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Territorial Behavior

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I. Territoriality in Marine Mammals

“Territoriality” refers to the exclusive use of fixed space, which entails obtaining, defending, or advertising occupancy of the space. All agonistic social interactions occur within a spatial framework, but by themselves do not constitute territorial behavior. “Home range” refers to the space used by an individual or group (whether or not it is used exclusively), without attendant behavior in defense or advertisement (Fig. 1). As in other animals, territoriality in marine mammals can evolve if space is defensible, enabling monopolization of resources within that space. Territoriality is absent in most marine mammal species simply because no whales are territorial; the polar bear (*Ursus maritimus*), marine otter (*Lontra felina*), and most Sirenia also are not territorial. The best known examples of territoriality are breeding males in: one population of dugong (*Dugong dugon*; in Shark Bay, Western Australia; Anderson, 2002); sea otter (*Enhydra lutris*); and many pinnipeds. Superficially, territoriality appears to characterize the land-breeding elephant seals (*Mirounga* spp.) and gray seal (*Halichoerus grypus*; some populations also breed on ice), because males are fairly sedentary when hauled out (Fig. 2). All marine mammals that are territorial when breeding are polygynous; polygyny is most extreme in land-breeding pinnipeds, because density of breeding females can be very high (Fig. 3; Boness, 1991; Boness *et al.*, 2002). Territoriality is expressed differently even between closely related species, is rigid or invariant in any species, and varies intraspecifically through short-term opportunistic behavior, throughout development, seasonally, and geographically. Territoriality away from the breeding site and outside the breeding period occurs but has been studied little. Key papers are Bartholomew (1970), Stirling (1983), Boness (1991), Miller (1991), Boness *et al.* (2002), and Tyack and Miller (2002).

II. Development of Territorial Behavior

Territoriality involves complex behavioral patterns used repeatedly in interaction and communication, which emerge in play early in life. The complex underwater vocal displays of territorial male bearded seals (*Erignathus barbatus*) appeared at 4–5 years of age in several captive males, but not in females. Sexual differences in behavioral development have been documented in most detail for fur seals and sea lions (Otariidae), in which pups segregate by sex, male pups are more aggressive than females, and male pups engage in more play-fighting and territorial displays (Gentry, 1974). Those social interactions occur even in the appropriate topographical context for breeding territoriality; e.g., in the Steller’s sea lion (*Eumetopias jubatus*), “Pups located themselves on opposite sides of any available ridge and used boundary display postures, open mouth

lunges, and other ... behavior characteristic of boundary defense in adult males” (Gentry, 1974, p. 402). Young male otariids and walrus (*Odobenus rosmarus*) of all ages engage extensively in play-fighting (and for walruses, other display forms as well) throughout the year.

Territorial male otariids appear to try to influence females to stay on their territories by “herding” (Section VIII). Such behavior appears early in life, and male pups preferentially direct this behavior toward female pups (e.g., New Zealand fur seal, *Arctocephalus forsteri*). Herding is expressed also by non-territorial or peripheral males during the breeding season; for example when they encounter females outside breeding aggregations. In all otariid species, non-territorial males (including sub-adults) may rush simultaneously into (“raid”) breeding aggregations, and herd or interact with females in various ways before they are chased away by territorial males (Peterson, 1968; Campagna *et al.*, 1988a; Section VIII). Outside the breeding season, juvenile and sub-adult male otariids occasionally herd pups or young juveniles, at wintering haulout sites or colony sites (e.g., New Zealand fur seal). An extreme form of this behavior has been noted in several otariid species, in which non-territorial (generally sub-adult) males carry pups away in their mouths following raids on breeding sites (Campagna *et al.*, 1988b; Kiyota and Okamura, 2005). In the southern sea lion (*Otaria flavescens*), males may carry pups to the ocean, and then to non-breeding areas where the males herd and mount them, sometimes over several days; about 6% of pups treated in this manner die as a result (Campagna *et al.*, 1988b).

Breeding territoriality in otariids develops within the context of strong colony and natal-site fidelity (Section V), which become increasingly precise with age [e.g., for male northern fur seals (*Callorhinus ursinus*) aged 2–6 years]. Male northern fur seals start to haul out near the breeding site when they are 2-years old, and hold their first territories at about 7 years of age; first territories tend to be located peripherally, and are occupied late in the breeding season (Gentry, 1998; Kiyota, 2005). Over successive breeding seasons, territories become stabilized in location and size, and are established progressively earlier in the season.

III. Territorial Functions

Non-breeding territoriality is poorly documented and understood. Male otariid territoriality occurs at some non-pupping sites during the breeding season (Miller, 1991). Many minor disputes over space take place throughout the year at both breeding colonies and non-breeding haulout sites, where individuals of various classes tend to use and interact agonistically repeatedly at the same sites. Non-breeding (winter) territoriality in some individuals of some seal (Phocidae) species may provide exclusive (or priority) access to breath holes in stable ice. The function of another form of territoriality also is not known: mature male otariids may return to occupy their territorial sites for several days in the fall, weeks after abandon them (Section V).

The best known, most dramatic, and most interpretable forms of territoriality in marine mammals are shown by breeding adult males, which establish territories seasonally where females copulate. The ultimate function of male territoriality in all cases is to gain access to estrous females; proximate functions that mediate male reproductive success are more difficult to identify and are both varied and variable. For example, male pinnipeds may change locations in response to female movements, attend and defend isolated lone females, or even defend and copulate with female carcasses.

In many otariids, males hold territories where females give birth and remain on land until they enter estrus; in such cases, male

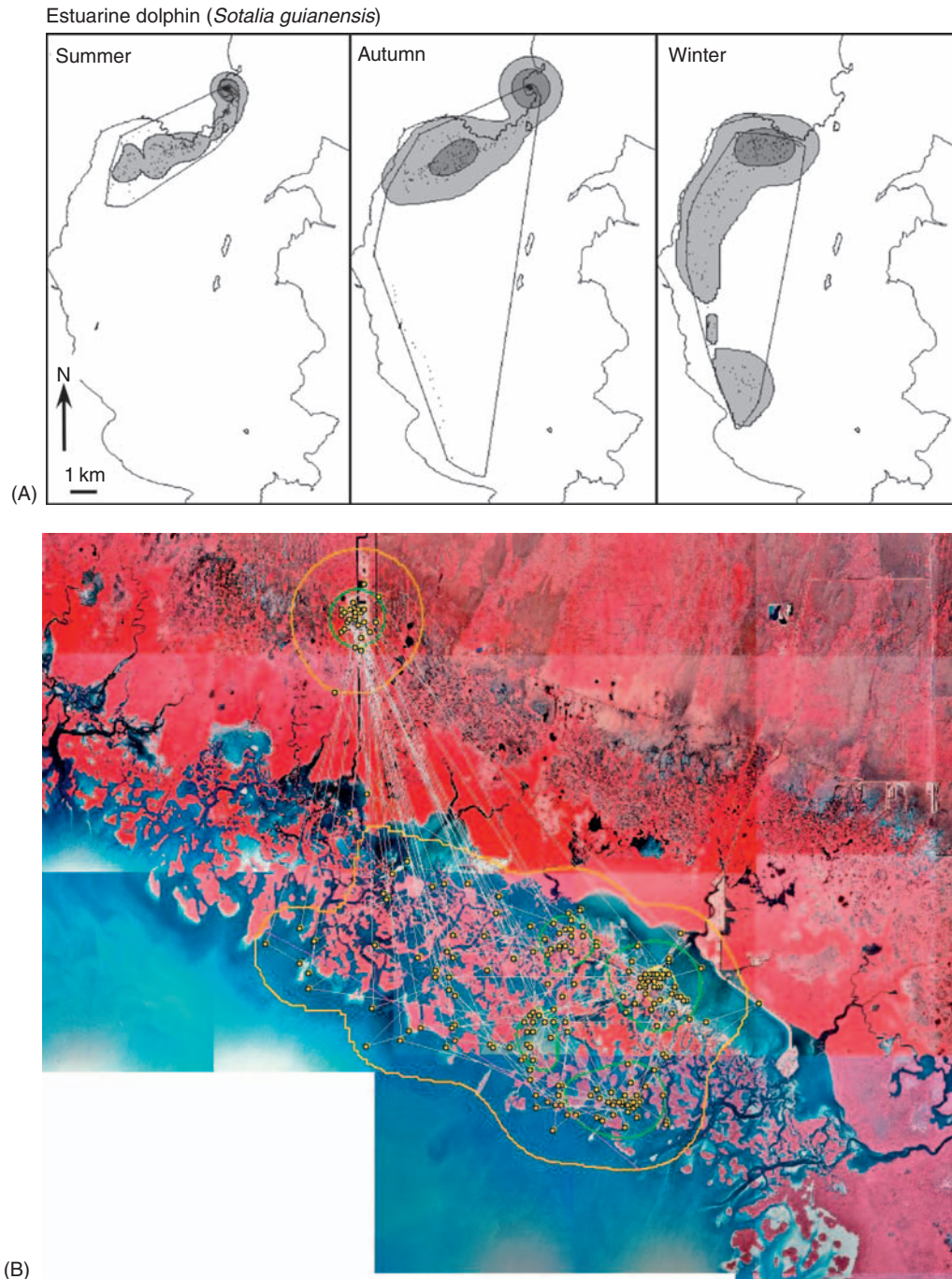


Figure 1 Most marine mammal species are not territorial: they occupy undefended home ranges, which typically incorporate systematic seasonal movements and regular smaller-scale movements between habitats. (A) Group home ranges of estuarine dolphins (*Sotalia guianensis*) in Norte Bay, southern Brazil in 2002, illustrating size, shape, and seasonal changes in home range. Home ranges were estimated by: (i) the minimum convex polygon method; and (ii) fixed kernel analysis, with dark and light gray areas representing 50% and 95% levels, respectively. (B) Home range of one adult female West Indian manatee (*Trichechus manatus*) in southern Florida in a dry period (March 2 to May 31, 2001), when it made many trips between marine-coastal feeding areas (seagrass beds), and freshwater rivers and creeks (the species needs regular access to freshwater for drinking and osmoregulation). White lines connect successive high-quality fixes by Argos satellite; colored lines reflect fixed kernel analysis, and depict 95% (orange), 50% (green), and 10% (yellow) levels. (A) After figure 3 of Wedekin et al. (2007); (B) after figure 56 of Stith et al. (2006).

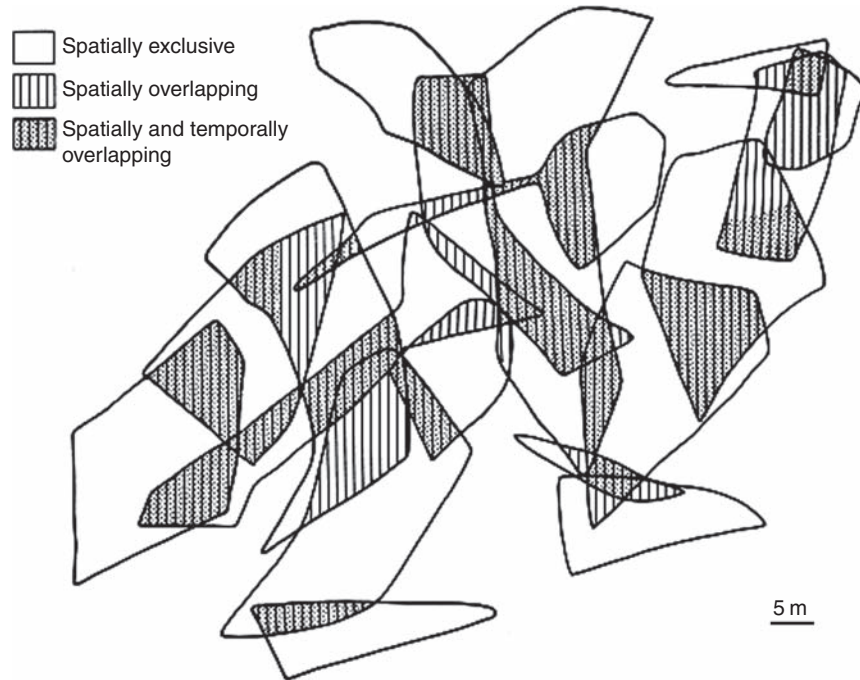


Figure 2 The spacing system of breeding male gray seals (*Halichoerus grypus*) on land resembles territoriality but is structured on attendance (“consortship”) of females, but not defense of space *per se*. This figure shows areas used by adult males attending females in a study area on Sable Island, Nova Scotia, in the 1975–1976 breeding season. After figure 9 of Boness and James (1979).



Figure 3 Female fur seals and sea lions (*Otariidae*) return seasonally to particular terrestrial sites on islands free from predation, to give birth and raise offspring. These factors have enabled the evolution of male territoriality and polygyny; the tendency of females to aggregate when ashore increases polygyny levels further (see text). This photograph illustrates a breeding aggregation of northern fur seals (*Callorhinus ursinus*) at the Little Polovina rookery, Pribilof Islands, Alaska, in July 1948. Photograph by Edward C. Johnston, Fish and Wildlife Service, U.S. Department of the Interior. Photograph courtesy National Marine Mammal Laboratory (NOAA, National Marine Fisheries Service).

territories hold resources that are needed by females (sites for pupping, reuniting with pups between foraging trips, and nursing). However, territoriality is fluid in many populations, because breeding animals must move regularly for thermoregulatory reasons or

due to tide levels, or because the breeding substrate is homogeneous and hence territorial boundaries are ill defined (Section IV; Boness, 1991; Miller, 1991; Boness *et al.*, 2002). In the Juan Fernández fur seal (*Arctocephalus philippii*), females move to the sea when it is

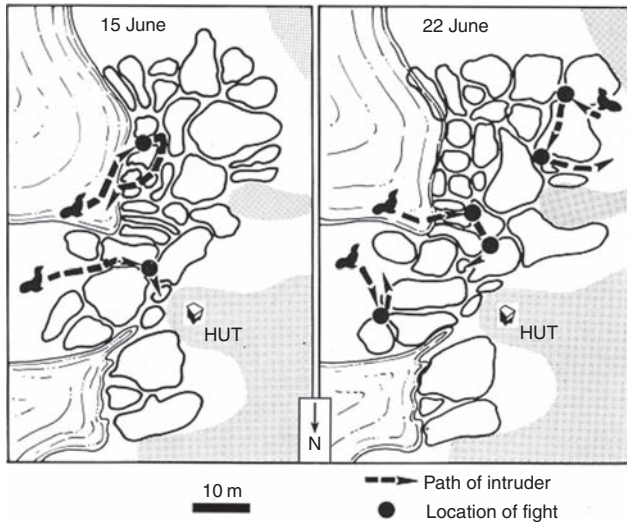


Figure 4 Territories are small and fairly fixed in size, shape, and location in many species of fur seals and sea lions (Otariidae). This figure depicts territories (in outlines) and some territorial behavioral events of male northern fur seals (*Callorhinus ursinus*) at Kitovi rookery, Pribilof Islands, Alaska, in 1962. “HUT” is the point of observation. After figure 11 of Peterson (1968).

hot but remain close to the colony; males may hold inland, shoreline, or completely aquatic territories in this species. The most reproductively successful male southern sea lions hold territories where females can thermoregulate: within tidepools, or along the high water mark where the substrate remains wet. Resource-based territoriality is expressed clearly in sea otters. Adult male sea otters establish territories seasonally in or near areas of high female density. Male territories hold multiple resources used by females, including prey, resting areas, protection from wind and waves, and protection from harassment by other males (Garshelis *et al.*, 1984).

The distinction between territories with and without resources needed by females blurs in many cases. In the Weddell seal (*Leptonychotes weddellii*), mature males set up and defend territories seasonally in traditional areas of stable ice where females congregate, give birth, and later enter estrus; females need access to water for foraging, so these access points can be considered as the key defensible resource on which male territoriality is based (Harcourt *et al.*, 2007). Similarly, male ring seals (*Pusa hispida*) hold underwater territories that are near or encompass the birth lairs of several females (Stirling, 1983; Stirling and Thomas, 2003). Male harbor seals (*Phoca vitulina*) establish territories near female haulouts, or on access routes to and from those haulouts (Boness *et al.*, 2006). At an extreme, male territories may hold no resources needed by females, and male reproductive success depends solely on female visitation for purposes of copulation (e.g., Shark Bay dugongs; walrus; bearded seal). In some situations (e.g., walrus), the presence of males near a small number of females can be construed as defense of females, rather than of space (Sjare and Stirling, 1996).

IV. Spatial Aspects of Territoriality

Discrete, clearly defined territories are most apparent on small temporal scales, in situations of crowding, in species that have good locomotory abilities so can efficiently patrol or defend their territories, and where environmental features (e.g., topographical irregularities)

occur that can be used by the animals to demarcate territories. Such conditions are lacking in the lives of cetaceans, especially open-ocean species, so territoriality does not occur in that group. River dolphins, with their spatially restricted distributions, or species that feed on concentrated prey that are sedentary or spatially predictable, may prove to be territorial, but this is not known at present. In Scotland’s Moray Firth, year-round resident bottlenose dolphins (*Tursiops truncatus*) may be territorial and exclude seasonal (winter) visitors from deep waters, which are most favorable for feeding; group territoriality also has been suggested for this species in Ecuador.

Most species of otariids breed on crowded colony sites and hold small territories; territories of male Hooker’s sea lions (*Phocarctos hookeri*) are often no more than 3 m in diameter, for example, and some northern fur seals hold territories that are little larger in diameter than a male’s body length (Figs 3 and 4). Larger territories occur in related species (e.g., about 200 m² in male Steller’s sea lions). Small aquatic territories are held by Juan Fernández fur seals adjacent to breeding aggregations on land, and by walrus adjacent to mixed herds on ice (Miller, 1991; Sjare and Stirling, 1996). In general however, aquatic territories are large: more than 100 m in length in some male Weddell seals, up to 1 km across in male sea otters (Pearson *et al.*, 2006), and up to 10 km across in some male harbor seals. Many aquatic territories are non-contiguous, but contiguous territories invariably overlap some extent, both in linear and in more complex spatial arrangements (Fig. 5; Boness *et al.*, 2006).

Phocids are specialized for aquatic locomotion, so their locomotion on land is slow and energetically costly. The poor locomotory abilities and large size of the two species of elephant seal usually preclude territoriality, although in small confined areas or rough terrain, defense of space and of females amount to the same thing. In contrast, fur seals and sea lions can move quickly and efficiently on land, so offer many clear examples of terrestrial territoriality.

Precise delimitation of territories occurs at many breeding sites of otariids, because rocks, fracture lines, and other natural features are present; in these situations, territorial boundaries may be stable within and across years. On featureless terrain (e.g., sandy beaches), territories are less clearly defined. Territories of northern fur seals are smaller in exposed terrain, and larger in protected terrain (Peterson, 1968). Aquatic territories also are influenced by physical environmental structures. In species that breed in association with ice, underwater features of ice or fractures or leads in ice may be important in determining territorial density, size, and shape. In the walrus, male territories are established in the water adjacent to mixed herds on ice, which may be stable land-fast ice (e.g., in the Canadian Arctic) or unstable drifting pack ice (e.g., Bering Sea).

V. Temporal Aspects of Territoriality

Territories of fur seals and sea lions are most clearly defined at the peak of breeding, when territorial density is highest and territorial size is smallest (Figs 3, 4, and 6).

Absence of females from their territories sometimes leads to territorial desertion by male otariids, but more commonly males attempt to acquire a new territory where females are present. In the Hooker’s sea lion, males establish territories several times during the breeding season in response to movement of the female aggregation down the beach. Southern sea lion males defend territories early in the breeding season but gradually change to defense of females as the season progresses (Campagna and Le Boeuf, 1988).

Male otariids may haul out at the site of their future territory before territorial behavior begins and, in many species, males

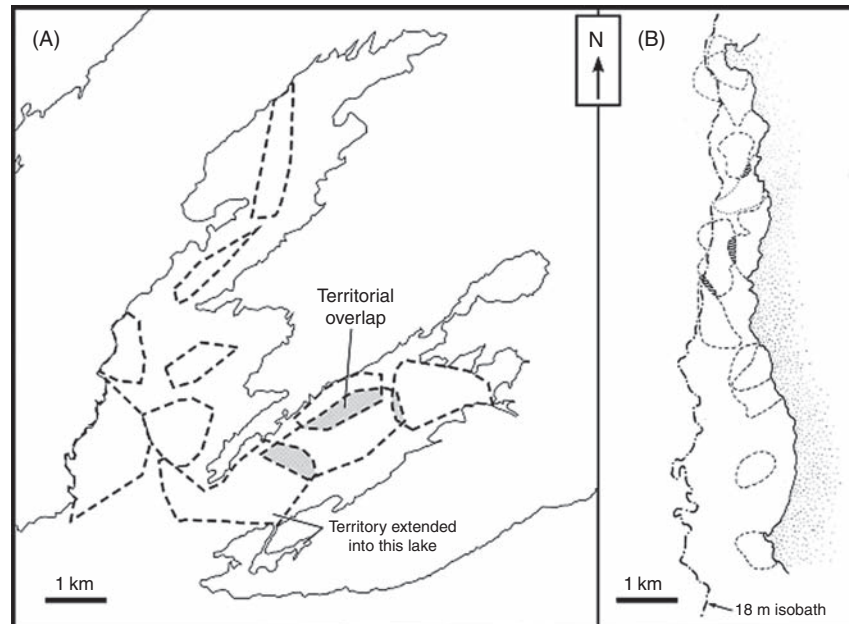


Figure 5 Size, shape, and configuration of marine mammal territories are influenced by the physical environment. Aquatic territories held by adult male sea otters (*Enhydra lutris*) hold multiple resources needed by females. They are large, overlap, and exhibit more complex spatial arrangements in enclosed waters [(A) Prince William Sound, Alaska, 2003; “lake” is a tidal lagoon] than along coasts [(B) central California, 1978–1982; overlapping territories held in different years are shown with areas of overlap not cross-hatched]. (A) After figure 1 of Pearson *et al.* (2006); (B) after figure 2 of Jameson (1989).

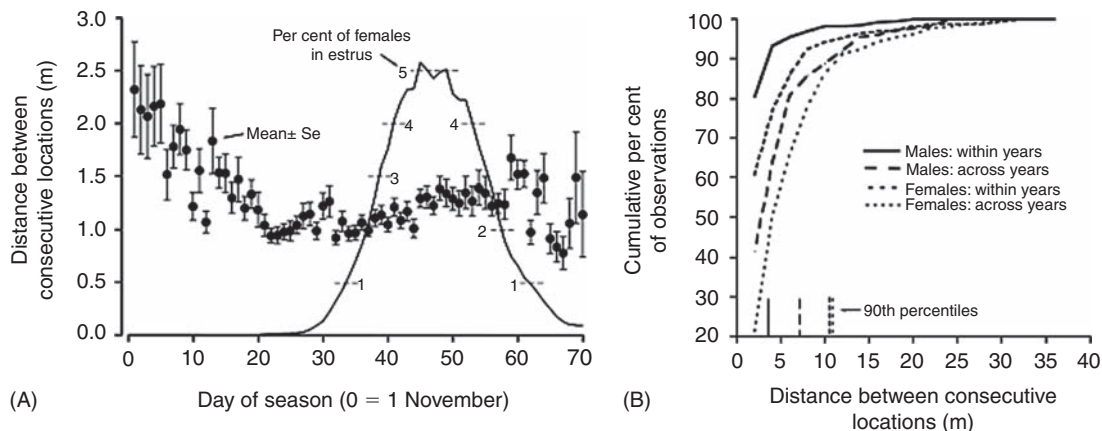


Figure 6 Territories are smallest and males move least at the peak of breeding in fur seals and sea lions (*otariidae*), and males tend to return to the same sites every year, as illustrated by the Antarctic fur seal (*Arctocephalus gazella*). (A) Movements of territorial males become increasingly localized within a breeding season. (B) Males have high site fidelity both within and across years, and their site fidelity is greater than that of females on both temporal scales. After figures 2 and 1 (respectively) of Hoffman *et al.* (2006).

also return to their territories after the breeding season has ended (Fig. 7A). Territorial occupancy may be continuous for weeks or months, or males may leave the territory for periods for thermoregulatory or other reasons, and then return (Fig. 7B; Gentry, 1998). Territorial occupancy is highly variable in the Hooker's sea lion, and males move extensively within and between breeding sites (Fig. 7C);

this is similar to behavior of breeding males in the non-territorial gray seal on Sable Island, Nova Scotia.

Male otariids habituate to neighboring males and engage in fewer and less aggressive interactions with neighbors over time. A similar effect occurs even across years between returning territorial neighbors (e.g., Steller's sea lion; Miller, 1991).

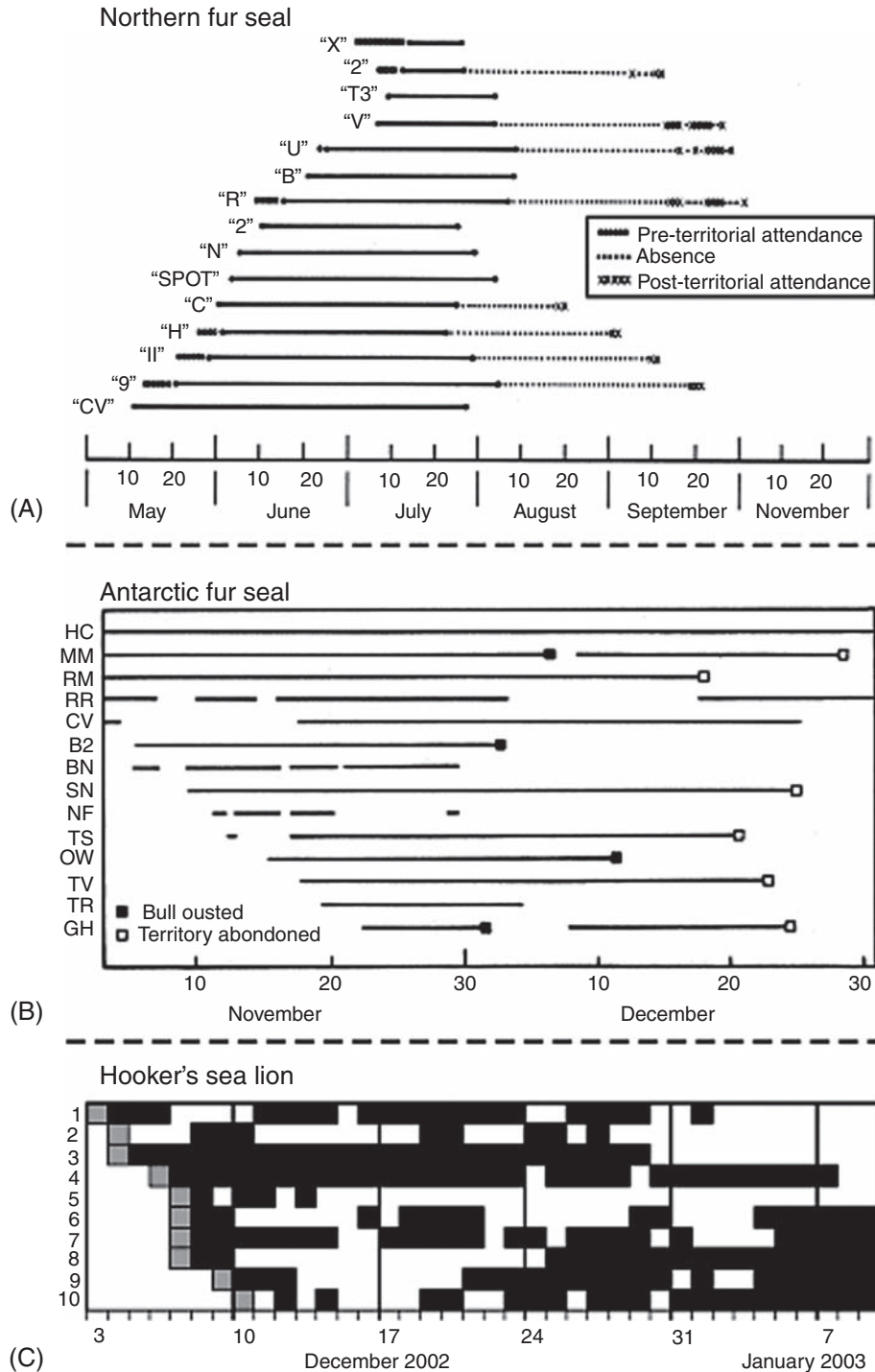


Figure 7 Attendance patterns of territorial male fur seals and sea lions (*Otariidae*) vary within and across species. Territorial attendance patterns are shown for: (A) 15 northern fur seals (*Callorhinus ursinus*) at Kitovi rookery, Pribilof Islands, Alaska, in 1962; (B) 14 Antarctic fur seals (*Arctocephalus gazella*) on Bird Island, South Georgia, in 1975–1976; and (C) 10 Hooker's sea lions (*Phocartos hookeri*) at Enderby Island, Auckland Islands, in 2002–2003 (shaded squares represent days when males were marked). (A) After figure 12 of Peterson (1968); (B) after figure 2 of McCann (1980); (C) after figure 3 of Robertson et al. (2006), respectively.

Long-term fidelity (philopatry) to territorial locations has two components. First, there is a tendency for males to return to breed near the site of their birth (natal philopatry). Second, males tend to return in successive years to where they first established a territory. Both forms of site fidelity are well documented in otariids; e.g., about 50% of returning male antarctic fur seals (*Arctocephalus gazella*) occupy a territory that is within half a body length of the territorial site held in the previous year (Fig. 6B). Site fidelity by breeding males occurs also in species that breed in association with land-fast ice (e.g., ring seal, Weddell seal; Harcourt *et al.*, 2007), or near land (e.g., harbor seal, sea otter); male sea otters hold territories in the same location for up to 7 successive years. Site fidelity even occurs in aquatically territorial phocids that display away from land or land-fast ice: some individual male bearded seals returned seasonally to the same territorial display areas every year of the 16-year-long study by Van Parijs and Clark (2006). The extremely strong natal- and territorial-site fidelity shown by otariids, coupled with their high breeding densities, results in kin breeding in proximity to one another.

VI. Territoriality, Mating Strategies, and Mate Selection

Land-breeding pinnipeds were central to Bartholomew's (1970) model of pinniped polygyny. His model remains as the core paradigm to explain otariid polygyny and territoriality, which assumes lengthy uninterrupted male territoriality, when males fast and expend much energy in territorial display and defense. However, many variations occur in territorial behavior, as noted earlier: thermoregulatory factors influence movements of males and females, and males may hold aquatic or semiaquatic territories (Juan Fernández fur seal, southern sea lion, California sea lion *Zalophus californianus*, etc.); males may vacate their territories for periods ranging from hours to days, even in classically territorial species like the northern and antarctic fur seals (Fig. 7); males may change from territoriality to female defense later in the season (southern sea lion); and so on. Variation in territoriality is paralleled by variation in male mating behavior and success.

Especially in otariids, male reproductive success is closely tied to possession of territory, and territorial males (a) account for most fertilizations and (b) fertilize most females that pup on their territories (Hoffman *et al.*, 2003; Kiyota *et al.*, 2007). Scattered observations over many years have pointed to mating in other situations, however: young male northern fur seals mate with females late in the breeding season, after the main period of reproduction; some mating occurs before pupping in the Cape fur seal (*Arctocephalus pusillus pusillus*) and New Zealand fur seal; and males mature sexually (i.e., physiologically) years before they are large enough to compete for territories. Recent molecular evidence has confirmed that fertilizations occur regularly outside the territorial structure, and involve non-territorial males (Hoffman *et al.*, 2003; Kiyota *et al.*, 2007); furthermore, female antarctic fur seals actively seek and mate with territory holders that are heterozygous and unrelated to them (Hoffman *et al.*, 2007).

Male behavior varies in other territorial species, but its relationship to mating success is not known. Some male bearded seals in Alaska change from being territorial in 1 year to non-territorial in another (Van Parijs and Clark, 2006); in Svalbard, most males are territorial when land-fast ice is extensive. It is not known whether such variability in territorial and mating behavior (a) reflects distinctly different strategies or a continuum, (b) represents evolved adaptations or behavioral plasticity, or (c) is related to male age or other characteristics (e.g., phenotype; in the non-territorial gray seal, males of different body sizes adopt different mating tactics).

VII. Obtaining, Defending, and Advertising Territories

Dramatic and potentially injurious fights between males occur in all territorial species, particularly when new males attempt to establish themselves. Severe injuries or even death can result, so fighting is uncommon, and most interactions between territorial males instead take the form of display (Peterson, 1968; Miller, 1991; Gentry, 1998).

Territorial male dugongs in Shark Bay repeatedly patrol the margins of their territories along fixed routes (Anderson, 2002). Acoustic displays can travel long distances (especially under water) and are energetically cheap to produce, but long-distance sounds are lacking from the diverse vocal repertoire of this species. Patrolling males perform various distinctive behaviors, e.g., they may swim upside-down or rear high out of the water; fights also occur. Male sea otters likewise patrol their large territories, and announce their presence by exaggerated kicking, splashing, and grooming (Garshelis *et al.*, 1984); males interacting near territorial boundaries may engage in mutual porpoising, and they sometimes fight. Like dugongs, sea otters have a rich vocal repertoire, but also lack sounds for long-distance communication (Miller, 1991). In contrast, walrus and aquatically territorial phocids possess acoustic signals that travel under water for long distances (Fig. 8).

Long-distance underwater sounds of territorial pinnipeds tend to be stereotyped, and to convey little behavioral information; nevertheless, they must be informative to several classes of receiver (e.g., non-territorial males, females), not just other territory holders (Miller, 1991; Tyack and Miller, 2002). Long-distance sounds are not universal in aquatically territorial species; for example, high vocal activity and long-distance sounds probably have been selected against in the ring seal, to minimize detection by polar bears (Stirling, 1983; Stirling and Thomas, 2003). Otariids are highly vocal and have rich vocal repertoires (Phillips and Stirling, 2001). Vocalizations of territorial male otariids are transmitted over medium to short distances; the stereotyped "full-threat call" (Phillips and Stirling, 2001, p. 423) is the loudest, and carries the farthest. Many male calls have been interpreted simply as communication of "threat" but carry much richer behavioral information. Most call types of male otariids are variable, have complicated syntactical arrangements, and are used in multiple social contexts (Miller, 1991; Tyack and Miller, 2002). Many morphological specializations for sound production occur in marine mammals but have evolved to serve general communicative functions, not functions related to territoriality *per se* (discussed later).

Optical signaling, likewise, is complex in territorial marine mammals and involves numerous morphological features. The distinctive appearance of adult male otariids is communicatively important in the context of territoriality. For example, in contrast to females or young males, adult male Hooker's and California sea lions are much darker than females or young males, and adult male southern sea lions have especially distinctive manes (Fig. 10B; Miller, 1991). Many other morphological adaptations for communication occur in marine mammals, including optical patterns of the pelage, sound-producing structures, and weapons (Miller, 1991; Tyack and Miller, 2002). Some structures may have become enlarged, strengthened, or otherwise modified for use in fights (e.g., claws of bearded seal; lower canines of otariids; Miller, 1991), and tusks (upper incisors) have evolved as optical display structures in the walrus. However, no morphological features have evolved specifically to serve territorial functions, as such features (e.g., tusks) have evolved independently in marine mammals with diverse non-territorial systems (Fig. 9A, B).

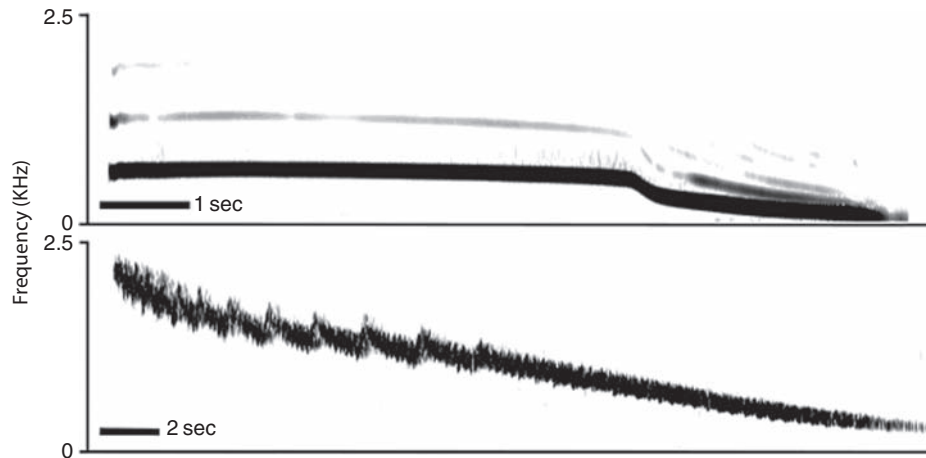


Figure 8 Adult males of some species of seals (*Phocidae*) utter sounds that travel for long distances under water, and function to advertise territorial occupancy. Spectrograms are shown for vocalizations of: (A) wintering territorial male Weddell seal (*Leptonychotes weddellii*), at McMurdo Sound, Antarctica; and (B) breeding male bearded seal (*Erignathus barbatus*), at Scalbard. (A) Courtesy of J.M. Terhune; see Rouget *et al.* (2007); (B) courtesy of C.M. Lydersen and K.M. Kovacs.

Some optical displays of otariids are relatively passive and undirected (e.g., the distinctive nose-up upright resting posture of otariids), but most optical displays are active and directed toward specific individuals. In otariids, these involve motor patterns such as distinctive head-and-neck swinging in locomotion, or rapid and complex sequences of feints, oblique stares, sprawls, facial expressions, etc., in displays between neighbors across territorial boundaries (Fig. 10A,B).

Chemical communication is probably important in all land-breeding territorial species of marine mammals but is virtually unstudied. Facial glands are unknown in sea otters, but the species has well developed anatomical (neural) characteristics for olfaction, and individuals often actively smell the air. Facial glands (many associated with vibrissae) occur in walruses, phocids, and otariids, and are known to vary seasonally in size and secretory activity in some species. Male otariids emit distinctive odors during boundary displays between neighbors, apparently from the oral cavity, and have distinctive body odors during the breeding season, but the anatomical source and functions of the smell are unknown. Breeding male ring seals hold underwater territories that are near or overlap with areas used by breeding females. During the breeding season, adult males of this species acquire a strong odor which is the origin of terms like “tiggak” (“stinker”) among Inuit, and “gasoline seal” among trappers. Male ring seals may actively deposit secretions from facial glands on entrances to their breathing holes and sub-nivean (“below-snow”) resting lairs, as well as within the latter.

The roles of taste or use of the vomeronasal organ (VNO) in marine mammal communication are unknown, although the VNO is absent in Sirenia but present and well developed in pinnipeds (see SENSORY BIOLOGY, OVERVIEW). Otariids commonly exhibit slow, repeated, tongue extrusion following agonistic displays (e.g., boundary displays or fights involving males; females, juveniles, and even pups also express the behavior), suggestive of behavior of other mammals that are known to use the VNO in chemical communication (at the very least, tongue extrusion is a conspicuous optical signal and likely has become ritualized as an optical display).

Tactile communication in marine mammals likewise is important but essentially unstudied (Miller 1991). Breeding males of all species engage physically and contact one another extensively in biting, wrestling, or pushing. Male sea otters and Weddell seals often try to bite the opponent’s penis, and fractured bacula (penis bones) of mature male sea otters are relatively common (see “Baculum” article). In phocid species that fight aquatically, the rear flippers (necessary for aquatic locomotion) are frequently bitten and injured in fights; walruses use the tusks in fights at and below the water surface (all sex and age classes of the walrus use tusks in numerous other agonistic contexts, of course).

VIII. Costs of Territoriality

Territoriality carries benefits and costs. In dispersed aquatically territorial species, most costs fall on territory holders, which must expend energy and time to establish, maintain, and advertise a territory, and must occasionally fight with other males. In fur seals and sea lions, some costs fall also on pups and on breeding females.

Territorial males must balance needs to be vigilant, advertise and defend territories, and signal about their own behavioral and physical attributes. Male sea otters hold large territories, and do not use long-distance advertisement, so must spend much time patrolling; on average, territory holders spent 17% of their time in this activity in Prince William Sound, Alaska (Pearson and Davis, 2005). In one long-term study, territorial male northern fur seals spent 1.5% of their time in overt interactions with neighbors; however, other types of activities also serve territorial functions, such as simply moving around the territory (1.7%), or resting in an upright position (21.1%; Gentry 1998). In the New Zealand fur seal, males spend about 14% of their time upright, compared with 5% for females (Miller, 1991).

The impact on males of time and energy spent in territorial activities is compounded by other factors: effects of fasting or reduced food intake; and time spent as a territory holder. On average, territorial male northern fur seals fast and do not drink for about a month (maximum 87 days), and decline in body mass by about one third

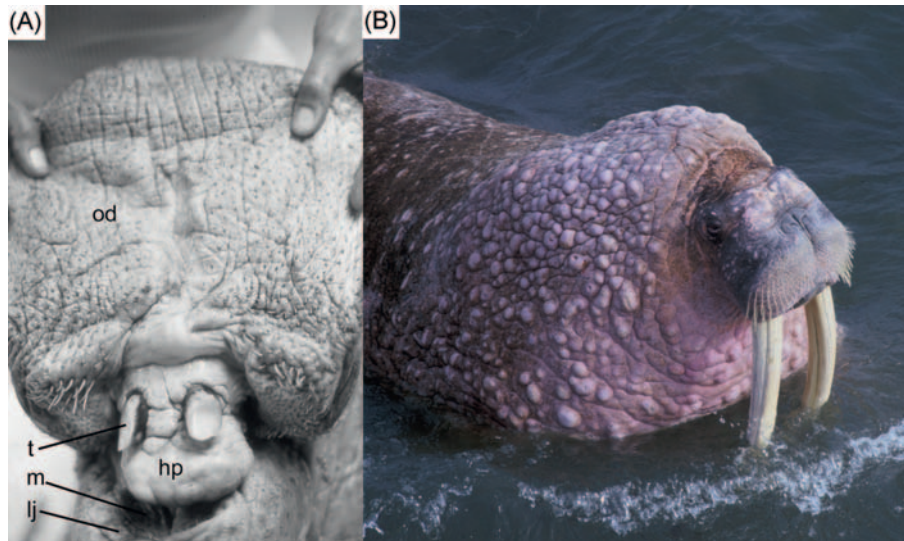


Figure 9 Specialized morphology has evolved in marine mammals to serve communication and other social functions, but occurs in diverse social systems and is not restricted to territoriality. (A) Male dugongs (*Dugong dugon*) possess tusks (upper incisors) that are used in fights between territorial males in Shark Bay, Western Australia, and between males elsewhere in the species' range, where the species is non-territorial (hp, horny pad on upper jaw; lj, lower jaw; m, mouth opening; od, oral disc, pulled forward to expose tusks; t, tusk). (B) Adult male walrus (*Odobenus rosmarus*; Alaska), which are territorial in parts of the range, develop conspicuous tubercles on the forequarters with age, which may act as an optical signal of male quality (as suggested for scarring in odontocetes by Macleod (1998)). (A) photograph by P.K. Anderson, from figure 4 of Domning and Beatty (2007); (B) photograph by Bill Hickey, courtesy of U.S. Fish and Wildlife Service.

over that time. This loss in body mass is equivalent to about 0.7% of initial body mass per day, similar to some other species: about 0.8% in the antarctic fur seal and the aquatically territorial Weddell seal. Breeding male harbor seals do not fast completely, and body mass declines more slowly (about 0.4% per day), but overall costs can be high (one male lost 30% of his initial body mass over the breeding season).

Costs and risks of territoriality include the danger of suffering severe physical injury. Most (80–90%) of antarctic fur seals found dead in a study on South Georgia had died as a direct or secondary consequence of fighting injuries, especially to the foreflippers or dorsal surface of the forequarters. Fitness of adult female and pup fur seals and sea lions also is affected by male behavior. For otariids, it is believed that female aggregation on land has been selected for, to reduce harassment by males and to protect pups from males (Chilvers *et al.*, 2005; Kiyota and Okamura, 2005). The significance of harassment is evident in the incidence of injuries and deaths in adult female Hooker's sea lions: greater than 80% of females have permanent scars inflicted by males, and annual mortality of adult females is about 0.5% due to male attacks (Chilvers *et al.*, 2005); infanticide by males also occurs (Wilkinson *et al.*, 2000).

Mortality rates of males are similar to those of females until social maturity is attained and males begin territorial activity. Male mortality increases at that time, and thereafter remains much higher than for adult females: 32% vs 15% in Galápagos fur seals (*Arctocephalus galapagoensis*); 30% vs 10–15% in northern fur seal; 30% vs 12% in Cape fur seals; and 50% vs 8% in Antarctic fur seals. This pattern

is presumed to be due largely to direct and indirect effects of male territoriality.

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Figure 10 Specialized communicative behavior has evolved in territorial marine mammals, but is based on general mammalian patterns that are not specific to territorial systems. (A and B) Ritualized boundary display; (A) followed by upright “full-neck display”; and (B) between neighboring territorial male Guadalupe fur seals (*Arctocephalus townsendi*). Note the long pelage on the forequarters. © P. Colla.

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Thermoregulation

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T Marine mammals have developed methods to retain heat in cold seas using a suite of physiological, biochemical, anatomical, and behavioral methods. Yet, they must be able to lose excess heat when they are on land or extremely active in the water. If the problem was one of solely evolving methods to stay warm in a cold ocean, it would be easier to wrap themselves in deep blubber and fur or to stay very active and not to have deal with the consequences of heat loading. However, the difficulty of that solution is that the animal would get too warm, which in turn would cause problems with metabolic regulation, reproductive chemistry and neural function. Thus, the thermoregulatory mechanisms that have evolved in marine mammals function not only to conserve heat, but also to dump it when necessary. As poorly insulated humans, we

must bring our artificial insulation with us and use exposure suits, wet suits and a variety of human-made insulative materials if we are to spend any significant time in the sea. For marine mammals, the insulation (blubber or fur) is already on board and serves multiple purposes beyond just thermoregulation.

I. The Physics of Heat and Temperature

The terms "heat" and "temperature" are often incorrectly exchanged for one another, yet they have very different physical aspects. "Heat" is the energy that reflects the molecular motion of atoms and molecules. As energy, heat can flow from an area where the energy is high (an object that is "hot") to an area where the energy is low (something that is "cold"). We quantify how hot something is by using a variety of temperature scales (Kelvin, Celsius, and Fahrenheit). Thus, the temperature of an object is our definition of the level of heat energy contained by that object. The unit of heat energy is the calorie, and a single calorie is defined as the amount of heat necessary to raise 1g of water by 1°C. In common usage in the United States, the calorie associated with food and dieting is actually the kilocalorie (kcal; 1000 calories). In strict scientific terms, a single calorie is defined as 4.184 Joules (J).

As with any energy that flows, there is resistance that impedes the flow of that energy. In the field of thermoregulation, that resistance is insulation (the inverse of insulation is thermal conductance). Thus, poor conductors are excellent insulators. Blubber, for example, makes an excellent insulator and conducts heat poorly. Materials such as silver are poor insulators and thus conduct heat very well. Relatively, water is a better insulator than silver by 1000x. The point that is relevant to marine mammals is that air is a better insulator than water by 25x. In other words, water conducts heat away from a warm body 25x more effectively than air. This becomes an important point for the discussion of how fur works to help keep some marine mammals warm.

One final physics description is the definition of how heat flows from a warm to a cold object. Heat will flow when there is a temperature gradient between two sides of a conducting material in relation to the magnitude of the temperature gradient, the thickness of the material, the inherent thermal conductance of the material and the area that is exposed to the gradient. In biological terms, this means that heat would flow from the interior of a warm blooded mammal through the fat and skin to the cold outside air or water. Since water conducts heat 25x times more effectively than air, this means that heat flows out of a warm object in cold water much more efficiently than it does when that same object is in air. Thus, as humans, we can easily stand around outside in 70°F air, but would find being in 70°F water very cold after a while. This principle states that the thicker the insulator, the less heat flow and the larger the temperature gradient, the greater the driving force. Therefore, to stay warm, an animal would want an effective insulator, a small surface area (reduced appendage size, rolling up into a ball, etc.), a low temperature gradient (seek a warmer area or allow the body temperature to fall, i.e., hibernators) and have a thick insulator. An excellent general discussion of the physics of heat and energy transfer can be found in Schmidt-Nielsen (1997) and in Kooyman (1981) and Pabst *et al.* (1999) for marine mammals.

II. What Is "Thermoregulation"?

Having discussed the physics of heat, the next step is to define the act of regulating temperature (thermoregulation) in the biological realm. In the broadest sense, animals can be classified as either *endotherms* or *ectotherms*, although some animals cross between