site abandonment (Smith et al. 2007). In contrast, post-denning bears on Wrangel Island ranged up to 1 km from dens, and they created extensive networks of trails and daybeds during a gradual departure (Uspenski and Kistchinski 1972).

14.3.6 Post-denning Behavior

There are limited data on the activity of females and cubs after emergence but prior to den abandonment (Hansson and Thomassen 1983; Amstrup and Gardner 1994; Ovsyanikov 1998; Smith et al. 2007, 2013). Maternal groups continue to spend the majority of their time (~81%) in the dens after initial emergence (Hansson and Thomassen 1983). More information is available on females than their cubs (Smith et al. 2007). Nursing represents 3.6% of daily activity, but there are no focal observations of cubs nursing. While outside the den, females are inactive 66% of the time and cubs 42% (Hansson and Thomassen 1983). Although the sample size is small, there is no correlation between weather and polar bear activity outside of the den in northern Alaska (Smith et al. 2007). Using the den site after initial emergence may enable cubs to gain body mass and strength before the den is abandoned (Fig. 14.13; Hansson and Thomassen 1983; Messier et al. 1994).

14.3.7 Response to Human Activity at Maternal Den Sites

Most carnivorans respond to humans by moving away with little energetic cost (Linnell et al. 2000). However, displacement of hibernating polar bears is energetically costly, increases exposure to predation, and may compromise reproduction (Linnell et al. 2000). When disturbed, female bears are more likely to abandon dens in the autumn because they have less to lose than the period immediately preceding or following the birth of the cubs (Belikov 1976; Amstrup 1993). As a result, their

Fig. 14.13 Mother and cubs denned in black spruce in Western Hudson Bay, Canada. Photo credit: © Daniel J. Cox/Arctic Documentary Project

Fig. 14.14 A polar bear at a den entrance encounters a Tucker Sno Cat on Alaska's North Slope. Photo credit: © T. Smith/byu.edu

tolerance to anthropogenic disturbance likely increases through the winter (Amstrup 1993). The reproductive cost of disturbance is higher in the spring if it results in premature den abandonment and the subsequent death of cubs, which may result from: (1) hypothermia, (2) poorly developed muscular strength and motor skills, or (3) some combination of these factors (Hansson and Thomassen 1983; Robbins 1993; Amstrup and Gardner 1994; Ovsyanikov 1998; Linnell et al. 2000). However, linking human disturbance to den abandonment has been difficult because bears occasionally abandon dens in areas devoid of human activity, making cause-and-effect difficult to prove (Amstrup 1993; Amstrup and Gardner 1994; Rode 2018).

A few studies have documented the response of denned polar bears to human activity (Amstrup 1993; Smith et al. 2007, 2013; Larson et al. 2019). Denned polar bears are tolerant of human disturbance—including industrial activities—on the North Slope of Alaska (Amstrup 1993; Smith et al. 2007). They showed no overt response and appeared tolerant of a wide variety of human activities (e.g., humans on foot, snowmobiles, trucks, and aircraft) near dens (<1.6 km) (Fig. 14.14; Larson et al. 2019). Den abandonment because of incidental human activities near dens and the subsequent loss of cubs has yet to be documented on the North Slope.

A number of studies have assessed human disturbance of denned polar bears using indirect methods (Blix and Lentfer 1992; MacGillivray et al. 2003; Lunn et al. 2004; Owen and Bowles 2011). Artificial dens absorb sound and vibration, so activities such as seismic testing, drilling, and vehicular transport at a distance >100 m are unlikely to disturb denned bears (Blix and Lentfer 1992; MacGillivray et al. 2003). However, helicopters and some ground vehicles (Hägglunds track vehicles) are detectable in dens at ~1000 m. Although the hearing range and sensitivity of polar bears has been measured, more research is needed on the effects of sound on denned bears to enable more informed decisions regarding human activity in the vicinity of maternity dens (Kriebel et al. 2001; Owen and Bowles 2011).

14.4 The Effect of Climate Change on Reproduction

If sea ice continues its current trajectory of decline, up to two-thirds of existing polar bear populations may disappear by the middle of the twenty-first century (Amstrup et al. 2008, 2010; Amstrup 2011). One of the major effects of diminishing sea ice will be the inability of females to access traditional denning areas because of open water (Derocher et al. 2011). In addition, there will be a concomitant decline in the availability of seals, which prevents females from achieving the mass gain (primarily fat) necessary for reproduction (Derocher and Stirling 1992). Adequate pre-denning body mass ensures that parturient females can fast for up to seven months, during which time they will give birth and nurse cubs before they resume feeding (Nelson 1980). However, prey availability is expected to decline as sea ice becomes less stable during the winter and spring, which reduces habitat for ringed seal pupping (Stirling and Smith 2004). The polar bear population in WHB declined 22% (from 1200 to 935) from 1987–2004 (Stirling et al. 1999; Stirling and Derocher 2007). This decline is correlated with an increasingly early break-up of sea ice, which reduces access to prey (Gagnon and Gough 2005; Stirling and Derocher 2007). Similarly, polar bears in the SBS declined 25–50% because of diminishing sea ice and reduced availability of seals from 2001–2010 (Bromaghin et al. 2015).

Climate change is expected to enhance rainfall during winter and spring, which will negatively affect both polar bears and seals (Stirling and Smith 2004). With dwindling prey and associated nutritional stress, there likely will be an increase in infanticide and cannibalism, both of which have been documented in the SBS and Svalbard (Amstrup et al. 2006; Stone and Derocher 2007). As the climate warms and sea ice becomes less stable, males will have difficulty tracking females, which will disrupt breeding (Stirling 2011). As stated by S.C. Amstrup in the *New York Times*, “[a]s the sea ice goes, so goes the polar bear” (Broder and Revkin 2007). Sea ice is essential habitat for polar bear survival. Climate change will cause the demise of polar bears if changes in sea ice habitat continue on their current trajectory.

14.5 Future Research

Further research is needed to understand how climate change will affect all phases of the polar bear reproductive cycle. The negative effects associated with climate change on the lifecycle of polar bears, especially maternity denning, may be severe (Stirling and Derocher 2007). Effective management of human activities near polar bear dens is essential to mitigate potential effects, especially with regard to noise (Owen and Bowles 2011). Data regarding polar bear responses to anthropogenic activity near maternity dens have been anecdotal and opportunistic. We need hypothesis-driven, experimental research investigating the response of bears to disturbance, including energetic costs and reproductive stress (Owen and Bowles 2011; Larson et al. 2019). We understand basic aspects of polar bear reproductive and denning behavior, but we have a poor understanding of the effects of human disturbance. Unfortunately, climate change may cause the demise of polar bears before we can more fully understand and mitigate these adverse effects.

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Chapter 15
Polar Bear Maternal Care, Neonatal Development, and Social Behavior

Megan A. Owen

Abstract Polar bear maternal behavior and neonatal development are difficult to study because maternal dens are secluded and generally inaccessible. As a result, much of what we know comes from polar bears in zoos. Altricial polar bear cubs (litter size 1–3) 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. Because females fast and lactate while caring for neonatal cubs, they lose ~44% of their body mass during the denning period. Maternal attentiveness to cubs accounts for $<15\%$ of the daily activity budget in the den and includes nursing, licking, positioning cubs, and postural changes to ensure cubs stay warm. The female shelters the cubs on her chest, covering them with her limbs to provide thermal insulation and warmth while affording proximity to teats for nursing. With a fat content of ~36%, milk provides the energy and nutrients needed for rapid maturation. Polar bear cubs vocalize ~25% of the time, usually associated with nursing while in the den. When cubs emerge from the den after 12 weeks, they have a litter mass that is similar to the gestational mass of other similarly sized mammals for the same period. Cubs nurse for up to 2 years, although they also eat seals captured by the female. Polar bears have a highly developed olfactory capacity, and exposure to sibling and maternal scent may reinforce kin recognition. Generally solitary, polar bears demonstrate social flexibility. Social interactions outside of reproductive contexts are largely associated with concentrated resources, such as food or habitat, and there is a range of characteristic social interactions in these settings, from adult social play to aggression, tolerance, and avoidance. Climate change and the loss of sea ice will affect polar bear social interactions, pre-denning energy storage, the timing of denning and parturition, maternal behavior, and cub survival.

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15.1 Introduction

Polar bears (*Ursus maritimus*) are generally solitary except during courtship, breeding, and while rearing offspring, but loose aggregations may form under some circumstances, particularly among adult males summering on land (Stirling and Derocher 1990; Derocher and Stirling 1990; Ovsyanikov 2005). Polar bears are non-territorial and range widely depending on sea ice conditions and prey availability. Traditionally, the study of animal behavior involves direct observation of focal animals with an adequate sample size to describe inter- and intra-individual variation based on age, sex, reproductive status, body condition, and environmental conditions (Altmann 1974; Owen et al. 2017). For polar bears and other cryptic, elusive, or geographically remote species, these traditional methods are often infeasible. Innovations in sensor technology and recorders (e.g., automated trail cameras, animal-borne sensors, passive environmental sensors) have enhanced our understanding of species that historically were unobservable (Wilmers et al. 2015; Allen et al. 2016; Studd et al. 2019). Nevertheless, polar bear life history (solitary, wide-ranging, amphibious) and habitat (Arctic sea ice) pose significant challenges for behavioral research. As a result, we have a poor understanding of how climate change will affect polar bear behavior and reproduction (Beever et al. 2017). There are few documented observations of two of the most critical aspects of the polar bear's life cycle—neonatal development and mating—but more information exists on the social interactions of polar bears nearshore and on land at concentrated food resources (Latour 1981a, b; Lunn 1986; Derocher and Stirling 1990).

In the wild, maternal care and neonatal development are almost completely hidden by the secluded and ephemeral nature of maternal dens, which has precluded both direct and indirect (e.g., video-audio surveillance) observation. As a result, much of our understanding has come from observations of denning females in captivity, assessments of females and cubs after they emerge from the den, and through insights from other bear species (Greenwald and Dabek 2003; Snyder et al. 2003; Dewing 2005; Kenny and Bickel 2005; Smith et al. 2007; Hall and Swaisgood 2009; Smith et al. 2013; van Gessel 2015). Because of their phylogeny and life history, polar bears demonstrate characteristics that reflect their terrestrial lineage and are more distinctly like other Ursidae than with the taxonomically related Pinnipedia (Rybczynski et al. 2009). Thus, the comparative descriptions in this chapter are framed primarily in the context of the Ursidae.

Sea ice dynamics influence polar bear encounter rates, and changes in sea ice stemming from climate change may negatively affect breeding success (Regehr et al. 2010; Molnár et al. 2014). Changes in sea ice also may increase the number and density of bears on land (Regehr et al. 2007; Rode et al. 2015; Atwood et al. 2016). While on land, polar bears are attracted to whale carcasses and refuse dumps around settlements, a behavior that increases intraspecific encounters and changes social-demographic spacing (see Chap. 17; Regehr et al. 2007; Rode et al. 2015; Atwood et al. 2016; Atwood 2017). This increases the chance of injuries from aggressive encounters with conspecifics (e.g., Amstrup et al. 2006).

In this chapter, I focus on maternal behavior and neonatal development during the 12-week maternal care period within the den. Technological advances for monitoring bears in captivity have provided new insight into their behavior, which is relevant to our understanding of the reproductive and intraspecific interactions of wild polar bears. The behavior of captive polar bears, even in an artificial situation, provides valuable information, which can be obtained by systematically collecting data on courtship, breeding behavior, and social spacing (Renner and Kelly 2006). An understanding of the behavioral mechanisms associated with maternal care and neonatal survival and the range of plasticity associated with these behaviors have shed light on selective pressures, which have shaped polar bear life history and inform predictive models of population persistence under rapid environmental change (Wong and Candolin 2015). I further describe the social interactions of polar bears both within family groups and among adult bears while aggregating on land.

15.2 Maternal Behavior and Neonatal Development

15.2.1 Gestation and Altriciality

Neonatal Ursidae are among the most altricial of eutherian mammals (Ramsay and Dunbrack 1986). Compared with the neonatal Arctic Pinnipedia, which are born on shore-fast ice or pack ice (e.g., walrus [*Odobenus rosmarus*], ringed seals [*Pusa hispida*], and bearded seals [*Erignathus barbatus*]), polar bear neonates are born at an earlier stage of development and are more dependent on maternal care and protection (Bowen 1991). The offspring of Arctic Pinnipedia develop sufficient strength and coordination to enter the water relatively quickly—within a few hours postpartum in the case of bearded seals and walrus pups and about two weeks for ringed seal pups (Bowen 1991; Kovacs 2009). This precocial ability to swim may have evolved in response to polar bear predation.

Eco-physiological constraints may have shaped the evolution of a short gestation period and associated neonatal altriciality for bears in general; these constraints also may have affected the developmental switch for neonates from transplacental to transmammary nourishment (Ramsay and Dunbrack 1986). This characteristic of bear reproduction reflects an adaptive response to the period of fasting associated with pregnancy and hibernation observed in Holarctic bear species (e.g., American black [*Ursus americanus*], brown [*Ursus arctos*], and polar bears). However, giant pandas (*Ailuropoda melanoleuca*), sun bears (*Helarctos malayanus*), Andean bears (*Tremarctos ornatus*), and sloth bears (*Melursus ursinus*) also exhibit a short gestation and altricial cubs, even though the peripartum fast is shorter (Spady et al.

2007). This indicates a phylogenetic explanation rather than one based on eco-physiology (Li and Smith 2020). However, female polar bears and brown bears in better body condition give birth sooner after breeding, indicating an eco-physiological influence on the duration of diapause rather than the duration of intrauterine gestation and the degree of fetal development (Robbins et al. 2012). This supports the hypothesis that short gestation among bear species reflects phylogenetic inertia, while the duration of diapause may be adaptive (McKitrick 1993; Li and Smith 2020).

Among the Ursidae, there is a range of maternal effort and attentiveness that is correlated with the degree of offspring altriciality and the duration of the peripartum maternal fast (Swaisgood et al. 2004). Altriciality is positively correlated with the degree and duration of obligate maternal care during postpartum denning, as indicated by the highly attentive maternal care of giant pandas whose cubs have the smallest birth mass, shortest intrauterine gestation period, and greatest altriciality among the Ursidae (Zhu et al. 2001; Snyder et al. 2016; Li and Smith 2020). The duration of the peripartum fast is negatively correlated with maternal effort because female energy conservation is critical for cub survival. This manifests in the recumbent body posture and passive maternal care (e.g., minimal postural changes and less overt manipulation of cub position) of the Holarctic bear species (Trivers 1974; Dewing 2005; Owen et al. 2013). Among bear species, the first weeks of life are particularly demanding on maternal attention and resources. In giant pandas and sun bears, maternal attentiveness decreases 2–3 weeks postpartum, while it is consistent and sustained in black and brown bears over the first eight weeks of denning, potentially reflecting a persistent need to conserve maternal energy stores (Dewing 2005; Owen et al. 2013).

15.2.2 Maternal Behavior

Video recordings of captive female polar bears with their cubs in artificial dens indicate that maternal care, cub dependence, and development exhibit greater similarities to black and brown bears than to other bear species (Fig. 15.1; Greenwald and Dabek 2003; Snyder et al. 2003; Kenny and Bickel 2005; Hall and Swaisgood 2009; van Gessel 2015). However, maternal behavior varies among individuals, which may be associated with age, experience, body condition, or other factors (Stirling and Derocher 1990; Derocher and Stirling 1994). Environmental changes that compromise body condition at the onset of denning, or the perception of threat during denning, may influence maternal behavior (Bennett and Murray 2014). Finally, the presence of zookeepers and the availability of food and water (whether consumed or not) may influence maternal behavior, so caution is warranted in extrapolating the behavior of captive bears to those in the wild.

Female polar bears fast and lactate while caring for neonatal cubs. Energy for the female's metabolic requirements and milk production comes from stored fat, so

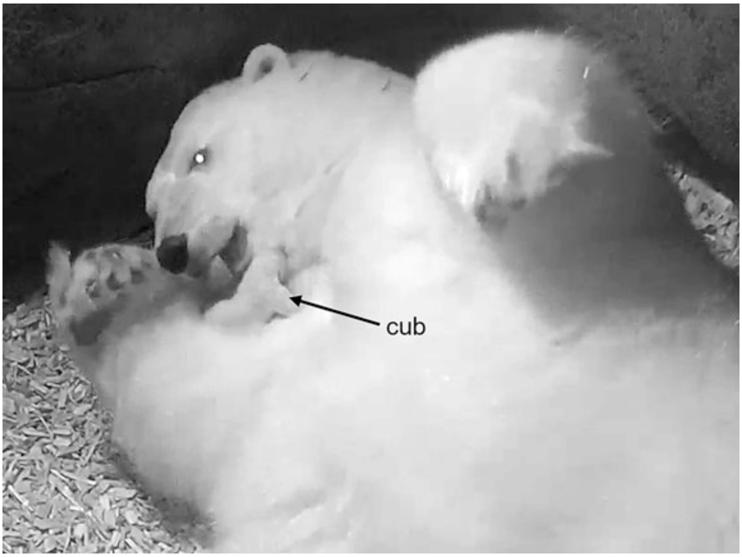

Fig. 15.1 Captive polar bear mother grooming her 2-week-old cub. Image courtesy of Erlebnis Zoo, Germany

energy conservation during the denning period is essential (Atkinson et al. 1996). While denning, females rest 75–85% of the time. Denning brown bears in the wild show higher levels of activity before parturition, but this has not been reported for polar bears (Friebe et al. 2014).

Captive female polar bears exhibit low levels (1–5%) of daily, self-directed activity (e.g., grooming, standing) during the postpartum denning period, with a gradual increase towards the end. Maternal attentiveness to cubs accounts for <15% of the daily activity budget within the den, which includes the facilitation of suckling, licking, positioning cubs, and postural changes to ensure cubs stay warm (Kenny and Bickel 2005). The female usually lays supine (facing upwards), wrapping neonates in her forepaws for warmth and access to nipples for suckling (Owen unpub. obs). Neonates emit plaintive vocalizations immediately after birth, which elicits female attention (R. Meyerson, pers. com.). In the absence of cub vocalizations, maternal attentiveness decreases, suggesting a direct association between offspring vocalization and maternal response. Females rarely vocalize. In a rare instance, a parturient female at the Dierenrijk Zoo in the Netherlands emitted vocalizations indicative of stress during the first three days postpartum (van Gessel 2015). Notably, this primiparous female did not demonstrate maternal care and its cub soon died.

Polar bear neonates are incapable of thermoregulation (i.e., maintaining a core body temperature of ~37 °C) and rely on bodily contact with the female for warmth (i.e., kleptothermy) (Blix and Steen 1979). This thermal dependence on the female decreases by the time the cubs are two months of age (Greenwald and Dabek 2003). Polar bear mothers shelter cubs on their chest and belly, covering cubs with their limbs to provide thermal insulation and warmth while affording proximity to teats for nursing. As a result, cubs in captivity are rarely visible on video monitors for the first 1–3 weeks postpartum. By six weeks of age, the growing cubs are easier to monitor.

Neonates require maternal facilitation to defecate. The female licks the anogenital region of the neonates to promote excretion and then consumes the feces. This also has been observed during the first two weeks postpartum in other bear species (Snyder et al. 2003; Hall and Swaisgood 2009; Owen et al. 2013). Beyond stimulating defecation and keeping offspring clean, maternal consumption of the excreta provides a means for recycling water and nitrogen during the fasting period (Oftedal et al. 1993). In contrast, female urination and defecation cease while fasting in the den both in the wild and in captivity.

When cubs emerge from the den after 12 weeks, their litter mass is similar to the gestational mass of other similarly-sized mammals over the same duration of development. Hence, the female polar bear creates an extrauterine environment for the development of altricial cubs using her body for warmth and nutrition in the den (Ramsay and Dunbrack 1986). By 12 weeks of age, cubs in captivity weigh 6–10 kg, with no clear pattern associated with rearing factors (either human/hand or mother reared), sex, or litter size (Kenny and Bickel 2005). Based on cub size and cub survival in the wild, there is no evidence that polar bear mothers differentially invest in male versus female neonates, but direct behavioral data to support this finding are lacking (Derocher and Stirling 1998). If maternal body condition or other factors prompt early emergence from the den, cub survival may be compromised if adequate growth and development have not occurred (Amstrup and Gardner 1994; Derocher and Stirling 1994; Rode et al. 2018). Further research is needed on the influence of maternal behavior and energetics during denning and how they are influenced by body condition and climate change (Pagano and Williams 2019).

15.2.3 Neonatal Behavior

Polar bear cubs are born in a maternal den during the winter (i.e., early January), but the range of dates is unknown (Derocher et al. 1992). Captive bears in the northern hemisphere give birth from October–February (Spady et al. 2007). Litter size ranges from 1–3. Twins are the modal litter size, and singleton litters are more common than triplets (Wiig et al. 2015). Litter size is not correlated with latitude (Derocher 1999). The postpartum denning period provides approximately three months of post-natal growth and development within or in proximity to the security, warmth, and seclusion of the den.

Altricial polar bear cubs (birth mass of ~650 g) have limited coordination and sensory capacity, sparse fur, and are completely dependent on the female for nourishment, warmth, and protection (Fig. 15.1; Blix and Lentfer 1979; Amstrup 2003; Kenny and Bickel 2005). Polar bears are born with their eyes closed and are incapable of coordinated movement (Kenny and Bickel 2005). The degree of neonatal altriciality, coupled with the abrupt transition to the locomotor and

Table 15.1 Milk fat content (%) among some bear and marine mammal species

Species	Mean milk fat content (%)
Polar bear (*Ursus maritimus*)	36[a]
Brown bear (*Ursus arctos*)	25[b]
Giant panda (*Ailuropoda melanoleuca*)	20[c]
Ringed seal (*Pusa hispida*)	38[d]
Bearded seal (*Erignathus barbatus*)	49[e]
Northern fur seal (*Callorhinus ursinus*)	53–72[f]
Galapagos fur seal (*Arctocephalus galapagoensis*)	32–35[g]
Beluga whale (*Delphinapterus leucas*)	27[h]

[a] Derocher et al. (1993)
[b] Farley and Robbins (1995)
[c] Oftedal and Gittleman (1989)
[d] Lydersen and Kovacs (1999)
[e] Kovacs (2009)
[f] Ashworth et al. (1966)
[g] Trillmich and Lechner (1986)
[h] Lauer and Baker (1969)

thermoregulatory demands of life outside the den, anchor a period of obligate rapid physical growth and behavioral development for cubs while in the den.

In the first weeks of life, movements are limited to shivering and squirming, which likely facilitate heat generation and access to teats for nursing, respectively. Neonates begin to show coordinated movement (e.g., head and neck) by about two weeks of age (Kenny and Bickel 2005). Coordinated movements of the body are apparent by the 4th week of life, with the onset of crawling beginning by 27–30 days of age (Owen unpub. obs.). By the end of the 12-week denning period, the cubs are able to follow the female and to thermoregulate. The rapid period of postpartum growth for neonates in the den is marked with important developmental milestones that reflect adequate acquisition of body mass, physical coordination, and behavioral development. Energy and nutrients for this rapid maturation are provided by milk, which is ~36% fat, the highest fat content of any bear species—comparable to the milk in some Pinnipedia (Table 15.1; Oftedal and Gittleman 1989; Derocher et al. 1993; Hedberg et al. 2011; Davis 2019). In Galápagos fur seals (*Arctocephalus galapagoensis*), the fat content of milk is positively correlated with the duration of maternal absence while at sea (Arnold and Trillmich 1985). In contrast to Pinnipedia, polar bear maternal attendance is virtually constant until weaning, with cubs relying on maternal milk to supplement their nutritional needs for upwards of two years (Blix 2016). Rapid cub growth makes lactation the most energetically costly part of reproduction, far exceeding the energetic costs of gestation (Gittleman and Thompson 1988; Clutton-Brock et al. 1989; Oftedal and Gittleman 1989; Molnár et al. 2009). As a result, females lose ~44% of their body mass during the denning period (Derocher and Stirling 1994). While den emergence varies throughout their circumpolar range, it primarily occurs from early March to early April, with females and cubs remaining near the den for an additional 1–4 weeks (Smith et al. 2007; B. Kirschhoffer unpub. obs.). Cubs continue to nurse for up to two years, although they also share seal meat obtained by the female (Blix 2016). While the dependence on milk diminishes over time, there is no evidence that the fat concentration of polar bear milk changes during the period of maternal care while on the sea ice (Derocher et al. 1993).

Although acoustic communication is common among many marine mammal species, it is only prominent in polar bears during the postpartum denning period (Tyack 1998; Stirling and Thomas 2003). By far, the most prominent feature of neonatal behavior is persistent and energetic vocalization. Bear cubs produce a range of vocalizations, which indicate need or contentment to the mother. While some vocalizations are unique to individual bear species, several call types are similar among species, with intensity and persistence loosely correlated with the degree of need or distress. Bear vocalizations are poorly described or categorized, although recent research has improved our understanding of the behavioral significance of neonatal vocalizations (Pokrovskaya 2013; Baotic et al. 2014). Captive polar bear cubs vocalize ~25% of the time during the 12-week denning period (Owen unpub. obs.). This is less than that observed in black (50%), brown (40%), and sun bears (40%) (Dewing 2005; Hall and Swaisgood 2009; Owen et al. 2013). Polar bear litters of two cubs are more vocal than singletons, but maternal activity varies little between singleton and twin litters.

The vocal repertoire of Ursidae neonates includes plaintive calls (e.g., cries, squawks, and squalls) and vocalizations that appear to signal contentment (Hall and Swaisgood 2009; Baotic et al. 2014). One vocalization in the latter category is described as a hum (i.e., a low, steady continuous sound like that of a purr; Peters et al. 2007). Humming is a relatively loud, rhythmic, and persistent emission documented in all bear species except the giant panda (Peters et al. 2007). In polar bears, maximum energy (amplitude) occurs at 280 Hz, which is consistent with the spectral parameters documented in other bear species (i.e., <500 Hz; Peters et al. 2007; Derocher et al. 2010). The mean maximum frequency of humming in polar bears is 850 Hz (Derocher et al. 2010). While the specific function of this vocalization is unknown, it is generally associated with nursing. This hum may signal successful feeding or may serve as a form of tonic communication that stimulates milk excretion (Peters et al. 2007).

Chuffing is another vocalization made by adult bears and cubs (Wemmer et al. 1976). In the mother-offspring context, the chuffing by females may promote contact. In the wild, it has been documented in older cubs within and outside of the den. The reliance on acoustic communication for the successful rearing of neonates is one reason that concerns persist regarding the effect of anthropogenic noise on cub survival (Perham 2005; Nachtigall et al. 2007; Owen and Bowles 2011; Owen et al. 2020). While anthropogenic noise may have significant non-auditory effects (e.g., stress, behavior change), it is unclear whether it could compromise cub survival by masking vocalizations, especially given the proximity between mother and cubs in the den and the intensity of cub vocalizations. Given the increasing occurrence of polar bears on land and the expansion of industrial activities in the Arctic, further research is needed (Ellison et al. 2012; Moore et al. 2012; Erbe et al. 2016; Southall et al. 2019).

15.3 Social Behavior

Polar bear cubs interact with their mother and littermates, and this is an important period for learning critical life skills (e.g., hunting, navigation) during the extended mother-offspring association (typically 2.5 but up to 3.5 years) (Macdonald 1983; Ramsay and Stirling 1988; Derocher et al. 1993). Once young cubs achieve a degree of coordination, play behavior (i.e., movements that do not result in the acquisition of a resource or resolving a need) can be observed in the den at 8–10 weeks postpartum. Play behavior includes paw swats and biting. Self-play and exploratory behavior, both tactile and olfactory, become more prominent at approximately eight weeks of age. After emergence from the den, the repertoire of play behavior expands greatly and is described elsewhere (see Chap. 14). While cubs do not participate in hunting during their first spring on the ice, yearlings and 2-year old cubs do (Stirling and Latour 1978). Although 2-year old cubs spend less time hunting than their mothers, their kill rate is similar to that observed for adults, demonstrating the importance of socially-facilitated learning prior to weaning (Stirling and Latour 1978).

With a modal litter size of two, most polar bear cubs engage in social behavior with siblings before they emerge from the den and until the dissolution of the family unit, or as long as littermates survive. Pre- and post-den emergence interactions with littermates provide opportunities to develop and refine social competence, including the development of agonistic and non-agonistic behavior (Bekoff 1972). There are anecdotal observations of siblings staying together after weaning, but it is unknown whether siblings will recognize one another once they are adults.

Polar bears have a highly developed olfactory capability, and intraspecific chemosignaling is an important means of managing social interactions (Figs. 15.2 and 15.3). Ontogenetic exposure to sibling and maternal scent during early intrafamilial interactions may support kin recognition (Hain and Neff 2006; Mitchell et al. 2018). Thus, both maternal and sibling cohabitation may serve to imprint kin recognition and provide olfactory evidence of relatedness, which could facilitate appropriate avoidance or tolerance behavior as adults. Olfactory recognition of kin has been documented in the giant panda and would be advantageous for the polar bear (Gilad et al. 2016).

In contrast to the tight-knit existence of polar bear females and their offspring, interfamilial interactions occur but are rare. For example, in a relatively dense maternal denning area in Kongsøya, Svalbard, tolerance among post-emergence family groups was documented, but overt social interactions or inter-litter play behavior was not observed. Even play behavior between littermates was <5% of the activity budget (Hansson and Thomassen 1983). In a similarly dense denning area on Herald Island, Russia, family groups did not interact (Ovsyanikov 1998). Den abandonment occurred when a younger female was approached by an older one, which may have been perceived by the young female as a threat to her litter (Ovsyanikov 1998). On Wrangel Island, Russia, non-breeding adult females may kill and eat cubs (Uspenski and Kistchinski 1972). These observations indicate a

Fig. 15.2 Female polar and her yearling offspring investigate the pawprints of an unidentified conspecific during the fall migration while waiting for Hudson Bay to freeze near Churchill, Manitoba, Canada. Image courtesy of J. Simerson

Fig. 15.3 An adult female polar bear engaged in olfactory investigation of paw prints while following the trail of an unidentified conspecific. Image courtesy of J. Simerson

complex relationship among polar bear behavior, population density, nutritional status, and resource availability (Amstrup et al. 2006).

Adult polar bears are generally solitary but engage in social behavior through direct interactions during breeding and intrasexual competition (see Chap. 14) or when in loose aggregations relative to concentrated resources (Latour 1981b; Derocher and Stirling 1990; Miller et al. 2015). Polar bears taking advantage of concentrated food sources (e.g., whale carcasses or garbage dumps associated with human settlements) exhibit intraspecific tolerance, moderate aggression, and submissive behavior when feeding on supplemental food sources. On the Beaufort Sea coast of Alaska, whale remains or bone piles (typically bowhead whale, *Balaena mysticetus*) can attract large congregations of polar bears (Herreman and Peacock 2013; Miller et al. 2015). Temporal partitioning of feeding occurs, and females with offspring are the most aggressive towards conspecifics when challenged and are more likely to feed when lone males are absent (Miller et al. 2015). Similarly, at a garbage dump near Churchill, Manitoba, Canada, females with offspring were more aggressive than bears without offspring (Lunn 1986). Additionally, social tolerance was exhibited among family groups with limited interactions. One instance of apparent cooperation between mothers was observed when females took turns feeding at the dump while the other waited nearby with young of both litters (Lunn 1986).

Polar bears risk some degree of intraspecific aggression to exploit relatively predictable resources, such as garbage dumps. The predictability and quantity of food indicate their potential energetic value, and the social transmission of the location of such resources is likely (Lillie et al. 2018). Knowledge of evolutionary novel foraging resources may spread through populations via social associations, such as mothers and offspring, or through social networks (Schakner et al. 2017; Lillie et al. 2018). Social networks have been documented in both solitary species and species that occur in low density. For example, information transmission through such networks has been documented in both black and brown bears (Mazur and Seher 2008; Morehouse et al. 2016).

Adults also engage in social behavior outside of face-to-face encounters, navigating to find or avoid conspecifics through olfactory communication. Anecdotal observations and limited empirical evidence indicate the capacity to assess the sex and reproductive status of conspecifics through olfaction and, if consistent with other bear species, other information may be discernable (e.g., kinship, age, competitive potential) (Fig. 15.3; Stirling and Derocher 1990; Owen et al. 2015). In a paired discrimination test, captive male and female polar bears could discriminate the sex of wild pedal scent donors. Males can discriminate among females available for mating, as indicated by chemosensory investigation, such as sniffing and flehmen (Owen et al. 2015). The latter behavior is indicative of reproductive status assessment as it facilitates the deep inhalation and passage of non-volatile compounds over the vomeronasal organ. The vomeronasal is an accessory olfactory organ for detecting pheromones emitted by conspecifics (Boschat et al. 2002; Tomiyasu et al. 2017). Olfactory communication may be critical for the avoidance of potentially aggressive conspecifics, especially for mothers with dependent young. Adult males have been observed attacking family groups and cannibalizing cubs and females (Taylor et al. 1985; Derocher and Wiig 1999; Amstrup et al. 2006).

The most prominent social behavior in polar bears is the occurrence of congregations while on land. Adult male polar bears, which are typically solitary on the sea

Fig. 15.4 Males engaged in social play or ‘sparring’ while waiting on land for the fall freeze-up of the Hudson Bay to begin, near Churchill, Manitoba, Canada. Images courtesy of J. Sheppard

ice and can cause life-threatening injuries during intrasexual competition for mates, form dense aggregations along the coast when forced on land in the summer (Latour 1981b; Ovsyanikov 2005; Derocher 2012; Stirling et al. 2016). Although these groups are highly fluid, aggregations typically consist of ~14 individuals (Derocher and Stirling 1990). These males often establish resting areas where they will lie within a few meters of one another (Ovsyanikov 2005; Derocher 2012). Individuals within these aggregations also exhibit play behavior (i.e., ‘sparring’) with one another (Latour 1981a). These interactions largely consist of structured motor patterns consistent with aggressive interactions but lacking the follow through and power that would accompany true aggressive interactions. This may provide an opportunity for males to practice their competitive skills (Fig. 15.4; Derocher and Stirling 1990). The primary social function of these aggregations is unknown, as few species of carnivores display such tolerance among adult males even during non-breeding periods (Latour 1981b; Derocher 2012). Males of greater mass tend to aggregate more frequently, which suggests that these social aggregations may diminish in some areas if adult males become energetically challenged by climate change (Derocher and Stirling 1990; Molnár et al. 2010).

15.4 Effects of Climate Change on Neonatal Behavior and Development

Climate-driven sea ice losses may decrease polar bear litter size throughout their circumpolar range by reducing maternal fat stores, leading to reduced cub survival (Derocher and Stirling 1994; Molnár et al. 2011; Stirling and Derocher 2012). Reductions in litter size and cub survival have been observed in the Western Hudson Bay, Southern Beaufort Sea, and Baffin Bay subpopulations, where significant sea ice losses have occurred in recent decades (Regehr et al. 2007, 2010; Laidre et al.

2020). Climate change also may influence the timing of parturition (Robbins et al. 2012). If maternal body condition causes den emergence before cubs gain adequate physical and behavioral maturity, they may not survive, especially if shore-fast ice is not available for foraging (Rode et al. 2010; Freitas et al. 2012). The timing of den emergence also may be negatively influenced by the integrity or stability of snow dens because of rain or unusually warm weather (Clarkson and Irish 1991; Stirling and Smith 2004).

15.5 Conclusions and Future Research

Our limited understanding of polar bear maternal behavior and neonatal development primarily results from logistical constraints, which prevent the use of traditional methods for behavioral research. Technological advances will facilitate new methods for monitoring polar bear life history, including individual variation and their sensitivity to environmental change (Wong and Candolin 2015). This is especially true for foraging success and its effect on body condition, maternal care, and the development and survival of altricial neonates. Because cub maturity at the time of den emergence may have a significant impact on survival, improved data are needed on parturition dates. Additionally, some historic denning areas overlap with human activities (including industrial-scale activities), and research is needed on the effects of anthropogenic activity and associated noise on maternal behavior, cub development, and the energetic costs of disturbance. Changes in sea ice extent and freeze-thaw dynamics may influence population density and communication modalities (e.g., chemosignaling) in such a way as to affect mate-search efficacy and reproductive rates. While we have a basic understanding of polar bear sensory systems, further research is needed on pedal scent communication and the potential for warming air temperatures to degrade chemosignals. A better understanding of polar bear behavior is essential as their habitat changes. Behavioral plasticity may afford polar bears the best chance of survival in the face of rapid sea ice losses, but such plasticity may drive polar bears into increasing conflict with humans, including overlap with human settlements (see Chap. 17).

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Chapter 16
Polar Bear Behavior in Response to Climate Change

Jon Aars

Abstract Although the Arctic has experienced previous periods of warmer climate, the rate of sea ice loss in recent decades is likely faster than polar bears have ever experienced. 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. Although seals are their primary prey, polar bears feed opportunistically on a variety of marine and terrestrial prey and vegetation. Recently, the greatest change in their feeding behavior has resulted from spending more time on land as seasonal sea ice recedes. Additionally, polar bears will encounter new prey as some temperate species extend their ranges northward. Changes in polar bear movements and habitat associations because of climate change vary among subpopulations. In several areas, the loss of sea ice has altered migration routes, required long-distance swimming between hunting and denning areas, and resulted in some denning areas becoming inaccessible. Because polar bears do not occur in regions 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.

Keywords Adaptation · Behavior · Climate · Den · Foraging · Habitat · Mating · Microevolution · Plasticity · Polar bear · Sea ice

During the past three decades, climate change has led to an ice-free season that is weeks or months longer than historical periods in several areas occupied by polar bears (Regehr et al. 2016; Stern and Laidre 2016). The Arctic has been warming at a rate about twice the global average and, in addition to the longer ice-free season,

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there has been an increase in habitat fragmentation and a decrease in multiyear sea-ice, factors that affect sea-ice dependent Arctic mammals (Fig. 16.1; Laidre et al. 2015). This rapid change means that any response in 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 (*Ursus maritimus*) despite their marked specialization as a marine predator that depends on sea ice-associated seal species.

16.1 Changes in Feeding Behavior

Polar bears are the most carnivorous bear species and prey on sea ice-associated seals, mainly ringed seals (*Pusa hispida*) (see Chap. 13). However, they are opportunistic and may eat almost anything. More than 80 species of mammals, plants, birds, fish, and invertebrates have been identified in polar bear diets (Derocher 2012). While their diet may include plants and terrestrial prey when on land, they now spend more time ashore, which increases the frequency of terrestrial foraging. This change in diet has implications for how polar bear subpopulations will survive in the future.

Most data on polar bear foraging have relied on indirect methods rather than direct observations. A Canadian Arctic study of more than 1700 live-captured bears used fatty acid analyses to identify prey species for ten polar bear subpopulations (Thiemann et al. 2008). The data show that polar bears exhibit geographic variation in foraging, but relationships between sea ice conditions and prey dynamics are complex. There are considerable differences in foraging among the sexes and age groups, with adult males hunting larger prey, such as walrus (*Odobenus rosmarus*) and bearded seals (*Erignathus barbatus*), compared to younger males and females of all ages (Thiemann et al. 2008). Walruses (and to a lesser degree, bearded seals) are less sea ice-dependent than ringed seals, suggesting that adult males have an advantage over females and younger males as sea ice is reduced. In Svalbard, bearded seals were more important to polar bears than ringed seals in the summer (Derocher et al. 2002). Conversely, bearded seals were of minimal importance in some areas in the spring, and ringed seals were the most important prey based on scat samples from more than 100 bears collected from 2003-04 (Iversen et al. 2013). Two studies in Svalbard showed a significant change in polar bear foraging. One observed that polar bears on the west coast of Spitzbergen, the most western and largest island in the archipelago, increased consumption of bird eggs in summer (Prop et al. 2015). Farther east in Svalbard, the other study also observed that bears now spend more time in areas with colonies of ground-nesting birds (Hamilton et al. 2017). At the same time, bears spent less time hunting ringed seals at glacial fronts in summer, even though these areas are still used by seals (Hamilton et al. 2017). However, the sea ice is now mostly absent in front of glaciers during the summer, meaning bears no longer have a stable platform for hunting seals. Even in spring, many of the glacial fronts have been without sea ice in recent years. In winter, icebergs from

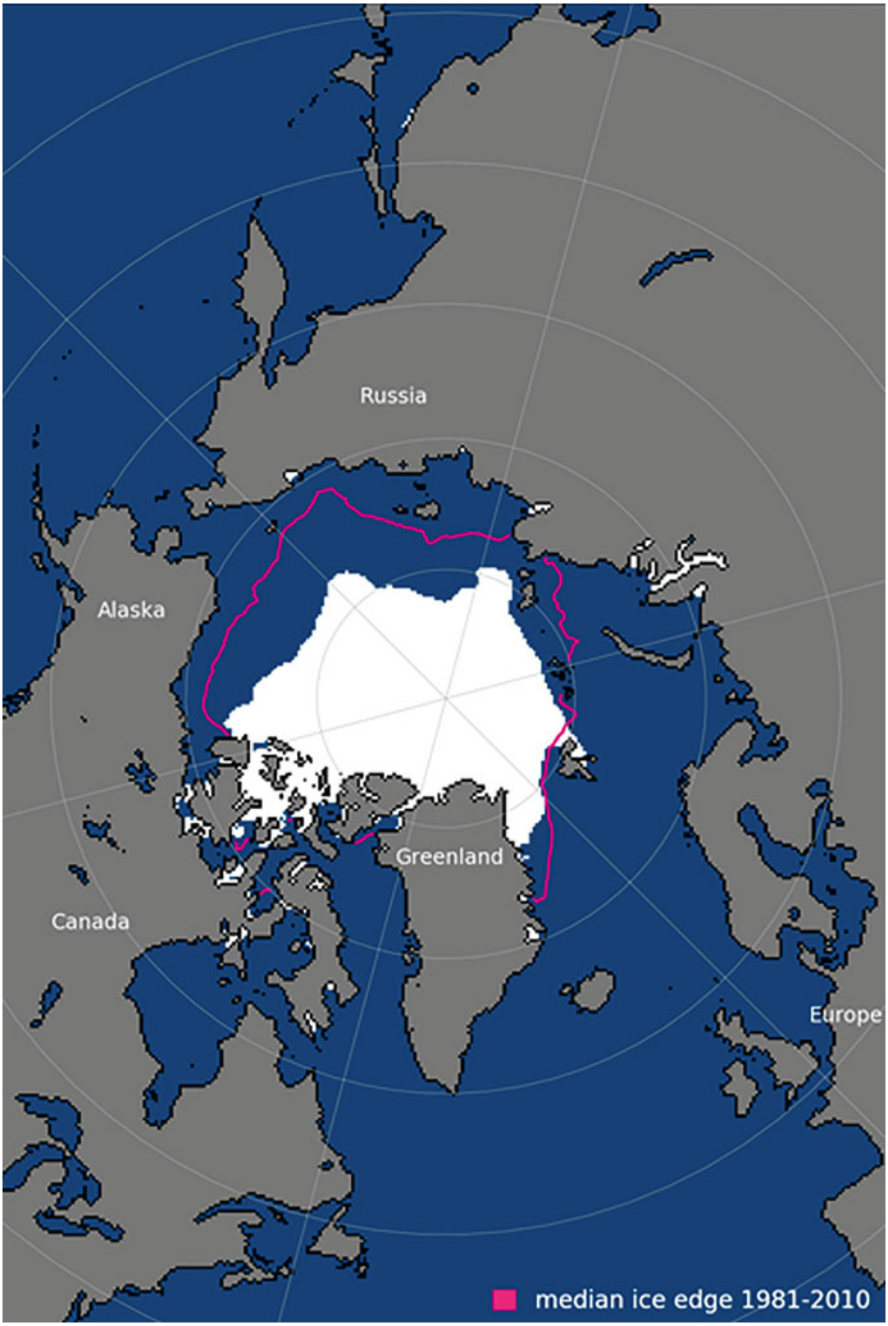

Fig. 16.1 Sea ice cover in September 2019 compared to the median cover from 1981–2010. Image from the National Snow and Ice Data Center, University of Colorado, Boulder

glaciers freeze into the sea ice, causing drifting snow to accumulate. Female ringed seals use these snowdrifts to make their lairs, and female polar bears with cubs hunt seal pups in early spring. In recent years, the sea ice habitat in front of the glaciers has melted by early spring, forcing polar bear mothers to hunt in other areas, potentially traveling farther north to reach the ice edge.

Bowhead whales (*Balaena mysticetus*) are also an important resource for polar bears and may provide food for extended periods when sea ice is scarce (Laidre et al. 2018). In some areas, subsistence whale hunting means carcasses are regularly available, but in other areas, dead whales may wash ashore. Historically, whale carcasses may have been more important when periods of warmer climate led to significant reductions in Arctic sea ice habitat, but fewer whale carcasses will be available in the future because whaling greatly reduced stock sizes (Laidre et al. 2018). In the Beaufort Sea, polar bears frequently feed on bowhead carcasses from subsistence hunting (Amstrup 2003). In good ice years, this resource is important for some bears during the summer, but it will likely increase in importance as the length of the ice-free season increases (see Chap. 13). Bears may change their home range significantly when they learn that whale carcasses are regularly available (Lillie et al. 2018).

While large whales are only a food source as carcasses, polar bears will hunt and kill smaller whales (Amstrup 2003). Both narwhals (*Monodon monoceros*) and beluga whales (*Delphinapterus leucas*) are associated with sea ice, and their abundance may decline as the sea ice declines. Polar bears wait along leads and near small areas of open water for narwhals, which occasionally become trapped in the sea ice. In Svalbard, polar bears killed white-beaked dolphins (*Lagenorhynchus albirostris*), which became trapped in the sea ice during a period of cold spring weather (Fig. 16.2; Aars et al. 2015). These dolphins normally do not occur so far north at that time of the year, and their presence likely resulted from recent climate changes when many species have expanded their range northward. However, it is uncertain whether white-beaked dolphins and other more southerly species will become significant prey for polar bears in the future. Increased open water resulting from climate change likely will reduce the foraging success of polar bears on smaller, sea ice-dependent whales.

In Svalbard, observations of polar bears killing reindeer (*Rangifer tarandus*) were previously rare (Derocher et al. 2000). More recently, reindeer killed and scavenged by polar bears are more common (Aars unpub. obs.). A local hunter in Svalbard observed several kills or remains of kills, and it is likely that a few bears have specialized in hunting reindeer during periods with little sea ice and reduced access to ringed seals (T. Sandal, pers. com.). It is difficult to determine whether polar bears are hunting more reindeer or whether this results from more people observing them. In the future, reindeer may become more common in Svalbard as a warmer climate increases the duration of the growing season. However, it remains to be seen whether reindeer become an important food source for polar bears. Svalbard differs from other areas with large ungulates because competing predators, such as brown bears (*Ursus arctos*) and wolves (*Canis lupus*), are absent.

Fig. 16.2 A male polar bear with a recently killed white-beaked dolphin. There is a small hole in the ice to the left of the dolphin, probably where it surfaced to breathe. Another partially eaten dolphin was found nearby (Aars et al. 2015)

Walruses are less sensitive to sea ice loss than many Arctic marine mammals. Although they are challenging prey to kill because of their large size and defensive behavior, walruses may be an important prey for polar bears in some areas. Polar bears will scavenge dead or debilitated walruses and also prey on calves. On rare occasions, large polar bear males will successfully kill adult walruses. Before being hunted by humans to near extinction, walruses on the west coast of Spitsbergen (Svalbard) may have sustained large numbers of polar bears (Lønø 1970; Kovacs et al. 2014). Hence, walruses may offer an increasingly important food source as sea ice becomes less abundant and bears are stranded on land for longer periods. Polar bears frequently stay close to walrus colonies in the summer, and walruses react to bears, indicating they are a threat (Øren et al. 2018). On Wrangel Island in the eastern Russian Arctic, large aggregations of walruses are important for an increasing number of polar bears on land in summer (Ovsyanikov 2005).

In Western Hudson Bay, polar bears prey on harbor seals (*Phoca vitulina*), which are absent from much of the high Arctic but may move farther north as the climate warms (Thiemann et al. 2008). The most northern population of harbor seals occurs in western Svalbard (Merkel et al. 2013). During the summer, a few polar bears overlap with this population, and some bears ambush the seals from the sea when they haul out onshore. It is likely that predation on harbor seals during the summer has increased in response to an increase in their availability and because polar bears in recent years have not had sea ice in summer from which to hunt ringed seals.

In the summer, polar bears also have been seen catching freshwater fish, such as Arctic char (*Salvelinus alpinus*) and fourhorn sculpin (*Myoxocephalus quadricornis*) (Dyck and Romberg 2007). This has led to a debate about the value of alternative food sources and the adaptability of polar bears in areas with loss of sea ice habitat. However, polar bears catching fish is not a new phenomenon. In Labrador in the summer of 1778, polar bears were observed catching salmon in a river, similar to the behavior of brown bears (Stirling 2011). It is likely that polar bears will depend more on fish in areas of declining sea ice, but some argue that fish alone cannot provide all of the energy they need (Stirling and Derocher 2012).

Polar bears may ingest material that has no nutritional value, although it may contain certain minerals. I once observed a young polar bear during the autumn in Svalbard eating soil while it was recovering from immobilization drugs. Later the same day, I found a large scat from an adult polar bear that was composed solely of claylike soil. A trapper told me that he found several kilos of pebbles in the stomach of a polar bear, which was killed in Svalbard in the 1960s.

Polar bear prey do not need to be large. In Churchill, Canada, in October 2017, I observed a polar bear successfully hunting abundant meadow voles (*Microtus pennsylvanicus*) moving among pieces of wood, kelp, and stones in the littoral zone. If polar bears are on land for long periods, they may behave like brown bears, which are opportunistic carnivores willing to feed on small mammals and birds. When a polar bear's fat reserves are depleted, it likely will feed on any edible plant or animal to avoid starvation.

In winter and spring 2004, intraspecific killing was observed on three occasions, a behavior not seen previously during 24 years of research (Amstrup et al. 2006). Nutritional stress resulting from longer, ice-free seasons could have been the cause. Polar bears also may regard humans as prey and, with bears spending more time on land, the likelihood of aggressive encounters will increase (see Chap. 17).

16.2 Movements and Habitat Use

Loss of sea ice ultimately leads to changes in movements and habitat associations of polar bears. In seasonal ice areas, the amount of time polar bears are stranded on land has increased as the climate has warmed (Amstrup et al. 2008; Stern and Laidre 2016). In Western Hudson Bay, where all polar bears summer on land, the ice-free season increased by three weeks from 1979–2015 (Castro de la Guardia et al. 2017). In Baffin Bay, polar bears exhibited a 70% reduction in summer home ranges and used areas farther north because of a reduction in summer sea ice from 1991–95 and 2009–15 (Laidre et al. 2018).

The Barents Sea has experienced the greatest declines in sea ice of any region in the Arctic (Stern and Laidre 2016). Although polar bears follow the sea ice as it retreats north in summer, they exhibit two habitat preferences (1) an offshore pelagic zone along the ice edge where seals are hunted year-round, especially in the summer and autumn, and (2) a near-shore zone in Svalbard year-round (Mauritzen et al.

2001). Many of the pelagic bears migrate between Svalbard, where females den or where sea ice in winter makes it possible to hunt, and the western Russian Arctic. However, the seasonal ice edge is now located much farther north than it was three decades ago, and this has forced polar bears to hunt farther north (Lone et al. 2018a). In the past, Svalbard was connected to the sea ice year-round. In recent years, open water has separated the archipelago from the ice edge almost annually and in some years well into winter. Although historical data are scarce, polar bears did not swim far to reach the ice edge. In recent years, we have documented bears swimming between Svalbard and the ice edge, which may exceed 100 km and require several days (Lone et al. 2018b). Long swims have been associated with reduced sea ice in other Arctic subpopulations (Pagano et al. 2012; Pilfold et al. 2017). In the Southern Beaufort Sea, long-duration swims by polar bears have been reported, the most extreme of which was almost 700 km over nine days (Durner et al. 2011; Pagano et al. 2012). In 2018, sea ice disappeared entirely in the early summer between Svalbard and Franz Josef Land in the western Russian Arctic. A satellite-collared adult female swam for over a week, interrupted by a 20-h break about halfway. These examples demonstrate the remarkable swimming endurance of polar bears, especially because it is energetically expensive and increases heat loss (see Chap. 12). The estimated energetic cost of swimming is about five-fold greater than that of walking (Griffen 2018).

A few hundred bears reside in Svalbard year-round (near-shore bears). They do not have the same challenges as pelagic bears in moving to denning areas because they usually den close to their summer range. However, with longer ice-free seasons, near-shore bears now spend more time on land and increasingly depend on terrestrial food, which may have a lower energy content. Although pelagic bears expend more energy associated with walking and swimming, their diet of seals potentially provides more energy (Mauritzen et al. 2003; Blanchet et al. 2020). It is difficult to predict which strategy will prove most successful as the loss of sea ice continues. If the distance between the ice edge and Svalbard increases, it is likely that more bears will den in Franz Josef Land, which is closer to the ice edge.

16.3 Denning

In cold-temperate areas with limited food availability in winter, black bears (*Ursus americanus*) and brown bears exhibit obligatory denning. Both male and female polar bears may den for periods of several weeks if weather and prey availability are unfavorable (Amstrup 2003). However, only females giving birth occupy dens for several months (Amstrup 2003). There have been several studies on polar bear denning phenology (i.e., seasonality), mostly based on satellite-collared adult females. Location, ambient temperature, and some indices of activity provide useful indicators of denning events. Denning phenology varies geographically, with den entry mostly from September–November and den emergence from late February-mid-April (see Chap. 14; Amstrup 2003). Cubs are born by early January, but the timing varies with entry and emergence dates. The duration of time in a den will depend on maturation of the cubs and their ability to follow the female when she leaves the den and synchronization with the ringed seal pupping season. In spring, ringed seal pups are born in subnivean lairs above breathing holes where they remain for several weeks. The altricial pups are easier prey for polar bears than are adult seals. Because female polar bears fast for up to eight months, their fat reserves are low at the end of denning (Atkinson and Ramsay 1995). After emerging from the den, females must find prey to restore fat reserves and provide milk for growing cubs.

It is likely that variation in emergence dates among polar bear subpopulations is partly explained by geographic variation in the occurrence of ringed seal pupping, which indicates the importance of this food source. However, there is considerable variability in the dates of den emergence, indicating the influence of other factors (Hansson and Thomassen 1983). An early decline in sea ice because of a warmer climate could result in earlier ringed seal pupping. As a result, polar bears may enter the den, give birth, and emerge earlier. However, seasonal light levels may limit how much earlier seal pupping and den emergence can occur. In addition, phenological shifts are complicated by what happens before denning. A female must accumulate sufficient fat to fast and produce milk for one to three cubs during the winter.

Changes in the phenology of maternity denning indicate that climate does play a role, but patterns are complex and vary among areas. Polar bears in Baffin Bay from 2009–15 had a mean denning period about one month shorter than in the 1990s, which resulted when females entered dens considerably later (Escajeda et al. 2018). Denning females in the Chukchi Sea, which were in better body condition than females in the Beaufort Sea, emerged from dens later in spring (Rode et al. 2018). Even though sea ice availability would indicate greater food availability, bears did not enter dens later in years with extensive autumn sea ice. However, in the Barents Sea, the start of denning was found to begin later in autumn in years with colder weather (higher Arctic Oscillation index) during the previous spring (Sulich 2019). These females also emerged later if they were older than 10 years. This may result from young females having lost young cubs or having to start hunting earlier if their fat reserves were low in early spring. It also may indicate that bears will shift their denning phenology to earlier in the year as the climate warms and access to seals is further reduced. In Western Hudson Bay, females now emerge from dens several weeks earlier than decades ago (Derocher 2012). In addition, the locations of dens are moving farther north.

In the Southern Beaufort Sea, where most polar bears previously denned in the multiyear ice, they increasingly do so on land as the seasonal sea ice moves farther north (Fischbach et al. 2007; Olson et al. 2017). A reduction in multiyear ice and the greater geographic movement of thinner ice because of sea currents (a den may move hundreds of kilometers from its origin) during the winter may now discourage bears from denning on the sea ice. In Svalbard, dens were common on isolated islands in the eastern archipelago. However, bears can no longer reach Hopen Island (an isolated southern island in the Svalbard archipelago; 76.5° N) because sea ice no longer forms around the island until late in the year (Derocher et al. 2011).

Previously, this island would have had more than 30 dens each year if the sea ice formed by early November. The northern island of Kongsøya, Svalbard (78.9° N) also has experienced a later return of sea ice in recent years, and few if any females now den there. Kongsøya had previously been one of the most important denning areas for polar bears in the Arctic and was protected from hunting in 1939. We do not know how the loss of traditional denning areas will affect the Barents Sea subpopulation. Many pregnant females may find suitable denning areas elsewhere, perhaps in Franz Josef Land in the western Russian Arctic. A genetic study from Svalbard indicated that flexibility regarding denning areas may be large, despite denning philopatry (Zeyl et al. 2010). When possible, polar bears prefer to den near the place of their birth. Although the distance from the ice edge may be within their swimming capability, the energetic cost of swimming long distances (i.e., >100 km) may deplete fat reserves essential for fasting and lactation in the den. In August 2015, my colleagues and I captured two adult females on Kongsøya and instrumented them with GPS satellite collars. There was no sea ice around the island, and both swam about 100 km to reach another island within one week. On Kongsøya, there was nothing to hunt, and the sea ice did not form for several months. Remaining on Kongsøya may have prevented the bears from gaining adequate fat reserves before denning.

In general, the availability of sea ice and food dictates both the distribution of polar bear dens and denning phenology, but these vary geographically depending on the type of habitat. In areas with considerable multiyear sea ice and few open leads, temporary reductions in sea ice may improve the bears' ability to hunt seals (Stirling and Derocher 2012). Flexible denning behavior may be important as the climate warms. For example, it was reported that a female with cubs emerged from a den as early as 8 January (Rode et al. 2018). In Svalbard, a female went into her den as late as 19 January and left with a cub on 1 May. Such plasticity indicates significant flexibility in denning phenology in response to environmental changes.

16.4 Weaning

In most areas, females stay with their cubs for a little over two years (until spring when females mate again). Although this was true for polar bears in Western Hudson Bay in the 1980s, a 3-year reproductive cycle is common in most areas if cubs survive.

16.5 Mating

Polar bears mate in spring, usually from February–May, with variation in timing among subpopulations (Amstrup 2003). Because of delayed implantation, the fertilized egg does not develop until autumn, and altricial cubs are small when born in mid-winter. Males roam over large areas searching for females, and because there may be two to three-fold more adult males than receptive females without cubs, competition among males is fierce (see Chap. 14). Females may mate with several males successively over several weeks, and males may guard females for longer periods, then search for new females. As with brown bears, within-litter multiple paternity may occur (Zeyl et al. 2009a). A reduction in sea ice may reduce the home range of males, the number of male-female encounters and copulations, and the variance in male reproductive success. Among polar bear subpopulations, the age at first reproduction varies from 4-6 years and probability depends on food availability (Stirling 2011). Differences in movements of females and males in ice-covered areas in spring may result from female hunting behavior, while males optimize the likelihood of encountering females (Laidre et al. 2013). The reduction in sea ice may lead to more isolated stocks and increased levels of inbreeding, which is normally rare around Svalbard (Zeyl et al. 2009b). The reduced mobility of males and females may further isolate subpopulations geographically.

While the mating season normally occurs in the spring, delayed implantation makes some plasticity possible. A highly unpredictable environment means cubs could starve if the female has insufficient fat reserves and is unable to catch prey. However, the female's condition can improve rapidly if food is plentiful (see Chap. 13) and, in such cases, being able to mate in summer rather than waiting until the following spring would increase her expected lifetime reproductive success. In one instance, a mating occured in late June in Svalbard involving a female that had lost a yearling cub earlier in the spring (Smith and Aars 2015). This female went into a maternity den the following winter. The possibility of mating in the summer may be important if diminished sea ice leads to unpredictable food availability in the spring.

16.6 Conclusions

Polar bears may change their behavior in response to a warmer climate and less sea ice. Most of the change will result from phenotypic plasticity rather than microevolution because the environmental changes are occurring over a few generations. While the ability to swim long distances is important in an increasingly fragmented sea-ice habitat, the energetic cost is large. The ability to maintain fat reserves will be critical during periods of reduced access to seals. Although several studies have shown a negative relationship between polar bear viability and residency on land, the importance of alternative terrestrial food sources is unclear. Because polar bears do not occur in any ice-free areas 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.

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Chapter 17
Human-Polar Bear Interactions

Todd C. Atwood and James M. Wilder

Abstract Human-wildlife interactions (HWI) are driven fundamentally by overlapping space and resources. As competition intensifies, the likelihood of interaction and conflict increases. In turn, conflict may impede conservation efforts by lowering social tolerance of wildlife, especially when human-wildlife conflict (HWC) poses a threat to human safety and economic well-being. Thus, mitigating conflict is one of the most consequential components of a wildlife management program, particularly for large carnivores. However, unlike other large carnivores, the causative factors and conservation consequences of interactions between humans and polar bears (*Ursus maritimus*) are poorly understood. Historically, mitigation of human-polar bear conflict has been a low management priority with the exception of a few locations where conflict had been a chronic concern. In part, this was because of low human densities in most of the Arctic and sea ice act as a physical barrier regulating the frequency of human-polar bear interactions. However, as the Arctic has warmed, anthropogenic activities have increased, and polar bears have become more reliant on land. As a result, mitigating interaction and conflict between humans and polar bears has become a growing concern. In this chapter, we 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. We first provide an overview of behaviors that contribute to the occurrence of interactions and conflicts. We then review historical and contemporary drivers of interaction and conflict and examine how climate-mediated changes to Arctic marine and terrestrial environments are likely to influence distribution and types of future incidents. We close by proposing a conceptual framework that conservationists and managers can use to

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mitigate the likelihood of future human-polar bear conflict in a rapidly changing Arctic.

Keywords Arctic · Attractant · Competition · Conflict · Global warming · Human-wildlife interaction · Mitigation · Polar bear · Sea ice

17.1 Human-Wildlife Interactions

Human-wildlife interactions (HWI) can be positive or negative and are rooted in direct or indirect competition for shared resources, usually habitat and food. Human-wildlife conflicts (HWC) are interactions, which result in negative outcomes for humans, wildlife, or both. HWC encompass a broad range of adverse interactions, including those that may result in injury or death, threaten economic security, and damage property, which makes this is one of the most salient and intractable conservation issues (Nyhus 2016). As the human population increases from 7.8 to 9.9 billion people over the next 30 years, coexistence with wildlife will become increasingly important for the conservation and management of biodiversity.

The conservation and restoration of many at-risk wildlife species will depend on mitigating HWC, particularly where they create community unrest and economic uncertainty because of regulatory burdens on industry. Amelioration and mitigation of HWC should be a relatively simple endeavor because a range of technical approaches and tools exist to prevent interactions from escalating into conflict (Van Eeden et al. 2018). Unfortunately, evidence for decisive and lasting resolution of HWC is rare, indicating that the causes of conflict are complex and deeply rooted. In part, the failure to mitigate HWC may result from the expectation that the response to wildlife conflict will be rational (e.g., the response to conflict will be based on thoughtful deliberation rather than emotion and retaliation; Wieczorek Hudenko 2012). Actual responses often depend on perceived risk and social influences rather than empirical assessments of injury or damage (Dickman 2010).

Conflicts between people and large carnivores receive a disproportionate amount of attention in media and literature. The attention is understandable, given that many large carnivores are both charismatic and capable of posing a direct risk to human safety. In some instances, the threat posed by human-carnivore conflict evokes actions and attitudes that undermine conservation and recovery efforts. For example, localized depredation of livestock by African lions (*Panthera leo*) and tigers (*Panthera tigris*) have resulted in retaliatory killings at spatial scales broader than those of depredations (Kissui 2008; Goodrich 2011). In Russia, retaliatory killings constituted 29.5% of all Siberian tiger mortalities recorded from 1970–90 (Goodrich 2011). Additionally, chronic HWC can foster the proliferation of negative attitudes towards wildlife by local people so that on-the-ground conservation actions become untenable (Naughton-Treves et al. 2003; Dickman 2010). Collectively, conflict-mediated lethal removals and the erosion of public support for coexistence can pose a challenge to conservation or restoration efforts.

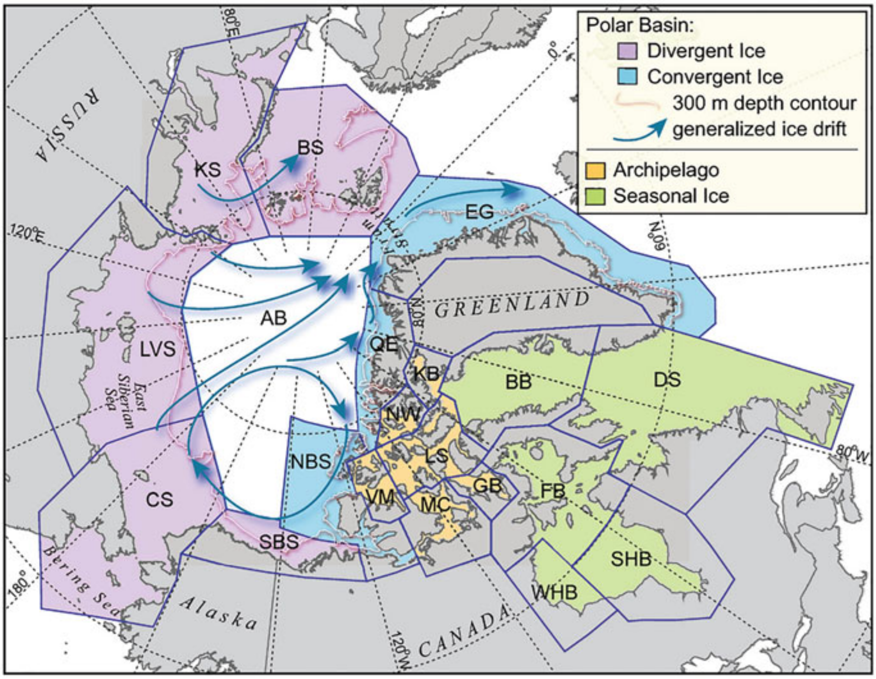

Fig. 17.1 Map of the 19 polar bear subpopulations. The map also shows the aggregation of the subpopulations into four ecoregions indicative of regional sea ice dynamics (Amstrup et al. 2008). The map includes a depiction of annual patterns of ice motion. Subpopulation acronyms: Arctic Basin (AB), Baffin Bay (BB), Barents Sea (BS), Chukchi Sea (CS), Davis Strait (DS), East Greenland (EG), Foxe Basin (FB), Gulf of Boothia (GB), Kane Basin (KB), Kara Sea (KS), Lancaster Sound (LS), Laptev Sea (LVS), M'Clintock Channel (MC), Northern Beaufort Sea (NBS), Norwegian Bay (NW), Southern Beaufort Sea (SBS), Southern Hudson Bay (SHB), Viscount Melville Sound (VM), Western Hudson Bay (WHB)

In marine ecosystems, HWC has been associated primarily with depredation of commercially fished species (Schakner and Blumstein 2013), with relatively little threat to human safety. Polar bears (*Ursus maritimus*) are a marine mammal predator with a circumpolar distribution, which encompasses 19 subpopulations and ranges over five Arctic nations: the United States of America, Canada, Greenland, Norway, and Russia (Fig. 17.1; DeMaster and Stirling 1981). Polar bears evolved during the Pleistocene to exploit sea ice as a means to access their marine mammal prey, which is primarily ice seals (see Chap. 11; Kurten 1964). Enhanced loss of sea ice habitat from anthropogenic climate change is the primary threat to the long-term survival of polar bears, and the availability of sea ice will continue to decline as long as greenhouse gas (GHG) emissions continue to rise (Schneider 1989; Amstrup et al. 2008; Atwood et al. 2016a). Historically, the ability of polar bears to remain in their sea ice habitat—a harsh climate with low human population density—has limited the interaction between polar bears and humans. However, the loss of sea ice is changing polar bear distribution and behavior while simultaneously increasing industrial development and recreation (AHDR 2015; Lillie et al. 2018; Rode et al. 2018). In turn, these concurrent changes in bear and human behavior are likely to increase the risk of interaction and conflict. Here, we review the factors and processes that have shaped historical and contemporary occurrences of human-polar bear interaction and conflict and provide the conceptualization of a process for mitigating risk to polar bears and humans in the future.

17.1.1 Interactions and Conflict: Key Terms and Definitions

There are a variety of terms and concepts used when describing HWC and its management. Over the years, various authors have emphasized the importance of clearly defining terms and using them consistently (Whittaker and Knight 1998; Hopkins et al. 2010). To that end, we adapted previous definitions when referencing terms, concepts, and circumstances for human-polar bear interaction and conflict (Table 17.1; Hopkins et al. 2010; Garshelis et al. 2017). The terms and definitions also have been used to describe interactions among humans and various species of

Table 17.1 Terms and definitions used to describe human-polar bear conflict and factors that contribute to its occurrence adapted from Hopkins et al. (2010)

Term	Definition
Aggressive interaction	Offensive or defensive behavior by a polar bear that is threatening to a human.
Anthropogenic food	Food or attractants with a human origin, either in production or placement.
Attack	Intentional contact resulting in human injury.
Conditioning	Learning involved in receiving a reward or punishment for a given response to a given stimulus.
Habituation	A waning response to a favorable or unfavorable stimulus or circumstance.
Human-polar bear interaction	An instance when a human and a polar bear are mutually aware of each other.
Human-polar bear conflict	An interaction (other than an attack) that causes the human to take evasive or defensive action, results in property damage or killing of pets, or results in the intentional harm or killing of a polar bear by a human.
Incident	An occurrence involving an interaction or conflict between humans and polar bears.
Diversionary feeding	Providing or relocating foods to divert polar bears from sites where they could cause conflicts with humans.
Supplemental feeding	Intentional feeding of polar bears primarily to enhance nutrition and welfare.

bears and allowing for easier comparisons and contrasts of factors influencing human-bear management concerns (Can et al. 2014).

17.1.2 Behavioral Components of Conflict: A Bear's Perspective

To understand the circumstances that influence HWC, research has focused on how and why animals differ in their responses to humans and exposure to anthropogenic activities (Sih et al. 2011; Wolf and Weissing 2012). Behaviors like boldness (e.g., exploratory behavior and reduced neophobia) and wariness (e.g., enhanced neophobia) may mediate the response of wildlife to humans (Sih 2013; Blackwell et al. 2016). For example, bold individuals, which tend to be innovative and quick learners, may tolerate anthropogenic disturbance, exploit human-modified landscapes, and routinely interact with humans (Tuomainen and Candolin 2013; Sol et al. 2013; Breck et al. 2019). In contrast, wary individuals may display a startle response to a disturbance, followed by a latency or failure to return to the area of disturbance or encounter (Van Oers et al. 2004). Finally, other behaviors such as boldness and wariness may influence HWI (e.g., escalation into conflict). Behaviors induced by exposure to anthropogenic disturbances may be adaptive when they foster persistence in changing or novel environments but maladaptive when they lead to conflict with humans. Thus, understanding the behavioral context for HWI is an important step in predicting and mitigating HWC.

Various species of Ursidae have been described as "curious," particularly in the context of interactions with people and anthropogenic features. Curiosity can be viewed as a precursor to overt boldness or wariness and is often used to describe behavior in which an individual is investigating an object or situation. The behavior of a curious polar bear is similar to that of other bears, and it can involve moving slowly towards or circling an object while pausing to sniff the air. The bear often approaches the object from downwind with its head held high and ears pointed forward or to the side. Occasionally a bear may stand on its hind legs to investigate an object from a distance. Some of these behaviors can be difficult to interpret. For instance, circuitous movement from downwind can resemble stalking, while standing on hind legs can occur during fights with conspecifics and before initiating a charge (Fleck and Herrero 1988). Curiosity in polar bears may result from the lack of neophobia, including unfamiliarity with humans and anthropogenic features, and/or persistent foraging behavior (Gjertz and Persen 1987; Stirling 1988; Floyd 1999). Reduced neophobia and persistent hunting may predispose polar bears to habituation and food conditioning.

Bears are independent (i.e., individualistic social behavior), adaptable, intelligent, and highly mobile (McCullough 1982; Durner and Amstrup 1995; Deecke 2012; Ordiz et al. 2012). As a result, they encounter and exploit a wide range of resources and their tolerance for (or naïveté towards) humans and their associated activities are influenced by demography and nutritional condition. Most bears avoid human settlements because of the increased level of disturbance (e.g., noise, traffic, artificial light) common to developed landscapes (Gibeau et al. 2002; Elfström et al. 2014). Bears in or near human settlements are perceived as bold and either naïve (i.e., exploring a novel environment) or seeking food (Mueller et al. 2004; Elfström et al. 2014). Naïveté associated with age is considered an important factor explaining the disproportionate involvement of subadults (individuals 2–4 years of age) in human-bear interactions (Stenhouse et al. 1988; Towns et al. 2009; Alldredge et al. 2015).

Another factor in human-bear conflicts is nutritional stress. Black (*Ursus americanus*), brown (*Ursus arctos*), and polar bears are attracted to developed areas when natural foods are scarce and individuals are nutritionally stressed (Elfström et al. 2014; Johnson et al. 2015; Wilder et al. 2017). Repeated use of developed areas can result in habituation to human activities. If bears gain access to human-derived foods, they may become food-conditioned (i.e., associate people or settlements with food). This, along with habituation, is the most common behavioral process explaining the occurrence of bears in developed landscapes (Peine 2001; Spencer et al. 2007).

17.1.3 Behavioral Components of Conflict: A Human Perspective

Research on HWC has characterized attitudes and beliefs regarding the social tolerance of wildlife (Treves et al. 2006). This information can be useful for gauging the public reaction to management actions for mitigating HWC, although it provides little insight into human motivation (McCleery et al. 2006). Nevertheless, understanding community attitudes to HWC is crucial because successful mitigation usually requires changing human behavior.

Although there is a variety of human behavior that contributes to HWC, the most important is the disposition and security of attractants (Can et al. 2014). The presence of anthropogenic attractants (e.g., garbage, livestock, crops) is considered the primary cause of human-bear conflicts (Spencer et al. 2007). The frequency of conflicts is often greatest along the margins of expanding settlements and activity, where people may be naïve about the need to manage wildlife attractants. For example, an increase in the number of conflicts between humans and black bears in Nevada was caused by the availability of garbage associated with urban expansion into previously undeveloped wildlife habitats (Beckmann 2000). Similarly, the probability of interactions between humans and black bears at urban-wildland interfaces in Montana was highest in areas characterized by moderately dense single-family homes, which provided an array of potential attractants, including garbage, fruit trees, and bird feeders (Merkle et al. 2011). The traditional approach to managing attractant-mediated conflict around human settlements is hazing. This may provide short-term success but often fails to address the root causes of chronic conflict. More recently, several agencies and organizations have investigated approaches that rely on educational outreach and incentives to modify human behavior to better secure and dispose of potential attractants (Gore et al. 2006, 2008; Pienaar et al. 2015; Proctor et al. 2018).

17.2 Historical Drivers of Human-Polar Bear Interactions and Conflict

17.2.1 Subsistence Hunting and Arctic Exploration

The historical distribution of polar bears, which is mainly limited to observations by Arctic explorers and whalers, indicates that they ranged over the ice-covered seas of the Northern Hemisphere as far south as St. Paul Island (57°N) in the Bering Sea and Newfoundland in the North Atlantic Ocean (Ray 1971; Smith et al. 1975). This extensive and inhospitable environment, which was largely free of competitors and predators (except for coastal regions frequented by Indigenous Peoples), provided habitat for polar bears. The prehistorical record of human-polar bear interactions is sparse and mostly limited to interpretations of art and carvings discovered through archaeological investigations of sites used by coastal hunter-gatherer societies (Ryan et al. 2014).

Archaeologists have used animal effigies created by the Dorset Paleo-Eskimos of the eastern Arctic to infer historical relationships between hunter-gatherer societies and animals. The Dorset People occupied the Canadian Arctic and Greenland between 450 BCE and 1250 CE and made carvings from bone, antler, ivory, wood, and soapstone that represented spiritual relationships with their surroundings (Betts et al. 2015). Polar bears were the most common animal effigies, and the diversity of motifs suggests a wide range of interactions between bears and the Dorset. For example, effigies have been inferred to depict ritual slaying, subsistence use, and bear behavior (McGhee 1974; Maxwell 1985; Betts et al. 2015). Other archaeological evidence suggests polar bears and the Dorset competed for seals, and that bears may have raided meat stores and killed Dorset (Sutherland 2001). Reports from other regions of the Arctic suggest similar relationships between prehistorical hunter-gatherer societies and polar bears (Dikov 1988; Ackerman 1998).

The historical record of human-polar bear interactions began with European Arctic exploration. A comprehensive review of the history of polar bear attacks on humans dates back to William Barents' second expedition into the Russian Arctic in 1595 (Wilder et al. 2017). Over a 145-year period (1870–2014), 73 confirmed polar bear attacks resulted in 20 human fatalities and 63 human injuries. It is difficult to glean information from the primary sources on what may have precipitated many of these interactions, and accounts seem to be mostly limited to interactions that escalated quickly into conflict. A central theme in these incidents is a description of predatory behavior by a bear resulting in an attack, followed by attempts to drive the bear from the victim, and culminating with the deaths of the victim and/or bear (Wilder et al. 2017). It is important to consider that interactions resulting in conflict, particularly injury or death, may have been recorded more often than benign encounters. Nevertheless, historical reports of attacks on people indicate that they were rare but often predatory in nature. Notably, 61% of bears that attacked humans were considered to be in below-average body condition (i.e., nutritionally stressed).

17.2.2 Human Population Growth

Reports of human-polar bear interactions and conflicts remained rare until the 1960s, when human populations, sport hunting, tourism, and exploration for oil, gas, and minerals began to increase in some areas. The circumpolar human population started to grow rapidly after World War II, with growth continuing into the 1990s but at a slower rate. For example, in Alaska, the human population above the Arctic Circle increased 4% year^{-1} from 1940–90, then slowed to 1.3% year^{-1} from 1990–99 (AHDR 2004). Similarly, Arctic regions of Canada, Russia, and Greenland experienced population growth from the 1940s to the 1980s, followed by declines in growth rates after that (AHDR 2004). In contrast, human population growth in Arctic Norway was minimal and relatively stable through the 1990s (AHDR 2004).

As the human population in the Arctic increased, unregulated hunting in Russia and sport hunting in the USA, Canada, and Norway (Svalbard) caused polar bear populations to decline (Prestrud and Stirling 1994; Belikov and Boltunov 1998). In response, the Range States (i.e., USA, Canada, Denmark [Greenland], Norway, and Russia) signed the International Agreement on the Conservation of Polar Bears in 1973 (hereafter referred to as the Agreement), which restricted non-Aboriginal polar bear hunting. Russia banned polar bear hunting in 1956. After ratification of the Agreement, Norway banned all polar bear hunting, and the USA and Denmark stopped non-Aboriginal harvests (Peacock 2017). As a result, polar bear populations recovered over several decades (Derocher 2005; Peacock et al. 2013). The recovery of formerly over-harvested polar bear populations, in concert with continuing human population growth, exacerbated the risk of human-polar bear conflict.

17.2.3 Attractants

As the human population grew in the Arctic, subsistence, recreational, and industrial activities around coastal communities increased, which elevated the risk of human-polar bear interactions. From 1966–85, 366 interactions were recorded in the Northwest Territories and Manitoba, Canada. The majority (48%) were associated with hunting/subsistence activities, while the remainder occurred around residential communities (27%) or industrial and research camps (24%) (Fleck and Herrero 1988). Food was present at 78% (n = 324 interactions) of aggressive interactions (Fleck and Herrero 1988). No human injuries were recorded in 95% of the interactions, but 86% resulted in the death of the bear (Fleck and Herrero 1988). In some instances, the bear was killed to protect property, while at other times it was self-defense. Of 15 polar bears killed in Svalbard from 1993–96, six were shot near cabins or tents and two near research stations, although there was no information on the presence of attractants (Derocher et al. 1998). In Churchill, Manitoba, there is a long history of food attracting polar bears and ensuing management programs to mitigate the risk of conflict (Box 17.1).

17.2.4 Recreation

Historically, opportunities for recreational activities in areas inhabited by polar bears have been limited. Prior to 2001, six national parks in Canada were located within the range of polar bears and had habitat (e.g., maternal den habitat, summer, and fall refugia) regularly used by bears. Through the 1980s, non-aggressive human-polar bear interactions in national parks in Canada were rare and mostly occurred around cabins and camping sites (Fleck and Herrero 1988). Aggressive interactions were similarly rare and included bears breaking into cabins with attractants and one instance of an adult female with cubs following skiers (Fleck and Herrero 1988). Interactions between humans and polar bears recorded from 1986–2000 were unrelated to visitation rates but may have been influenced by the availability of sea ice and local bear densities (Clark 2003). From 1986–2000, 5% of the interactions with polar bears resulted in human injuries, while 2% resulted in human injuries from 1980–85 (Fleck and Herrero 1988; Clark 2003).

17.2.5 Industrial Development

Exploration of the Arctic in the late nineteenth century revealed areas that were rich in mineral resources. For example, reserves of coal, diamonds, nickel, and copper were discovered in the Russian Arctic. In Svalbard, coal mining began on Spitsbergen Island in 1899 (Avango et al. 2011). In the 1930s, Russian geologists found surface oil seeps on the coast of the Laptev Sea (Kontorovich 2015). By the mid-twentieth century, large oil and gas reserves had been discovered in Prudhoe Bay, Alaska, and in Canada's Mackenzie Delta in the late 1960s (Szabo and Meyers 1993; Spicer and Bath 2010). Large-scale oil and gas production began in Alaska and Russia (including Siberia and islands in the Kara and Barents seas) in the 1970s. This area remains the primary source of Arctic petroleum and gas, and most information available on industry-related human-polar bear interactions has come from Alaska (Andrew 2014).

Most human-polar bear interactions associated with industrial activities have been restricted to observations, which rarely escalate to conflict. However, aggressive interactions have occurred, and polar bear sightings around Alaska's oil and gas operations have increased over time. The U.S. Fish and Wildlife Service reported 321 and 313 polar bear sightings in 2007 and 2008, respectively, within the oil and gas industrial footprint. Those numbers were ~4-fold higher than the average annual sightings from 1994–2000 (Rosen 2009). Throughout the Arctic, 6% of all polar bear attacks from 1960–2014 occurred at industrial sites (Wilder et al. 2017). On November 30, 1993, a polar bear broke into the U.S. Air Force Distant Early Warning (DEW) facility adjacent to Prudhoe Bay, and mauled a worker (U.S. Fish and Wildlife Service, unpublished data). Investigators thought that the bear may have been attracted by whale meat belonging to Indigenous whalers, which was stored nearby. Other reports indicated that personnel at the DEW Line site may have been feeding the bear, which was a subadult male in poor physical condition (U.S. Fish and Wildlife Service, unpublished data). The mauling at the DEW Line site prompted the formation of a multi-agency task force to identify measures to mitigate human-bear interactions (including attractant management), which were effectively implemented throughout the greater Prudhoe Bay region. When human-polar bear interactions have occurred within Alaska’s industrial footprint, they have largely been interventions to deter bears from getting too close to people or infrastructure.

The response to human-polar bear interactions in the Alaskan oil fields has been largely to haze bears away from people or infrastructure. Such short-term behavioral changes likely have no impact on bear health or fitness. However, efforts to deter bears from infrastructure appear to have little lasting effect. The persistent, seasonal association of polar bears with industrial infrastructure may have mixed consequences. Under certain conditions, polar bears may indirectly benefit from associating with offshore oil facilities, which create leads in the ice that enhance seal hunting (Stirling 1988). Conversely, polar bears have been observed consuming spilled or leaked petroleum products and solvents used in extraction applications, both of which can cause mortality (Øritsland et al. 1981; Amstrup et al. 1989; St. Aubin 1990; Derocher and Stirling 1991; Hurst et al. 1991). Additionally, some bears use the coastal plain for maternal denning, and anthropogenic activities in proximity to dens may cause bears to abandon dens (Amstrup 1993). Pregnant bears typically enter dens by mid-November and emerge by mid-March, which overlaps with the opening of the tundra to cross-country vehicle traffic and the annual peak in industrial activities.

Box 17.1 Mitigation of Human-Polar Bear Conflicts in Churchill, Manitoba One of the best examples of the nexus between increasing human densities and human-polar bear conflict comes from the Hudson Bay region of Canada. The town of Churchill is situated on the western coast of Hudson Bay within the boundaries of the Western Hudson Bay (WHB) polar bear subpopulation. The area around Churchill has a long history of human occupation dating back to 1700 BCE (Brandson 2005). The town was established formally in the 1920s as a port facility and railway hub, then grew as the local economy diversified (Lemelin 2008). The human population in the region increased through the 1950s to include multiple settlements (including a military base), each with a refuse dump. Polar bears spent several months on land after the sea ice melted each summer, and the refuse dumps were attractants.

At the Fort Churchill military installation, a garbage dump was located ~1.6 km from apartments, while another dump was located within the perimeter of the town. People were observed photographing, feeding, and teasing polar bears, which were attracted to the garbage (Jonkel 1970). Concerns over public safety increased in the 1960s, spurred by a spate of attacks on people. The abandonment of some satellite settlements and the closure of their dumps in the 1960s and 1970s led refuse-seeking bears to focus their attention closer to Churchill. The escalation of human-polar bear conflicts exacerbated concerns over public safety and led to the establishment of the Polar Bear Control Program (now the Polar Bear Alert Program) in 1969 (Towns et al. 2009), which is tasked with reducing property damage and ensuring public safety in and around the town (Kearney 1989). A component of the program now includes the use of zones around Churchill to guide management responses. For example, Zone 1 includes the town of Churchill, Zone 2 is the inhabited perimeter of town, and Zone 3 is the remote area around town (Pilfold et al. 2016). Tolerance for bears is lowest in Zone 1, and animals are moved to the Polar Bear Holding Facility (Fig. 17.2). This facility was built in 1982 to temporarily house bears until the bay freezes (Kearney 1989). The humane mitigation of human-polar bear conflict has been a longstanding priority in and around Churchill.

Fig. 17.2 The Polar Bear Holding Facility in Churchill, Manitoba, Canada. Polar bears that come into Churchill are moved to the holding facility, where they are housed temporarily until the sea ice returns in the fall. Bears are captured as early as July and usually released in November. Image courtesy of Kt Miller/polarbearsinternational.org

17.3 Contemporary Drivers of Human-Polar Bear Interactions and Conflict

17.3.1 Climate Warming

The primary threat to the survival of polar bears is the progressive loss of sea ice (Amstrup et al. 2008; Atwood et al. 2016a; U.S. Fish and Wildlife Service 2017a). Likewise, it is also the contemporary and future driver of human-polar bear conflict. Global warming is transforming Arctic ecosystems through changes in nutrient cycling, precipitation regimes, ocean chemistry, floral and faunal community structure (and trophic interactions), ambient air and sea temperatures, and availability of sea ice (IPCC 2014; Stern and Laidre 2016; Bintanja 2018). Overall, (1) the Arctic is warming ~2.4-fold faster than the Northern Hemisphere average, (2) sea surface temperatures have risen by ~1.0 °C decade^{-1} since 1982, (3) the percentage of multi-year sea ice present has declined by 4.6 million km^2 since 1979, and (4) ice extent and volume during summer have declined at rates of 14% and 28% decade^{-1}, respectively, since 1979 (Comiso 2012; Lang et al. 2017; Hart et al. 2018; IPCC 2019). Based on current trends in GHG emissions (primarily CO_2) and the lag time for global climate processes to reach equilibrium, Arctic warming will continue for several decades even if emissions ended immediately (Allen and Stocker 2014; IPCC 2014). As a result, loss of sea ice resulting from a warming climate will remain a primary driver of human-polar bear conflict for several decades.

The loss of sea ice influences human-polar bear interactions primarily by displacing bears from offshore to onshore. The break-up of annual ice in spring gives way to a minimum extent typically by mid-September, followed by the reformation of ice in the fall (Barry et al. 1993). Patterns of sea ice phenology and availability have historically varied regionally. For example, the Seasonal Ice Ecoregion (SIE) (Fig. 17.1; Amstrup et al. 2008) has a long history of ice melting almost completely each summer and bears coming ashore until ice reforms in the autumn. In other regions (Divergent, Convergent, and Archipelago), ice was present year-round and, until recently, bears mostly remained on the ice (Fig. 17.1; Amstrup et al. 2008; Rode et al. 2015a; Atwood et al. 2016a). Arctic warming has caused the annual period of reduced ice availability (i.e., open-water period: the time between ice break-up and freeze-up) to increase at a rate of ~13 days decade^{-1} throughout the Arctic since 1979 (Stern and Laidre 2016). As a result, polar bears have modified their behavior and movements and become more reliant on land during the open-water period.

Even for polar bears accustomed to spending time on shore (e.g., those in the SIE), longer periods of open water result in a longer on-shore residence and corresponding declines in body condition caused by nutritional restrictions (Regehr et al. 2007; Obbard et al. 2016). Diminishing sea ice also is causing human behavioral changes, which have implications for successful coexistence with polar bears. As temperatures warm and sea ice declines, conditions in the Arctic become more favorable for economic development and recreation (AHDR 2015). Collectively, these changes in habitat availability and bear and human behaviors have spurred an increase in the frequency and breadth of human-polar bear interactions and conflict.

17.3.2 Attractants Revisited

Some attractants, such as garbage, are incidental in the sense that they are by-products of human activities and not intended to attract wildlife. Other attractants are intentionally dispersed to divert wildlife from areas where they are likely to cause conflict or to provide supplemental food periodically. Bears are more likely to exploit human food when their natural sources are scarce, which for polar bears is the open-water period when their ability to hunt seals is reduced (Baruch-Mordo et al. 2014; Johnson et al. 2015). Garbage dumps, which are spatially and temporally predictable sources of food, remain focal attractants for polar bears, and waste management continues to be a priority for mitigating human-polar bear conflict. As the duration of the annual open-water period has increased and access to marine mammal prey has been reduced, polar bears have become more reliant on food in and around settlements (Towns et al. 2009; Atwood et al. 2016b; McKinney et al. 2017).

In 2013, two polar bear attacks on humans occurred in Churchill, Manitoba. Subsequent interviews with resource managers and residents identified improper garbage disposal as one of several contributing factors (Schmidt and Clark 2018). Improper waste management practices included placing garbage on the street the night before pick-up (rather than the day of), a lack of bear-proof garbage containers, and improper garbage disposal practices at restaurants and other businesses, which are not unique to Churchill (Schmidt and Clark 2018). Communities in Alaska, Greenland, and Russia have experienced increased human-polar bear conflict, exacerbated by inconsistent garbage disposal and security regimens (Moshøj 2014; Wilder et al. 2017; Steer 2019).

Improved waste management will mitigate the risk of human-polar bear interactions, but long-term solutions will require altering human behavior, which will require better education on how to prevent human-polar bear conflict (Schmidt and Clark 2018). Educational outreach is the preferred management tool to reduce HWC, but its effectiveness as a stand-alone approach is questionable. For example, a "Bear Aware" education campaign in New York had no effect in changing human behavior to prevent attracting black bears (Gore et al. 2008). Yet, educational outreach paired with proactive communication and enforcement of wildlife ordinances (e.g., use of a bear-proof container, properly secured container or dumpster) proved effective in altering human behavior in Aspen, Colorado (Baruch-Mordo et al. 2011). Single-method approaches to changing bear behavior can be less effective than multi-pronged efforts. For example, the habituation of polar bears to sound deterrents (e.g., 12-gauge cracker shells) make it more difficult to mitigate chronic conflict (Schmidt and Clark 2018). Accordingly, management strategies that include proper aversive conditioning techniques or deterrents along with the removal of attractants are key to modifying bear behavior and reducing conflict (Marley et al. 2017; Wilson et al. 2017).

Intentional provisioning, such as diversionary and supplemental feeding, has been widely practiced in Europe to reduce HWC and sustain wildlife during periods of food scarcity. Feeding is often accepted by the public because it provides a non-lethal alternative to mitigating conflict (Kavčič et al. 2013). However, the efficacy and unintended consequences of feeding bears can vary based on the underlying circumstances. For example, the emergency feeding of black bears in the Tahoe Basin of California-Nevada following a drought-induced food failure seemed to reduce conflicts near the feeding sites (Garshelis et al. 2017). Similarly, diversionary feeding, implemented at a broad spatial scale every year regardless of natural food availability, is the primary strategy for reducing human-brown bear conflicts in Slovenia (Krofel and Jerina 2012). However, while human-bear conflicts in Slovenia were less prevalent where diversionary feeding was most intense (Garshelis et al. 2017), the availability of human-provisioned food likely contributed to higher reproductive rates and densities, which eventually created a demand for population control through an increased harvest (Krofel et al. 2012; Jerina et al. 2013).

In Alaska, diversionary and supplemental feeding of polar bears by locals occurs in the autumn in conjunction with subsistence whaling activities and likely helps to reduce conflicts when whales are brought to shore for butchering. However, this has the unintended consequence of increasing conflicts when bears run out of human-provisioned food (Box 17.2). While supplemental feeding may be applicable in emergency situations, the negative consequences of persistent feeding led to banning the practice in national parks in the USA, and the prohibition or removal of anthropogenic attractants has become the principal action to mitigate conflicts with bears in North America (Garshelis et al. 2017).

17.3.3 Tourism and Recreation

Although wildlife is threatened by anthropogenic activities, the popularity of nature-based tourism is increasing. According to the World Travel and Tourism Council (WTTC), travel and tourism contributed US$8.8 trillion to the total worldwide Gross Domestic Product (GDP) in 2018 and supported one in ten jobs worldwide (World Travel and Tourism Council 2019). Nature-based tourism, including wildlife viewing, is one of the fastest-growing sectors of tourism, and it has experienced a recent annual growth rate of 10–15% (Oviedo-García et al. 2017; Wearing and Schweinsberg 2018). In the Arctic, tourism and recreational activities, including the viewing of polar bears, have increased as sea ice has declined. Unfortunately, some of the growth in nature-based tourism is attributed to "last chance" tourism, which is motivated by the desire to see threatened or diminishing natural attractions (e.g., at-risk species, glaciers, coral reefs) (Hall and Saarinen 2010). Locations featuring "last chance" attractions often experience heightened visitation, which has spurred concerns about how such activities may affect polar bears (Rode et al. 2018).

It is difficult to estimate the types and intensities of recreational activities in the Arctic, as this information is often fragmented or unavailable. Arctic-wide, common recreational activities include hiking, camping, rafting, and hunting in the summer and autumn (Hall and Saarinen 2010; Rode et al. 2018). Because these activities are dispersed in time and space, they do not pose a substantial risk of conflict (Rode et al. 2018). In contrast, the commercial viewing of polar bears, which by its nature brings together aggregations of people and bears, may pose a larger risk of conflict. In Alaska, the numbers of commercial recreation and air operation permits issued by the Arctic National Wildlife Refuge (ANWR), many for polar bear viewing, have increased since the 1980s (U.S. Fish and Wildlife Service 2015). Polar bear viewing now exceeds all other recreational uses of ANWR by more than two-fold (U.S. Fish and Wildlife Service, unpublished data). In Svalbard, long considered a "bucket-list" destination by adventure travelers, guest arrivals in Longyearbyen have increased at a rate of 6.4% year^{-1} since 2008 (Quark Expeditions 2019). Most tourists moving beyond the limits of the Longyearbyen settlement travel by cruise ship, which doubled the number of port landings from 1996–2010 (Hagen et al. 2012). In Churchill, Manitoba, commercial polar bear viewing operations accommodate up to 10,000 people during a 4–8-week season (Churchill Polar Bear Tours 2019). In

Kaktovik, Alaska, the opportunity to view polar bears at the bowhead whale (*Balaena mysticetus*) bone pile (Box 17.2) led to the development of a nascent but fast-growing eco-tourism industry where the number of visitors during a three month season increased from 260 to 2557 from 2011–2015 (U.S. Fish and Wildlife Service 2017b). There are numerous examples where commercial brown and black bear viewing has occurred with little to no conflict (Barnes 2006; Coleman et al. 2013; DeBruyn et al. 2014; Massé et al. 2014). If well-managed, commercial polar bear viewing can provide economic benefit to local communities with relatively little risk of human-polar bear conflict.

Tourism can provide a much-needed economic stimulus to Arctic communities. In 2013, nature-related tourism in the Arctic generated US$388 million in Canada and greater than $6 million in Alaska (Maher et al. 2014), suggesting that the opportunity exists to generate substantial revenue in the future. In the context of conservation, recreational activities encourage learning and empathy, and they foster support for initiatives benefitting wildlife and their habitats (Zeppel 2010). However, the economic and educational benefits of recreational activities in the Arctic must balance potential negative effects on polar bears and the tundra (Forbes 1998; Rode et al. 2018). As polar bears spend more time on land, the proliferation of recreational activities will increase the risk of human-polar bear conflict.

17.3.4 Oil and Gas Exploration and Production

Probabilistic geology-based assessments suggest that the area north of the Arctic Circle may contain about 30% of the world's undiscovered gas and 13% of the world's undiscovered oil (Gautier et al. 2009). The continued decline of summer sea ice will allow greater human access to the Arctic Ocean, facilitating the extraction of oil and gas reserves. While these reserves are distributed throughout the Arctic, most exploration and development occurs in the nearshore region of Alaska's Southern Beaufort Sea associated with the coastal plain (i.e., the North Slope) and, to a considerably lesser degree, in Russia. In 2013, an offshore oil platform was built in Russia's Kara Sea, but little additional work has occurred since then (Tayloe 2015). In Alaska, exploration activity has steadily increased over the past decade and, as of 2018, oil and gas operations were occurring at facilities on four offshore artificial gravel islands (Oooguruk, Nikaitchuq, Northstar, and Endicott-Duck Island) and on the coastal plain within the Prudhoe Bay and Kuparuk fields and the National Petroleum Reserve-Alaska (NPR-A) (Fig. 17.3; Smith et al. 2017). In the winter of 2018–19, the number of active exploration and production rigs on the North Slope reached its highest level in 20 years. The concurrent increase in North Slope industrial activity and decline in the availability of sea ice is associated with the occurrence of polar bears near infrastructure. For example, from 2010–16, 2373 polar bears were reported by industry to the U.S. Fish and Wildlife Service. No

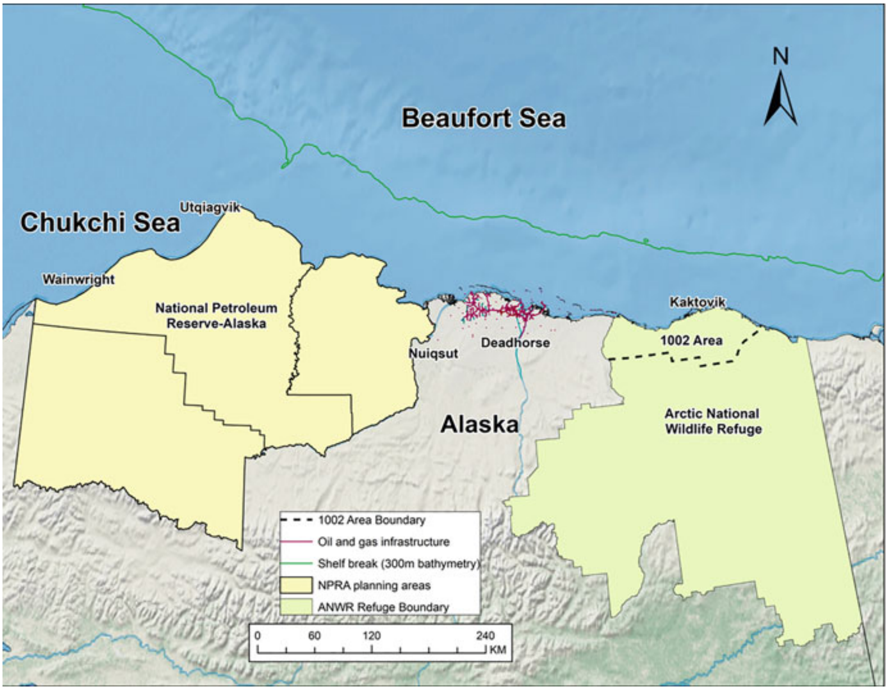

Fig. 17.3 The National Petroleum Reserve-Alaska (NPR-A) occupies 9.5 million hectares along the eastern North Slope region. The Arctic National Wildlife Refuge (ANWR) occupies 7.9 million hectares in the west. The Prudhoe Bay and Kuparuk oil fields occur in the Deadhorse region between the NPR-A and the ANWR

intervening action (e.g., hazing to mitigate the risk of conflict) by industry was reported for 84% of the bears (1978 bears) (U.S. Fish and Wildlife Service 2017c).

In December of 2017, federal legislation was passed in the U.S. to open 0.6 million hectares of the 1002 Area of the ANWR to oil and gas exploration and development (Fig. 17.3). Industrial development within the ANWR will result in an oil and gas industrial footprint spanning the east-west axis of Alaska's North Slope. In addition to increasing their time ashore in summer, a majority of Southern Beaufort Sea polar bears now use land for maternal denning in winter (see Sect. 14.3; Fischbach et al. 2007; Olson et al. 2017). The coastal plain of the ANWR has a disproportionate amount of high-quality denning habitat for polar bears, and the community of Kaktovik is located within the boundary of the refuge (Box 17.2; Durner et al. 2006). As a result, use of the refuge by polar bears is relatively common from summer through winter (i.e., August through March) (Atwood et al. 2016b; Pearce et al. 2018). Consequently, oil and gas exploration and development are likely to present a challenge to managers tasked with mitigating conflict and human disturbance of denned bears.

Box 17.2 Southern Beaufort Sea Polar Bears and Their Growing Reliance on Human-Provisioned Scavenge Subsidies There are three communities in Alaska (Utqiağvik, Nuiqsut, and Kaktovik), which harvest bowhead whales (*Balaena mysticetus*) from the Southern Beaufort Sea (SB) in the autumn. Unwanted remains from the harvest are placed at “bone piles” where they have attracted polar bears since at least the 1990s (Schliebe et al. 2008; Atwood et al. 2016b). The declining availability of sea ice in the SB has led to an increase in the proportion of the bear population coming ashore in summer and autumn. Since the late 1990s, the mean duration of the open-water period has increased by over one month, as has the mean length of stay on land by bears (Atwood et al. 2016b). The largest aggregation of bears typically occurs at the Kaktovik bone pile, which is situated ~2.5 km from the community. In 2012, an estimated 148 polar bears (16% of the SB population; Bromaghin et al. 2015) visited the Kaktovik bone pile in the autumn (Lillie et al. 2019). Interactions between humans and bears are common during the butchering of whales, and diversionary feeding is practiced to discourage bears from approaching the workers (Fig. 17.4; T. Atwood, pers. obs.).

At Kaktovik, polar bears mostly remain close to the bone pile while on land, even after whale remains have been depleted, until sea ice forms. People cure their whale meat outside of their homes, although the use of bear-proof food lockers has increased recently. When food is no longer available at the bone pile, some bears venture into town. Kaktovik maintains a Polar Bear Patrol, which is tasked with deterring bears from entering the community, but resources are limited for the effort needed. For example, the Polar Bear Patrol responded to 467 reports of bears in the community over a three-month period in the summer and autumn (August through October) of 2018. Unfortunately, documentation of human-polar bear interactions and conflicts in Kaktovik is limited, precluding an assessment of potential trends and outcomes. Although rare, “defense of life” kills occasionally occur.

A longer open-water period is expected to result in SB polar bears spending more time on shore and becoming increasingly reliant on the remains of whale harvests to ameliorate declines in body condition (Atwood et al. 2016b; McKinney et al. 2017). As a result, the aggregation of polar bears around the Kaktovik bone pile will continue to be a threat to safety for residents and bears, and concerned parties have considered options for mitigating the risk. Some favor eliminating the bone pile by pushing the unused whale remains into the ocean. Others see its value in sustaining bears through a period of food scarcity and in diverting large numbers of bears from coming into town to exploit whale meat at residences. Because the use of whale remains by bears is a learned behavior (i.e., mothers teach their cubs to exploit the bone piles; Lillie et al. 2018), it may be difficult to deter bears from the area should the bone pile be eliminated (rather than slowly phased out). A compromise

(continued)

Box 17.2 (continued)
(though costly) solution may be to place the unwanted whale remains farther from the community. For example, relocating bone piles ~50 km from Kaktovik could reduce the estimated number of bears present in the community by more than 75% (Wilson et al. 2017). Relocation and distribution of whale remains in a manner that resembles the distribution of beach-cast marine mammals may reduce polar bear-human conflict while encouraging more natural scavenging behavior by polar bears.

17.4 Mitigating the Risk of Future Conflict: A Conceptual Model

Proximate factors influencing human-polar bear interactions and conflict are varied but largely consistent through time and likely to be exacerbated by changes in human and bear behavior (e.g., increased development and recreation, growing dependence on land by bears) resulting from climate change. Because of the potential consequences for human safety and polar bear conservation, there is a pressing need to better understand the circumstances that lead to conflict, predict when and where conflict will occur in the future and use that information to develop effective interventions. Here, we introduce a conceptual model based on mechanistic links between environmental change and polar bear behavior, which can be adapted for use in predicting and mitigating human-polar bear conflict (Van Hemert et al. 2015; Atwood et al. 2016a). The model is comprised of the following components:

- Environmental drivers (e.g., climate change, air and sea temperatures)
- Primary effects (e.g., habitat change)
- Secondary effects (e.g., changes or modifications in bear and human behaviors)
- Polar bear responses (e.g., frequencies of interactions and conflicts)

This generalized framework can be expanded into more detailed, regionally relevant models as needed (Fig. 17.5).

The primary cause of accelerated climate change is GHG emissions. If they continue to rise unabated, climate models estimate that mean surface air temperature will increase 4–5 °C above preindustrial levels by the end of the twenty-first century, and sea temperature in the central Arctic Ocean will rise ~0.4 °C decade^{-1} (Collins et al. 2013; IPCC 2014; Barnhart et al. 2015; Alexander et al. 2018). As a result, the Arctic Ocean will be ice-free in summer for as many as five months (Douglas and Atwood 2017). It is unclear how such changes (e.g., ice extent, sea temperatures) to the physical environment will affect the marine food web. Ringed (*Pusa hispida*) and bearded (*Erignathus barbatus*) seals, the primary prey of polar bears, may shift their distribution northward where stable ice remains and sufficient snow cover accumulates for constructing birthing lairs (Harwood et al. 2015). It also is possible that subarctic seals, such as spotted (*Phoca largha*), ribbon (*Histriophoca fasciata*),

Fig. 17.4 (**a**) A polar bear feeding at the bowhead whale bone pile at Kaktovik, Alaska. The unwanted remains of subsistence-harvested whales are placed on a spit from September to October. Some polar bears may return to the bone pile in winter to search for food (Lillie et al. 2018). (**b**) Diversionary feeding of polar bears during the butchering of a bowhead whale at Kaktovik. Whales are butchered on shore, which attracts polar bears that wait for the bone pile to be stocked. Whalers often drag sections of blubber away from the butchering site to keep bears at a safe distance. Image courtesy of S. Breck

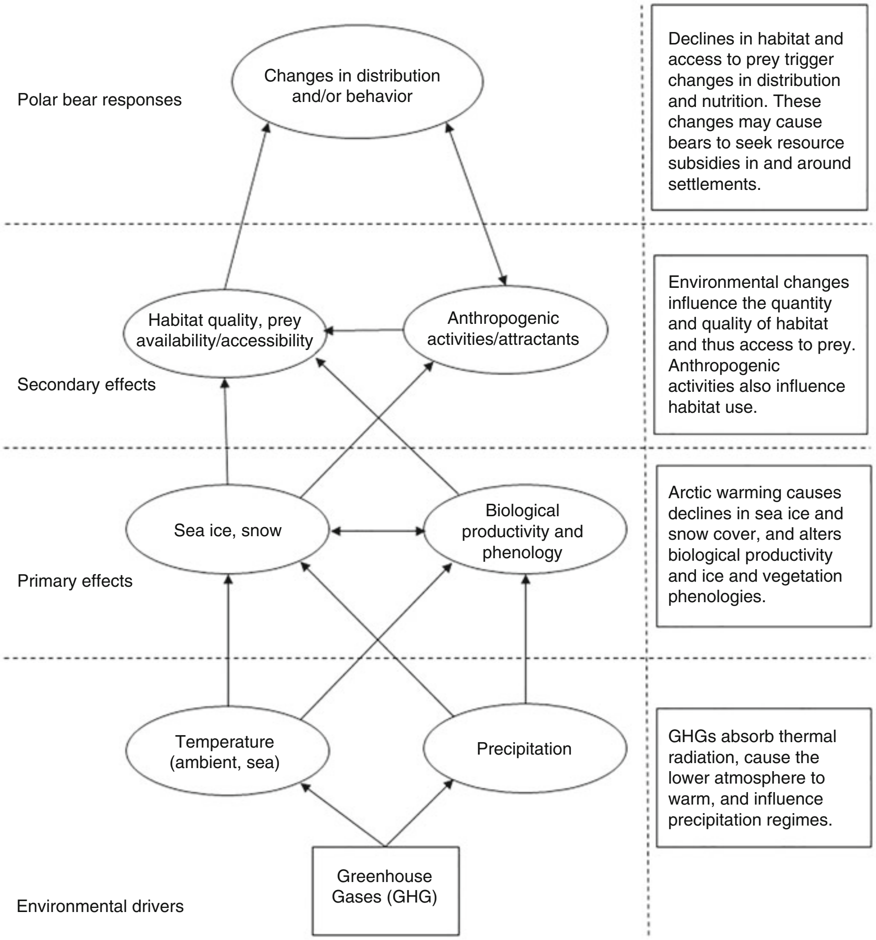

Fig. 17.5 Conceptual model of relationships and linkages between physical drivers of climate change and effects on habitat quality and quantity, anthropogenic activities, and polar bear responses. Adapted from Van Hemert et al. (2015)

harp (*Pagophilus groenlandicus*), and hooded (*Cystophora cristata*) seals could seasonally expand their ranges northward. However, without the sea ice to use as a hunting platform, polar bears are unlikely to benefit from such range expansions if the seals display pelagic behavior like they do in subarctic waters (Womble et al. 2014).

The continued loss of sea ice will drive more polar bears onto land (Rode et al. 2015a; Atwood et al. 2016b). If the Arctic Ocean eventually becomes ice-free in summer, all remaining polar bears will be forced ashore somewhere (Douglas and Atwood 2017). Polar bears, like most Ursidae, are adapted to a feast-and-famine lifestyle, which enables them to rely on accumulated fat reserves during periods when prey are scarce or inaccessible. However, there is a threshold beyond which fat reserves are depleted and bears become nutritionally stressed (Pilfold et al. 2016). In some subpopulations, declines in body condition have been associated with the loss of sea ice (Rode et al. 2010; Obbard et al. 2016). Energetic modeling suggests that food deprivation lasting longer than 5 months could result in a significant risk of reproductive failure and starvation (Molnár et al. 2010, 2014; Robbins et al. 2012). Polar bears experiencing extreme nutritional stress will be emboldened to seek food around settlements (Towns et al. 2009; Wilder et al. 2017). Thus, the interplay between the amount of fat reserves accumulated prior to the start of the open-water period, amount of time spent on shore, the availability of terrestrial food subsidies, and their proximity to human settlements will determine where human-polar bear conflicts are most likely to occur (Gormezano and Rockwell 2015; Rode et al. 2015b; Wilson et al. 2017).

So, where does that leave opportunities to mitigate future human-polar bear conflict? Our conceptual model provides a starting point for considering important drivers and interactions, which are likely to mediate human-polar bear conflict in the future (Fig. 17.5). Any attempt to assess threats to populations must integrate an appropriate level of ecological complexity. Specific analytic approaches, such as spatially explicit models of when and where conflicts occur, must then build on this framework to be useful to managers. Actions that target the effects of GHG emissions on human-polar bear conflict will be the most difficult to implement because they will require national and international attention. Even if widespread mitigation of GHG emissions is achieved, temperatures will continue to rise for ten years or longer because of CO_2 that has already accumulated in the atmosphere (Ricke and Caldeira 2014). In addition, stabilization of sea ice will require at least an additional 10–20 years (Amstrup et al. 2010).

Mitigation of GHG emissions and stabilization of sea ice habitat will not provide a timely reduction in the future risk of human-polar bear conflict (Allen and Stocker 2014). Until the climate-induced loss of sea ice habitat is halted, efforts to mitigate conflict should focus on (1) management of attractants, (2) location, timing, and intensities of anthropogenic activities, and (3) educating people living in or visiting polar bear areas to reduce the likelihood of conflict. Mitigating human-bear conflict is of mutual interest for communities, resource managers, conservationists, and other stakeholders. We have an opportunity to address this concern before it becomes more widespread.

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