1 INTRODUCTION

Once upon a time, around 37 million years ago, when primitive fissiped carnivores were evolving from their miascid predecessors, some of them forsook their way of life on land and went to sea to find food. This move must have worked out well, because many of the descendants of these pioneers—the seals, sea lions, and walruses—are still making a living in the sea today. Of course, descendants of the carnivores that remained on land fared well, too. Because land and sea are such different environments, we might expect the two animal groups to have diverged in many ways since their separation. Indeed, it should be interesting to compare representatives of the two groups because of what they have in common, an ancestor, and because of the obvious differences in the environments in which they live. In this chapter, I point out some differ-
ences and similarities between seals and their terrestrial counterparts with respect to gross morphology, feeding and predatory behavior, reproductive behavior, and various aspects of social life. As is necessary when comparing two large groups of animals, I document points with examples from a few selected species. My selection is biased toward those species that have been studied most systematically, those that are of greatest theoretical interest, and those studies with which I am familiar.

The similarities between seals and land carnivores were obvious to laymen and early scientists (Fig. 9.1). Fifteenth and 16th century sailors described the seals they saw as marine carnivores and called them “sea lions,” “sea bears,” or “lobos de mar” (sea wolves). Linnaeus and several later taxonomists classified seals, sea lions, and walruses in the order Carnivora. However, as early as 1811, there was an attempt to place these animals in a separate order (Illiger, 1811). At present, many investigators class these marine mammals in their own separate order, the Pinnipedia (e.g., King, 1964). However, classification of these animals is far from settled. Some maintain that the new order is inappropriate and that pinnipeds should be considered merely a suborder of the Carnivora (McKenna, 1969). Others argue that the pinnipeds can be classified into two living families (walruses are placed in the same family as sea lions) under the superfamily, Canoidea, in the order Carnivora (Mitchell and Tedford, 1973).

Before I make specific comparisons, it may be useful to present a sketch of pinniped evolutionary history. Their history, although poorly documented, may provide clues to differences we might expect between them and terrestrial carnivores.

The earliest pinnipeds probably entered the sea in one of the following areas: the Arctic Basin, the northwest coast of North America, or the Tethyan-Mediterranean area (Matthew, 1939; Davies, 1958a; McLaren, 1960; Repenning, 1970). It is not clear whether seals and sea lions (including the walrus) were already differentiated at this time. The oldest pinniped remains are from the Miocene era, a time when they were already well adapted for aquatic life and when seals and sea lions were already distinguishable (Downs, 1956; Mitchell and Tedford, 1973). One opinion holds that all pinnipeds derived from canid or dog-bear stock (e.g., Matthew, 1939; Simpson, 1945; Davis, 1958a; Sarich, 1969). An opposing view is that sea lions and the walrus derived from ursine stock, and seals derived from lutrine stock (e.g., Mivart, 1885; McLaren, 1960; King, 1964; Repenning, 1970). This question is far from settled. Nevertheless, there is agreement that all pinnipeds are more closely related phylogenetically to members of the superfamily Canoidea of the order Carnivora—the
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dogs, raccoons, bears, weasels, and the like—than to the feloid carnivores.

After they entered the water, the distribution and diversity of pinnipeds were influenced by geomorphic and climatic barriers, distance between land falls, ocean currents, and water temperature (Davies, 1958a; King, 1964; Hendey, 1972). Davies (1958b) hypothesizes that pinnipeds are, and always have been, tied to a cold-water environment. He argues very persuasively that the distribution and differentiation of present-day northern pinnipeds reflects periods of expansion and contraction of sea and glacial ice that occurred during the Pleistocene era. Scheffer (1958, p. 37) points out that "as local shore lines and islands rose and fell and glacial barriers came and went, pinnipeds moved back and forth in order to maintain favorable breeding grounds along the edge of the sea." On land, many contemporary carnivores were being forced into extinction by periodic fires, floods, droughts, and dust storms.

Scheffer suggests that the early pinnipeds moved out along the shores of continents, from island to island and later to polar ice fields. The rate of evolution was faster at the frontiers of the advancing lines where immigration was unidirectional. He speculates further:

The primitive populations were small, composed of family groups, not very sociable. The members did not wander far, had no well-developed homing instinct, were not migratory, and did not need to rendezvous in special places in order to find mates. Polygyny had not developed in any of the pinniped stocks. The animals were perhaps smaller than most recent pinnipeds (Cope's rule), had less fat, lived in more temperate waters, and perhaps made crude dens in beach grasses and among boulders. The advancing pinnipeds met, from sea birds and cetaceans, little competition for food. They met no competition for breeding room, nor do they often today. Pinnipeds early lost the habit of feeding on beach organisms such as crabs, mussels, periwinkles, and blennies. [Scheffer, 1958, p. 36-37]

As each generic stock became isolated, it was transformed in response to the local physical and biotic environment and adapted to its peculiar niche. Among species frequenting isolated bays, gulfs, islands, inland seas, or lakes, there has been, and still is, rapid evolution.

In the last few centuries, the effect of commercial sealing upon island and continental pinniped populations has been catastrophic. Millions of seals have been slaughtered and entire breeding populations wiped out. It is doubtful that some species will ever recover genetically from undergoing such a severe population "bottleneck" (Le Boeuf, 1977). In one recently exploited species, absolutely no polymorphic variation was
found in 21 blood proteins from 159 seals representing five rookeries (Bonnell and Selander, 1974)! In this regard, some land carnivore populations have suffered a similar fate at the hands of man—for example, the wolf. The increasing range of human populations is changing the distribution of both land carnivores and pinnipeds.

Although pinnipeds are marine, all species have retained an attachment to land. In this respect, they differ from the Cetacea, descendants of a primitive ungulate ancestor, who have become completely aquatic. All pinnipeds give birth on land or ice, and some species spend the majority of their time resting out of the water.

Pinnipeds have exploited the marine niche for food. A few carnivores, such as the sea otter, *Enhydra lutris*, and the polar bear, *Thalarctos maritimus*, also obtain food from the sea, but they have not undergone the same degree of morphological transformation to aquatic living as the pinnipeds. The anatomical and behavioral adaptations of the pinnipeds to life in the sea clearly distinguishes them from the land carnivores. Since these adaptations influence their behavior on land, it is worth reviewing some of the major ones.

2 MORPHOLOGICAL COMPARISONS

Many morphological differences between pinnipeds and land carnivores are simply a reflection of the different environments in which they live. The average body size of pinnipeds is greater than that of carnivores. The smallest pinniped, the ringed seal, *Pusa hispida*, weighs 90 kg. The largest pinniped, the southern elephant seal, *Mirounga leonina*, weighs about 3629 kg and is 650 cm long (Scheffer, 1958). Several seal species are larger than the largest land carnivore, the grizzly bear, *Ursus arctos*, which weighs 771 kg (Erdbrink, 1953). Many land carnivores, such as the foxes of Africa (Bekoff, 1975), weigh less than 4 kg. The Fennec fox, *Fennecus zerda*, weighs less than 1 kg! The greater body size of pinnipeds evolved mainly in response to the marine environment. Large body size is better for heat retention in the cold sea. Moreover, since the water medium gives more support than air, large size could more easily evolve in the sea than on land.

The pinniped body is adapted for swimming and diving. Body shape is streamlined to reduce drag. The external ears are reduced or absent, external genitalia and mammary teats are drawn into the body, limbs are enclosed within the body and extremities are flattened—the tail is short and the head is flattened, and the eyes are situated well forward. The neck, in particular, is thick and muscular and considerably more flexible.
than in most large carnivores. The skin is adapted to a water environment (Montagna and Harrison, 1957), and the hair is flattened. Pinnipeds never groom the pelage with the mouth or tongue (Scheffer, 1958). The terrestrial carnivore body is a picture of contrast. The canid body, especially the large one, is designed for long-distance running (see Romer, 1966; Mech, 1970; Fox, 1975).

Subcutaneous fat forms a substantial part of all pinniped bodies. Skin and blubber make up more than 25% of the weight of the Weddell seal, *Leptonychotes weddelli* (Bruce, 1951) and almost 50% of the body weight of the southern elephant seal (Laws, 1953). Blubber provides reserve energy during fasts and lactation, thermal insulation, buoyancy, and the padding necessary for a streamlined profile. The proportion of body fat to total weight in land carnivores is apparently much smaller, even in dormant or hibernating bears, skunks, and raccoons.

Although the pinniped brain has not been studied in great detail, it is evidently large, like that of terrestrial carnivores, but more spherical and more highly convoluted (King, 1964). The sea lion brain resembles that of bears, while the seal brain looks more like that of cats and dogs. Compared to a dog's brain, the cerebellum is large, probably because of the increased coordination demanded in swimming. The auditory nerve is large and the olfactory lobes are reduced. Pinniped eyes (the walrus excepted) are larger than those of land carnivores, and they function well at low levels of illumination. Seal vision is excellent both in water and on land (Schusterman, 1972).

Pinnipeds have fewer and more uniform teeth than most land carnivores (except for the walrus, a special case once again). All species have the pronounced upper and lower canines but lack the carnassial cusps characteristic of land carnivores. The postcanines in most species are rudimentary pegs functioning to hold prey that is swallowed whole. Variation in pinniped teeth reflects the type of flesh the animal feeds on, and, as in many mammals, it is a useful taxonomic indicator. Generally, the teeth, mouth, jaw, and associated structures of pinnipeds are designed for grasping, tearing, and swallowing prey whole or in chunks, rather than for chewing, shearing, or crushing large bones. In contrast with land carnivores, the deciduous teeth of pinnipeds disappear before or soon after birth.

Pinnipeds have made numerous physiological adjustments to aquatic life that set them apart from land carnivores. These adaptations in respiration, circulation, renal physiology, and the like are important and interesting, but it would be too much of a digression to cover these topics here. Ridgeway (1972) provides an excellent review of marine mammal adaptation to the aquatic environment.
Pinnipeds deviated from land carnivores in form and function because of adaptations that took place as a result of seeking food in the sea. It is therefore most important to compare these two animal groups from the point of view of hunting and feeding habits, and in relation to their respective prey.

Both pinnipeds and land carnivores are meat eaters, but only the marine mammals eat flesh exclusively. Seals and sea lions feed mainly on crustacea, molluscs, fish, penguins, and other sea birds. Although diet varies with the species, the majority of pinnipeds feed on a variety of prey. The Alaska fur seal, Callorhinus ursinus, is the best studied pinniped from the point of view of food habits. Its catholic diet is representative of the wide range of fishes and squid eaten by the Otariids (the earred seals or sea lions and fur seals, as opposed to the Phocids, the earless, true seals). Alaska fur seals feed on more than 30 kinds of marine organisms: at least 27 species of fish, 1 species of octopus, and 5 species of squid (Fiscus, Niggol, and Wilke, 1961). The most common prey of fur seals are northern anchovy, Engraulis mordax, squid, and Pacific herring (Clupea harengus). Various rockfish, Pacific hake, Merluccius Productus, Pacific saury, Cololabis saira, salmon, Oncomorhynchus spp., and American shad, Alosa sapidissima, are eaten in lesser quantities. Hermit crabs, amphipods, and various diving sea birds (e.g., Rhinoceros Auklet, Cerorhinca monocolor, Red-throated Loon, Gavia stellata, and Beal Petrel, Oceanodroma leucorhoa beali) are eaten occasionally, but they seem to play only a minor role in the seals' diet (Niggol, Fiscus and Wilke, 1959).

Fur seals, like most other pinnipeds, are opportunistic feeders. What is eaten depends on the seasonal distribution and the abundance of prey. Since fur seals commonly feed on schooling fishes, stomach contents of several animals collected in the same area often contain only one type of fish. The Steller sea lion, Eumetopias jubata (Spaulding, 1964), and the California sea lion, Zalophus californianus (Fiscus and Baines, 1966), eat similar fishes and squid, especially where the feeding range of the three species overlaps. Steller males in the Bering Sea and off Alaskan islands supplement their diet with Alaska fur seal pups (Roger Gentry, personal communication).

Most true seals, such as the harbor seal, Phoca vitulina, and the grey seal, Halichoerus grypus, are mainly fish eaters, but they occasionally feed on an assortment of crustacea, octopus, eels, and molluscs (Spaulding, 1964; Kenyon, 1965; Anderson et al., 1974). The northern elephant seal, Mirounga angustirostris, is a deep diving seal that feeds primarily on squid,
skates, rays, small sharks, and ratfish, *Hydrolagus collier* (Huey, 1930; Morejohn and Baltz, 1970). The small ringed seal, *Pusa Hispida*, which inhabits the circumpolar Arctic coasts, feeds on up to 72 different species of small pelagic amphipods, euphausians, and other crustacea, as well as on small fish (King, 1964).

Only two of the 32 different pinniped species in King’s classification (King, 1964) are rather specialized feeders that exploit one type of prey species almost exclusively. The Crabeater, *Lobodon carcinophagus*, feeds on krill, small shrimp-like animals that it catches in quantity and strains from the water through its multicusped cheek teeth, much as a mysticete whale sieves krill through its baleen. The walrus, *Odobenus rosmarus*, feeds primarily on three genera of bivalve molluscs, *Mya*, *Saxicava*, and *Cardium*, for which it forages in shallow coastal waters less than 40 fathoms deep. Bivalves on the sea bottom are examined and sorted by the lips and whiskers; feet and fleshy parts are torn off and swallowed whole or sucked out. But when molluscs are scarce, the walrus may eat young ringed seals, bearded seals, *Erignathus barbatus*, and even young walruses. It is the only pinniped that apparently feeds on Cetacea. Occasionally a narwhal, *Monodon monoceros*, or a beluga, *Delphinapterus leucas* is eaten. However, it is not known whether walruses actually kill them or feed on corpses (King, 1964).

The diversity of foods eaten by canids and ursids is even greater than that of pinnipeds. According to Mech (1970), “probably every kind of backboned animal that lives in the range of the wolf has been eaten by the wolf.” Wolves, *Canis lupus*, eat mice, mink, muskrats, squirrels, rabbits, various birds, fish, lizards, snakes, grasshoppers, earthworms, and berries. But predation on small animals plays only a minor role in the wolf’s diet. The main prey of the wolf, like those of the African wild dog, *Lycaon pictus*, are large animals. The wolf’s primary prey in the United States and Canada are: white-tailed deer, mule deer, moose, caribou, elk, Dall sheep, bighorn sheep, and beaver. Wild dogs kill mostly Thomson’s gazelles, juvenile wildebeests and Grant’s gazelles (Estes and Goddard, 1967), and, occasionally, warthogs and zebras (van Lawick-Goodall and van Lawick-Goodall, 1971). African foxes feed mostly on rodents and small reptiles, birds’ eggs, insects and vegetable matter; jackals eat similar foods in addition to small mammals and carrion (Bekoff, 1975). Additional information on other canids can be found in Fox (1975).

Of all the land carnivores, bears have the most diverse tastes. The grizzly, before man virtually annihilated it, was an omnivorous opportunist *par excellence*. The California grizzly (Storer and Tevis, 1955) ate almost anything and everything that was available. This long list in-
cluded: meat, fresh or putrid from whales, water birds, fish, elk, deer, antelope, gophers, lizards, frogs, and domestic livestock; a wider variety of plant materials than herbivorous animals ate, some of which were various berries, clovers, nuts, wheat, corn, potatoes, tree bark, and various bulbs; and assorted foods like honey, ants and their larvae, yellow-jacket nests, and mushrooms. Polar bears, *Thalarctos maritimus*, have a much more restricted diet. Although they consume some vegetation and carrion during the summer (Russell, 1975), they feed primarily on the ringed seal during most of the year (Stirling and McEwan, 1975).

The remarkable thing about the feeding habits of the large canids is that the prey is often larger than the predator. In this respect, the large canids differ from all of the pinnipeds. Wild dogs, whose average weight does not exceed 18 kg, bring down impala and reedbucks that are double or triple their size (Estes and Goddard, 1967) and zebras that are even larger. Wolves weighing 36 to 45 kg kill moose and bison that may weigh over 500 kg. These canids overcome large prey by hunting in packs that range from a few animals up to a score or more of them. One dog usually selects a quarry from a retreating herd of gazelles, and the other dogs follow it. The quarry is coursed for 1 to 3 km until it becomes exhausted. The lead dog catches up to it and grabs it or bowls it over. Once overtaken, the prey is fallen on by all the following dogs, and it is dismembered and eaten with great dispatch. Wolves bring down deer or moose in a similar way (Mech, 1970). The first wolf to catch up to the fleeing prey attempts to grab hold of the rump, flanks, neck, or nose. Once the prey is down, others attack from every side. Although the technique may vary with prey species, the strategy of the individual quarry, and the composition of the hunting pack, it is clear that these pack hunters get help from each other in getting their food. Lone wolves or even small packs are at a disadvantage in bringing down large prey. In black-backed jackals, *Canis mesomelas*, Wyman (1967) observed that two hunters were more than four times as successful as one in bringing down gazelle fawns.

Like land carnivores, the size of prey eaten by pinnipeds varies greatly, but, except for the dubious possibility that walruses kill small whales, pinnipeds always kill and eat animals that are much smaller than themselves. Prey size determines how Alaska fur seals, Steller sea lions, and harbor seals eat their food. Small fishes less than 30 cm long, such as anchovy, herring, saury, or squid, are consumed whole under water (Niggol, Fiscus, and Wilke, 1959; Spaulding, 1964). Except for very small food items like lanternfish, the prey is swallowed head first. Larger prey measuring more than 30 cm long, such as hake, rockfish, or salmon, is brought to the surface, grasped by the head, shaken vio-
lently, and reduced to chunks that are swallowed piecemeal. As fur seals get older and larger, large fish up to 92 cm make up an increasingly high proportion of their diet (Spaulding, 1964).

Some pinnipeds feed in groups, but, unlike the case with canids, grouping does not enable them to exploit larger animals. Rather, grouping seems to make it easier for them to exploit large aggregations of small prey. Fiscus and Baines (1966) saw Steller sea lions leaving their hauling grounds in the vicinity of Unimak Pass, Alaska, in compact groups of several hundred to several thousand animals. They swam out to feeding areas, where they dispersed into smaller groups of less than 50 animals containing both sexes and mixed sizes of animals. Massings of this type fed on large schools of fish or squid. Casual observations suggest that groups of sea lions feed more efficiently on schools of fish because cooperation among the hunters enables them to herd and control the movements of the school. When large fish schools are absent, sea lions feed singly or in small groups of two to five animals. Similar behavior has been observed in the California sea lion (Fiscus and Baines, 1966; Michael Bonnell, personal observation).

Before Steller sea lion females leave the rookery and their pups to go to sea and feed, they may engage in activities that resemble, and that may have an analogous function to, the prehunt greeting ceremony of wild dogs (Estes and Goddard, 1967; van Lawick-Goodall and van Lawick-Goodall, 1971). Several females may gather at water's edge, where they mill about restlessly in close contact with each other. They may vocalize repeatedly and engage in what appears to be low-intensity aggressive behavior before swimming off as a group to feed. In both species, these activities may reinforce group cohesion and unity as well as synchronize the time of departure.

Similarly, canids and pinnipeds may travel several kilometers to get a meal. Van Lawick-Goodall and van Lawick-Goodall (1971) report that wild dogs did not start their first chase until they were 8 km from where they started. The chase itself covered a distance of 5½ km. Wolves may pursue moose or caribou for up to 5 to 8 km but usually give up sooner (Mech, 1970). They may range up to 32 km from their den (Kelsall, 1957). Steller sea lions and California sea lions travel much further from their rookeries or hauling grounds to feed. The former have been seen feeding as far as 112 to 136 km from land (Kenyon and Rice, 1961) and the latter as far as 62 km from land (Fiscus and Baines, 1966; Le Boeuf, unpublished data). Usually, only small groups of less than 30 individuals are seen this far from land. Large groups of sea lions (100 or more) are seldom seen feeding more than 16 to 24 km from a hauling ground or rookery. It would be interesting to compare land carnivores and pin-
nipeds on the success of their respective hunting and fishing expeditions, but the difficulties inherent in observing seals feeding in the water makes this impossible at present. However, some indirect evidence is pertinent. Virtually all fur seals collected early in the day by the U. S. Fish and Wildlife Service had food in their stomachs (Niggol, Ficus, and Wilke, 1959).

Although both pinnipeds and the larger land carnivores are nomadic, the former travel greater distances in their annual feeding migrations. The record holder is the Alaska fur seal, which migrates from its breeding grounds in the Bering Sea to its winter feeding grounds along the shores of the eastern and western Pacific as far south as San Diego, California, and Hokkaido, Japan, a distance of some 5000 km. Wolves may follow caribou on their annual migrations (Kelsall, 1968).

Wild dogs and dholes, Ceron alpinus, prefer to hunt in early morning or early afternoon or evening, although hunts occur on moonlight nights as well (Estes and Goddard, 1967; van Lawick-Goodall and van Lawick-Goodall, 1971; Davidar, 1975). Wolves and bears may hunt by day or night. Most of the smaller foxes are nocturnal feeders (Bekoff, 1975). Fur seals and sea lions are primarily night and early morning feeders. Stomach contents of animals collected at various hours after sunrise show decreasing amounts of food. However, in some areas where large schools of fish are present, daytime feeding also occurs. Typically, the midday hours are spent resting, and feeding activities gradually resume in late afternoon (Niggol, Ficus, and Wilke, 1959; Spaulding, 1964). The harbor seal is a daytime feeder (Spaulding, 1964).

Canids eat great amounts of food in a single feeding bout. A wolf may gorge 9 kg of meat in a single meal; this may represent 20% of its body weight. However, estimates of a little more than half that amount per day per wolf may be more representative (Mech, 1970). Estes and Goddard (1967) estimate that wild dogs average 2.72 kg of meat per day, or approximately 6.7% of their body weight. But these canids may have to go without eating for several days at a time. Five to 7 day fasts have been recorded in wolves, and one wolf went for 17 days without food (Mech, 1970). It is common knowledge that domestic dogs can go for several days without eating, particularly when sexual activity is probable. Grizzlies and black bears in the more northerly parts of North America may go dormant for varying periods of time during the winter when food is scarce. In general, all of the land carnivores will feed regularly if possible. Even bears will actively feed throughout the year when food is available.

Most pinnipeds feed daily except at certain times of the year, usually the breeding season, when they undergo long fasts. Thus, feasts and
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famine are even more extreme in their annual cycle. When they are feeding, fur seals and sea lions ingest less food relative to body weight than the canids mentioned above. Spaulding (1964) estimates that fur seal, sea lion, and harbor seal food requirements range from 2 to 11% of body weight per day, with 6% being the average. During the breeding season, fur seal and sea lion males fast for approximately 6 weeks; harbor seals do not appear to fast during this time. The record for long fasts in pinnipeds goes to male northern elephant seals. They may go without food for 3 months (Le Boeuf, and Peterson 1969). Throughout this time they are actively fighting and attempting to copulate, and they may lose over 450 kg. Females of this species fast for an average of 34 days during the period in which they give birth and nurse their pups daily for 28 days (Le Boeuf, Whiting, and Gantt, 1972). A female’s total body weight may be reduced by almost 50% during this fast. During the nonbreeding season, males and females fast again for approximately 30 days while undergoing the annual molt.

Most canids and ursids scavenge for food at some time. Perhaps bears exploit carrion more than any other land carnivore. Carrion was a major part of the California grizzly’s diet more than 100 years ago, before man killed the grizzly and its prey. It is said that these bears kept the California coast clean of pinniped and whale carcasses that repeatedly washed ashore. There are numerous reports of 12 to 15 bears feeding at the same time on a single whale carcass (Storer and Tevis, 1955). Many of the larger land carnivores typically desert the remains of a kill and cache it away and return to eat from it later. Polar bears are an exception to this rule. They do not cache ringed seal carcasses that they kill, despite the fact that they may only feed on the blubber and leave the meat behind (Stirling and McEwan, 1975). In marked contrast to these feeding habits of land carnivores, pinnipeds do not cache food, nor do they scavenge, although the walrus may be an exception to this rule. Pinnipeds consume most of their prey entire and discard only the heads of large fish, particularly rockfish.

One drawback that pinnipeds experience in their marine habitat to which the larger land carnivores are relatively immune is predation. In carving their niche in the sea, pinnipeds became exposed to large predators who were also adapted to aquatic life and more formidable than themselves. At sea, the main predators on pinnipeds are large sharks, particularly the great white shark, Carcharodon carcharias, and the killer whale, Orcinus orca. All pinniped species living in the Pacific are preyed on by these animals. The degree of predation is unknown. When pinnipeds return to land or ice to give birth and nurse their young, they are vulnerable to predation by large land carnivores such as polar bears and
grizzly bears, perhaps wolves, and, of course, man. Small carnivores, such as foxes, and skuas, gulls, and hawks, may prey on their young. Being adapted primarily for locomotion in water, they are no match defending themselves against large land predators. Thus, it would appear that predator pressure was important in causing pinnipeds to breed in remote sanctuaries free from these predators; that is, offshore islands or rocks, sandbars and ice floes, and offshore breeding areas are limited. This is particularly true of the food-rich waters of the temperate north Pacific, the north Atlantic, and the circumpolar Antarctic.

4 SOCIAL BEHAVIOR AND REPRODUCTION

Given this set of circumstances, it is likely that pinnipeds were forced to share limited breeding areas, and this led to the high degree of sociality and the large social gatherings that we find in pinnipeds today. In terms of the sheer number of animals that congregate together, the pinnipeds are much more social than any land carnivore. As many as 2 million Alaska fur seals can be found every summer on two tiny Pribilof Islands in the Bering Sea. Three thousand northern elephant seals may be found packed together tightly on one beach on Isla de Guadalupe, Mexico, during the peak of the breeding season (Fig. 9.2). Two thousand California sea lions may be found sleeping together in close contact 1/2 km inland on San Miguel Island, California, during the nonbreeding season (Fig. 9.3). The largest wolf or wild dog packs are miniscule in comparison.

Pinnipeds are among the most polygynous mammals. Apparently, this mode of life developed very early in their history, and it was closely tied to their amphibious habits (Bartholomew, 1970). When females began clustering in time and space, the conditions became ideal for promoting male-male competition, polygyny, and sexual dimorphism (see Trivers, 1972). Males must have competed to mate with as many females as possible. Those who kept other males away from areas containing females sired more pups. In their short breeding seasons on traditional rookeries, fur seals and sea lions developed a social structure characterized by territoriality among males (Fig. 9.4 and 9.5). Males without territories do not copulate, or they copulate only rarely; those who secure the most well-placed territories—territories containing the most estrous females—do most of the breeding (Bartholomew, 1953; Gentry, 1970). Another system that developed was for males to dominate other males and thus gain access to more estrous females wherever they were situated. This was the strategy adopted by northern elephant
FIGURE 9.2 Approximately 2000 northern elephant seal males, females, and newborn pups gathered on Pilot Rock Beach, Isla de Guadalupe, Mexico on 5 February 1973, a week after the peak of the breeding season. An observer is located in the extreme foreground.
FIGURE 9.3 A large aggregation of California sea lions about 1/2 km inland from the water’s edge on San Miguel Island, California, during the nonbreeding season. Normally the sea lions would be sleeping in close contact with each other, but shortly before the picture was taken they were startled and rose up on their foreflippers.
FIGURE 9.4 Both California sea lion males and Alaska fur seal males are territorial during the breeding season, and on San Miguel Island they breed at the same time, and there is often interspecific competition over territories. The fur seal territories (circled in the foreground) are well defined spatially, and males actively herd females. California sea lions' territories are plastic and change with fluctuations in several variables. The sea lions are all other animals except those circled and those indicated by arrows; the latter are sleeping subadult male elephant seals.
Seal males. They fight for social status in a dominance hierarchy. The highest ranking male or males—depending on the number of females present—locate themselves nearest the females and keep all others away. One or a few of the highest-ranking males do most of the breeding in a harem; most males in a colony do not breed at all. One male may dominate a harem for several years and inseminate more than 200 females (Le Boeuf, 1974). Grey seal society is similar to that of elephant seals.

Thus, in most of the well-studied pinnipeds, males are polygynous and are either territorial or exhibit a dominance hierarchy during the breeding season. This is a reflection of the manner in which the largest and strongest males go about monopolizing a large number of females. Since size and physical aggression convey such a great reproductive advantage to males, these traits have become increasingly elaborated in time. Sexual dimorphism is greater in some seals and sea lions than in other mammals. For example, the Alaska fur seal male is five times larger than the female (Fig. 9.6).
Canids are "social" in quite a different way from pinnipeds. Social organization is characterized by seasonal or permanent pair bonds in foxes (Storm, 1965; MacPherson, 1969) and jackals (e.g., van Lawick-Goodall and van Lawick-Goodall, 1971; Eisenberg and Lockhard, 1972) and by cooperative hunting and group life in the wolf, dhole, and wild dog (Kleiman and Eisenberg, 1973; Mech, 1975). Black bears are essentially solitary, but female-cub associations are long lasting, and strong and female cubs inherit their mother's feeding territories (Rogers, 1974). Wolf packs are organized into separate male and female social hierarchies. Although the female hierarchy is more ambiguous, it is clearly more pronounced than the size-related dominance observed in female elephant seals. Hunting dog packs have similar hierarchies, particularly
during the breeding season, but it is the female hierarchy that is most evident (van Lawick-Goodall and van Lawick-Goodall, 1971). In wolves and wild dogs, the dominant breeding female may prevent subordinate females from breeding or may drive them out of the pack and kill their pups. Dominant females may also enlist the help of males, and they may prevent other adults from feeding the subordinate female or her young.

Although many canids and ursids are territorial in the sense that they defend a feeding or home range against other individuals or groups of individuals, this behavior is quite different from the defense of rigid individual territories by fur seal males and Steller sea lion males against conspecific males during the breeding season.

When it comes to reproductive behavior and parental care, pinnipeds and terrestrial carnivores differ in many ways. Most canids and ursids, like pinnipeds, have one estrus per year (Asdell, 1964; Kleiman, 1968). However, male-female sexual interactions in the land carnivores can be prolonged and complex. Canids exhibit extensive precopulatory courtship, frequent olfactory examination of the partners, and frequent urine and faecal marking (Kleiman, 1968). In some domestic canids, females actively solicit males (Le Boeuf, 1967). Canid copulation is characterized by a genital lock or tie. After intromission is achieved, the pair remains joined together by the genitalia and face in opposite directions for several minutes or as long as an hour. Females may be in estrus for several days and may copulate several times with different males. Usually, only the alpha female in a wolf pack breeds (Kleiman and Eisenberg, 1973; Rabb, Woolpy, and Ginsburg, 1967; Zimen, 1975, 1976).

In contrast, there is little or no courtship in pinniped sexual behavior (Le Boeuf, 1972). Male northern elephant seals pounce on females and attempt to force copulation at any time during the breeding season, regardless of the female’s reproductive condition (Cox and Le Boeuf, 1977). Sea lions and fur seals may investigate the female’s genitalia before mounting, but there is little parallel to the direct solicitation of males by females seen in the domestic dog (Beach and Le Boeuf, 1967; Beach, 1976). Male seals do not mark with urine or feces, and they do not exhibit a copulatory lock. Copulation duration is equally long in both animal groups, lasting 3 to 7 min in elephant seals and 15 to 20 min in Steller sea lions. Some phocid females are in estrus for several days; most otariid females (in which the males are territorial) copulate only once during the estrous period (Le Boeuf, 1972). Copulation is more convenient except in elephant seals, where the male mounts from the rear and to one side, perhaps a necessity because of the large bulk of the animals. Elephant seal males, like male wolves, prevent or interrupt each other’s copulations; female seals, unlike wolf bitches, do not prevent other females
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from mating, but they threaten, attack, and on occasion kill pups of neighboring females (Le Boeuf and Briggs, 1977).

Canids have a short gestation period of about 2 months and a litter size that ranges from 2 to 15, with 5 being the mode (Asdell, 1964; Kleiman, 1968). The gestation period of bears is 6 to 7½ months, and the litter size is usually 2 to 4 (Asdell, 1964). Wild canid pups are born in dens or burrows. Weaning from mother’s milk is at about 40 days in the domestic dog. But during the transition to solid food in most canids, the altricial young are provisioned by regurgitation feeding of partially masticated food. This is done by the parent male as well as by the mother in the smaller pair-bonding canids. In wolves and wild dogs, all adults in the pack, male and female, regurgitate to young pups as well as to the nursing mother not involved in the hunt. It is not clear how long this type of provisioning of the young goes on, but apparently it lasts until the young are able to obtain food on their own (see Mech, 1970; several reviews in Fox, 1975).

Females of all pinniped species give birth to a single pup once a year. They do not eat the placenta as the carnivores do. Within a few days or weeks after parturition, copulation takes place. Gestation, including delayed implantation, lasts 1 year. Thus, females give birth at about the same time each year and usually in the same place (except for seals that breed on ice). Most species give birth in the open, whether it is on sand, rock or ice; the ringed seal is an exception and gives birth in subnivean lairs in the pressure ridges of sea ice (Stirling and McEwan, 1975). Newborns of all species are physically well developed at birth. Pups are nursed for a minimum of 3 weeks (southern elephant seal, Laws, 1956) to more than a year (Steller sea lion, Gentry, 1970; walrus, Brookes, 1954). The northern elephant seal female is a mammalian phenomenon in that she doesn’t feed during the entire 4 week nursing period! Weaning is abrupt in species like the elephant seal and gradual in others like the Pacific sea lions. Apparently, mothers feed their pups exclusively by nursing; they have not been observed carrying food to the young or regurgitating to them. Females of several species that breed colonially will not nurse pups other than their own. Northern elephant seal females bite and sometimes kill orphaned pups that attempt to suckle them. Adoption of orphaned pups by females who have lost their own pups may occur in elephant seals, grey seals, and, rarely, in Steller sea lions. Unlike the canids, male pinnipeds that breed in colonies do not help in rearing or feeding the young. So far as I know, no male seal helps the female in any way. Quite the contrary, males are inadvertently responsible for a sizeable portion of pup mortality in elephant seals and
grey seals (Le Boeuf, Whiting, and Gantt, 1972; Le Boeuf and Briggs, 1977; Coulson and Hickling, 1964).

Evidently, there are fundamental differences in the social and reproductive behavior of these two related groups of animals. Two basic differences having to do with the origin of sociality and the rate of reproductive behavior stand out.

Social behavior seems to have quite a different origin in these two animal groups; that is, they must have been exposed to quite different selection pressures. In the carnivores, there developed a premium on grouping together, cooperating in the hunt, and feeding other pack members, because these behaviors increased the efficiency of predation (Wilson, 1975). Being social enhanced survival through the process of kin selection (Maynard Smith, 1964; Hamilton, 1964). On the other hand, pinniped sociality seems to have developed first because of a paucity of breeding sites free of predators; later, this trend became elaborated through the operation of sexual selection. It is unique to pinnipeds that feeding and breeding have always been spatially separated and have occurred in different habitats (Bartholomew, 1970). Unlike the typical terrestrial carnivore with an extensive home range in which mating also takes place, pinnipeds opted to travel great distances to breed on traditional sanctuaries. Since such sanctuaries were limited, females were forced to clump together; this situation predisposed males to maximize their reproductive success by attempting to inseminate as many females as possible (see Trivers, 1972). Successful males were belligerent and big. Unbridled male-male competition led quickly to extreme polygyny, sexual dimorphism, lack of parental behavior on the part of the male, sex differences in behavior, and continued gathering of a large number of animals for breeding. Once this system was started, the inertia of sexual selection kept it moving in the same direction. For example, females that move from the main aggregation of females are apt to be fertilized by a male who is unsuccessful in competing with other males—that is, a "marginal" male. If he is subordinate because of genetic factors, his progeny will be less successful in the next generation. Thus, any tendency of females to become less gregarious would be selected against and would be self-limiting (McLaren, 1967). Gregariousness in females should be positively reinforced as long as competition among males—whether for territories or for social status—results in the exclusion of some males (Bartholomew, 1970).

The second fundamental difference between pinnipeds and terrestrial carnivores has to do with reproductive turnover. In general, natural selection has favored two contrasting responses to the problems of
population replacement and the colonization of new habitats. According to MacArthur and Wilson (1967), in environments where there is little crowding and food is abundant, $r$-selection will favor animals that utilize the most food and rear the larger families—that is, those with a high population growth rate. On the other hand, when there is crowding and intense competition for food, $K$-selection will favor animals that can replace themselves with the lowest possible intake of food. The first is a strategy of productivity, and the second is one of efficiency of reproduction.

In general, pinnipeds appear to have been $K$-selected and terrestrial carnivores $r$-selected—Pianka's (1970) admonition that all organisms represent a compromise on this continuum is certainly applicable here. One of the most interesting correlates of $r$- and $K$-selection is the pair of complexes that Martin (1975) calls, respectively, the altricial and precocial complex. Pinnipeds conform to many of the attributes of the precocial complex. Only one pup is born per year (one every 2 years in the walrus, according to Brooks, 1954) and the young exhibit advanced physical development at birth. Alaska fur seals can locomote and vocalize within a moment of birth, and they are as advanced at birth as domestic dogs about 3 weeks old (Bartholomew, 1959). Northern elephant seal pups open their eyes and may exhibit the characteristic sand-flipping movements of the foreflippers before completely expelled from the birth canal. Harbor seal pups are able to swim and dive at birth (Bishop, 1967). Lactation is of long duration, lasting more than a year in some sea lions and the walrus. Even in seals having a relatively short nursing period, energy investment in the offspring may be enormous. Elephant seal milk is approximately 55% fat, and although pups are weaned at 4 weeks of age, they are left with a tremendous fat store (Fig. 9.7). These pups weigh more at weaning than they do a year later! Other attributes of the precocial complex are late sexual maturity and a long life. Most pinniped females ovulate for the first time at about 2 to 5 years of age; males reach sexual maturity at about 3 to 6 years of age (e.g., harbor seals, Bigg, 1969; Alaska fur seals, Bartholomew and Hoel, 1953; anonymous, 1975; northern elephant seals, Le Boeuf, unpublished data). In the colonial species, males do not complete successfully for females until much later in life, until approximately 10+ years of age in the northern elephant seal (Le Boeuf, 1974). Pinnipeds may live a long time. Harbor seals live for 20 to 29 years (Biggs, 1969). Alaska fur seals for up to 26 years (Niggal, Fiscus, and Wilke, 1959), and the life span of the northern elephant seal is typically about 14 years (Le Boeuf and Briggs, unpublished data). Like that in primates and other long-lived mammals,
FIGURE 9.7 A suckling northern elephant seal pup appears almost as large as its mother shortly before it is weaned. At this time, it is four or five times larger than it was at birth, and heavier than it will be a year later. Its sole nurturance has come from mother's milk. The mother has provided this enormous fat store to her offspring during a four-week period in which she did not feed.

the trend in pinniped reproduction has been toward quality rather than quantity.

Terrestrial carnivores, especially the smaller canids, exhibit the altricial complex. Most canids give birth in a shelter to a large litter of pups that are poorly developed and incapable of coordinated behavior except suckling. Gestation is short and lactation brief compared to most pinnipeds. Sexual maturity occurs at an early age, at the end of the second year in wild wolves (Mech, 1970), and at the end of the first year is some captive wolves (Medjo and Mech, 1976) and in the Arctic fox (Chesemore, 1975). Life spans are short compared to those of pinnipeds. Although wolves have lived 10 to 16 years in captivity (Young, 1944), 10 is considered very old (Mech, 1970). Seven is considered old age in large dogs (Fuller and DuBuis, 1962). The life span of foxes is considerably less, 6 years of age in the gray fox, Urocyon littoralis (Laughlin, 1973). Apparently, canids and ursids have been selected for quantity in reproduction. The paradoxically low fecundity rate in wolf and wild dog packs, where only one female may give birth, may be related to low availability of food. It is interesting to note that if only one female gives birth in a pack, it is usually the most dominant one. One might expect the fecundity rate to go up when food was abundant. Whether this
happens or not, the point is that the potential for a high reproductive rate is there.

Unlike land carnivores, pinnipeds must deal with problems that arise from making a living in two quite different habitats. The high metabolic rate and thick layer of blubber that are so adaptive in cold water create difficulties in thermoregulation on land, particularly when the ambient temperature is high, or after sustained activity has taken place. Numerous behavioral adjustments are important in preventing overheating (White and Odell, 1971; Gentry, 1973; Odell, 1974; Whittow, 1974). In addition, one negative consequence of the large social gatherings on land is that the animals are more vulnerable to disease and parasite transmission. The colonial breeding sea lions contain a wide variety of internal and external parasites (Dailey and Brownell, 1972). For example, seven species of trematodes, eight species of nematodes, one cestode, and various species of Acanthocephala, Acarina, and Anoplura have been identified in the California sea lion. Lungworm infestation is particularly heavy in this species and may be an important cause of juvenile mortality. Land carnivores do not seem to harbor the variety or the same high levels of parasite infestation as do these marine mammals. However, this comparison needs to be investigated more systematically.

5 SUMMARY

In summary, these two groups of animals have obvious similarities, some of which can be attributed to having a common ancestor. Pinnipeds bear the stamp of their canine, ursine, and lutrine relatives, especially in the structure of the head and the pronounced canine teeth. Most species in both orders are flesh eaters; they eat great quantities at a time, and they eat a wide variety of prey. However, subsistence in different habitats and exposure to differential selection for at least 20 million years have produced some even more obvious and interesting differences in social behavior. The larger canids evidently were selected to join social groups, in which there is a high degree of cooperation, because this allowed them to exploit large prey. Canids that prey on animals smaller than themselves are far less social, and kin-network welfare is reduced. Pinnipeds are social for a different reason. The most gregarious of them congregate in immense gatherings that may include thousands of individuals. These aggregations are located on offshore areas that are free from predators. Since these locations are restricted in number and size, it appears that pinnipeds were forced to group together in order to avoid predators. Once this step was taken, sexual
selection put a premium on continued social living; for example, males who dominated other males in the large social gatherings probably bore more offspring than those who pair-bonded with single females away from the group. The few pinnipid species that are solitary live in a habitat where there are few or no predators and where hauling-out areas, such as pack ice, are virtually unlimited. Finally, strategies of reproduction seem to differ in the two groups of animals. In general, the terrestrial carnivores appear to have been selected to produce a great quantity of offspring quickly, a strategy that works best in a varying environment, while pinnipeds appear to have been selected to produce fewer progeny of high quality, a strategy that is most characteristic of stable environments.

REFERENCES


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