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References

- Geraci, J., Harwood, J., and Lounsbury, A. (1999). Marine mammal die-offs: Causes, investigations and issues. In "Conservation and Management of Marine Mammals" (J. Twiss, and R. Reeves, eds), pp. 367–395. Smithsonian Institution Press, Washington, DC.
- Gulland, F. M. D., and Hall, A. J. (2007). Is marine mammal health deteriorating? Trends in the global reporting of marine mammal disease. *Eco. Health* **4**, 135–150.
- Harvell, C. D., et al. (13 authors) (1999). Emerging marine diseases—Climate links and anthropogenic factors. *Science* **285**, 1505–1510.
- Harwood, J. (1998). What killed the Mediterranean monk seals? *Nature* **393**, 17–18.
- Scholin, C., et al. (26 authors) (2000). Mortality of sea lions along the central California coast linked to a toxic diatom bloom. *Nature* **403**, 80–83.

Mating Systems

SARAH L. MESNICK AND KATHERINE RALLS

I. Introduction to Mating Systems

Marine mammal mating systems are diverse and variable. The key to understand this variation is the fundamental idea that individuals behave so as to maximize their lifetime reproductive success and that males and females are subject to different selective pressures (Trivers, 1972). In general, female mammals invest heavily in rearing a limited number of young during their lifetimes whereas males tend to maximize reproductive success by mating with as many females as possible to increase the number of offspring they sire. Recent reviews have both questioned this general conceptual framework (Roughgarden *et al.*, 2006), and supported it, although acknowledging that there is more complexity than originally envisioned (Clutton-Brock, 2007). Males and females do not necessarily always cooperate during mating, and sometimes may be in conflict. Together, the mating strategies of males and females define the mating system of a species. This article presents an overview of male and female mating strategies and describes how the different groups of marine mammals solve the problem of finding mates.

Mating systems have traditionally been categorized on the basis of whether the female and male form pair bonds, the duration of those bonds and the number of partners each sex copulates with during a breeding season or lifetime. To facilitate comparisons among marine mammals, in which males do not remain with their mates after mating (with rare exceptions, Danilewicz *et al.*, 2004), we focus on the number of partners for each sex during a breeding season. In *monogamous* systems, each individual has a single partner during the breeding season and in *polygamous* systems, some individuals have multiple partners. There are several types of polygamy: *polygyny*, in which some males have more than one partner; *polyandry* in which some females have more than one partner; and *polygynandry*, in which some females and some males have multiple partners.

Marine mammals, like most mammals, are predisposed to polygyny because of the fundamental disparity in reproductive biology between the sexes (Clutton-Brock, 1989). Females can produce only a limited number of offspring in their lives and they bear the energetic costs of gestation, lactation, and parental care. Males, however, provide little or nothing to the care of offspring and are free to devote their time and energy to competing for access to mates.

The potential for polygyny, and the extent to which that potential is realized, is determined to a great extent by the degree to which receptive females are aggregated in space and time. The distribution of females, in turn, is determined by phylogenetic constraints (such as the retention of terrestrial birthing in pinnipeds) and by ecological and social conditions. Among the most important of these conditions are the distribution of resources necessary for breeding, predation pressure, and the costs and benefits of group living. Several types of polygynous mating systems have been identified in marine mammals. In populations where females are clustered and their movements are limited in space and time, males generally compete to monopolize females. They may defend resources that are vital to females such as parturition sites (territoriality or resource defense polygyny) or they may defend females directly (female defense polygyny). When females are spatially or temporally dispersed, or are highly mobile, males are less able to control access to potential mates. In these situations, males may aggregate on traditional display sites and advertise for females (lekking) or they may search widely and spend little time with females except to mate (roving).

Females of many species also mate with more than one male during a breeding season and they may benefit in many ways by doing so (see below). Polygynandrous (or "promiscuous") mating systems have been described for a number of species. Frequent copulation may have a variety of functions, but not all mating behavior is for procreation; in many species, sexual behavior is an important component of the social fabric and often has little to do with fertilization.

II. Male Mating Strategies

Male competition for access to mates takes at least three general forms: aggressive interactions to limit the access of other males to females (contest competition), competition to disperse and find sexually receptive females (scramble competition), and competition in courtship to be chosen by the female (mate choice competition). Each of these behavioral strategies has, in turn, generated a number of morphological and physiological adaptations. For example, males are often distinguished by large body size, big canines, or tusks that can be used as weapons in combat with other males (Fig. 1). Among mammals, males generally disperse more widely than females and there is an increasing evidence that the pattern holds in marine mammals [e.g., Dall's porpoise (*Phocoenoides dalli*) and beluga (*Delphinapterus leucas*)]. Males are typically more persistent in courtship and are the more conspicuous and ornamented sex. They may attempt to entice and attract females through visual acoustic, and pheromonal displays (Fig. 2).

Several additional forms of male competition have also been described. Males may attempt to out-compete other males by producing higher quality or greater quantities of sperm or by removing other male's sperm (sperm competition). When a male cannot monopolize access to females by himself, males may cooperate and form alliances. These alliances, comprised of pairs of males or small groups, compete with each other for access to females and have been described in Indian Ocean bottlenose dolphins (*Tursiops aduncus*) from Shark Bay, Australia (Connor *et al.*, 1996), and common



Figure 1 Adult male northern elephant seals (*Mirounga angustirostris*) fight for positions in a dominance hierarchy that confers access to receptive females. Photograph by Sarah L. Mesnick.



Figure 2 A singing adult male humpback whale (*Megaptera novaeangliae*). Singing by humpback males presumably acts to attract females, although whether songs contain cues to mate quality remains in dispute. Singing may also function to space males in a breeding area or to aid in the establishment of dominance hierarchies. Maui. © Flip Nicklin (Minden Pictures). Photograph obtained under N.M.F.S. Permit No. 987.

bottlenose dolphins (*Tursiops truncatus*) from Sarasota Bay, Florida (Wells *et al.*, 1987), and are likely to occur in other species as well. Males may also form consortships, maintaining close proximity to a female until she comes into estrus. In common bottlenose dolphins from Sarasota Bay, Florida, such consortships have been found to correlate with the birth of offspring several months later. Species in which males are larger than females, possess dangerous weapons and aggressively pursue copulation, some males may forcibly coerce the female to mate (forced copulation), e.g., northern elephant seals (*Mirounga angustirostris*), Le Boeuf and Mesnick (1990). Males which are not competitive, because of their size, age, or experience, may employ alternative strategies to obtain access to females. Males may sneak copulations when alpha bulls are distracted or abduct females from the territories of dominant males (kleptogyny) as observed in northern fur seals (*Callorhinus ursinus*), Gentry (1998). Although competition between males receives the most attention, the possibility of male choice—the notion that males may prefer to mate with particular females—is an area that deserves further attention.

III. Female Mating Strategies

Females of most marine mammals produce only a single offspring at a time. The interbirth interval ranges from 1 year in most pinnipeds and small cetaceans to 5, 6, or even 7 years in larger toothed whales such as sperm whales (*Physeter macrocephalus*), killer whales (*Orcinus orca*), and short-finned pilot whales (*Globicephala macrorhynchus*). While females may maximize their reproductive success by being good mothers, they may also enhance their fitness by choosing males as mates that offer resources, protection, or genetic benefits. Multiple mating is also an important female strategy that may function to ensure insemination or to confuse paternity and reduce potential aggression directed toward young. Multiple mating may also enable females to promote sperm competition and exert cryptic female choice.

In other well-studied taxa, such as birds, females are highly discriminating in their choice of sexual partners. Moreover, females often choose in a similar way, so that a few males achieve many copulations and most other males achieve few or none. Females may choose among potential mates directly (based on resources, size, strength, dominance, or display) or indirectly (by mating with the winner of contests for access to females). Some marine mammal females actively seek out particular males and mate. For example, in California sea lions (*Zalophus californianus*), some females were observed to change pupping locations from one year to the next to remain with a territorial male who changed territory location (Heath, 1989). Females may also incite male–male competition. As a result of protesting male sexual advances loudly, female northern elephant seals instigate fights among males, and subsequently mate with the winner of these battles (Cox and Le Boeuf, 1977).

In marine mammals, it is difficult to establish the existence of female choice and even more difficult to determine why females might choose particular males with which to mate or to quantify the benefit to females of exercising choice. Direct benefits to the female, in the form of nutritional resources or parental care, are not known to exist in marine mammals. Females can benefit, however, by choosing males with higher quality territories, which provide better parturition or thermoregulatory sites, or by choosing males that provide protection from harassment by subordinate males (the bodyguard hypothesis; Mesnick, 1997). Females can also benefit by discriminating among potential mates on the basis of genetic benefits (Mays

and Hill, 2004). These include choosing males of the correct species, males with immunologically compatible genes, and males with “good genes” who can produce offspring of higher quality. Females can also choose males with better fertilization ability or virility.

Females may make very different decisions regarding which males they associate with, which males they mate with, and which male ultimately sires their offspring. In land-breeding pinnipeds, for example, a female may reside with one dominant or territorial male during lactation but later leave this male’s territory to copulate with another male elsewhere (extra-territorial copulation). In some species, such as the common bottlenose dolphin, sexual behavior is a frequent and important component of nonreproductive social life and has little to do with fertilization. As with males, female strategies need not be mutually exclusive and it is likely that different females will utilize different strategies depending on their age, dominance rank, and the number and quality of available mates.

IV. Taxonomic Descriptions

A. Pinnipeds

For all pinnipeds studied to date, the data support, or are highly suggestive of, a polygynous mating system (Boness *et al.*, 2002). Pinnipeds are predisposed to polygyny because they give birth on land, which results in the spatial clustering of females, and have an annual birthing cycle, which results in reproductive synchrony among females. The degree of polygyny varies both within and among species with the extent of reproductive synchrony and spatial clustering. Most species have a peak availability of receptive females lasting about 1 month but the availability of receptive females ranges from 10–15 days in harp (*Pagophilus groenlandicus*) and hooded (*Cystophora cristata*) seals to a period of several months for species that breed in tropical habitats such as monk seals (*Monachus* spp.) and Galapagos sea lions (*Zalophus wollebaeki*).

Variation in the degree of spatial clustering within and among species is due to a variety of factors including the spatial distribution of suitable breeding sites, whether mating takes place on land or at sea, the intensity of male harassment, predation pressure, and thermoregulatory pressures. Polygyny and sexual dimorphism are generally much more extreme in species that mate on land than in those that mate in the water and in species that reside in high latitudes than those that reside in lower latitudes (see article on Sexual Dimorphism).

1. Otariids Otariid females feed during lactation. Lactation is energetically costly, so females must raise their young on sites near highly productive marine areas. Because these sites are limited, and the season of maximum marine productivity may be short, females typically occur in dense aggregations (numbering from a few individuals to more than one thousand) on beaches or rocky shelves on islands. Mating occurs on land, although evidence of at least some mating at sea exists for a few species [e.g., Juan Fernández fur seal (*Arctocephalus philippii*) and the California sea lion]. The combination of dense female aggregations and terrestrial mating gives some males the opportunity to monopolize mating with many females. Sexual dimorphism among otariids is correspondingly extreme; males are on average 3 times, and up to 10 times, heavier than females and have other traits favored in physical combat over females: large canines, heavy chests, and dense manes.

The northern fur seal is among the most polygynous of the otariids: a single male at the St. George Island rookery mated with 161 females while hundreds of other males had no copulations at all (Gentry, 1998). The lowest levels of polygyny probably occur in

species such as the Juan Fernández fur seal, the South American sea lion (*Otaria flavescens*), the Galapagos fur seal (*Arctocephalus galapagoensis*), and Hooker’s sea lion (*Phocarcetos hookeri*), in which the ratio of sexually active adults ranges from two to six females per male (Boness *et al.*, 1993).

Male otariids typically defend territories containing resources needed by females—parturition and thermoregulatory sites—rather than individual females (Fig. 3). However, female defense has been demonstrated in at least one otariid, the South American sea lion. The two types of polygyny are difficult to distinguish and are not necessarily mutually exclusive. There is some evidence suggestive of lekking in at least three species, the California sea lion, the South American fur seal (*Arctocephalus australis*), and Hooker’s sea lion.

A male’s ability to acquire and defend a territory depends on his size and age, his ability to compete with other males, and his ability to fast during his tenure (contest competition). Under most circumstances, the boundaries of territories are fixed and are often delineated by natural breaks in the substrate. Males use a species-specific threat display when defending the boundaries of their territory. A male that secures a territory will probably, but not necessarily, mate with many of the females that give birth on his territory. Climate and topography also play an important role in determining a male’s mating success. Those males defending territories containing access to the water, tide pools, or shade typically acquire a disproportionately large number of females.

Most otariid bulls fast while maintaining their territories, sometimes for the entire 2–3-month breeding season [e.g., Steller sea lions (*Eumetopias jubatus*) and northern fur seals]. Some males return to the same territory in subsequent years, with remarkably high site fidelity, whereas others move to new territories or are not seen again. Territorial males may try to herd females to prevent them from leaving their territories but in most species, females determined to leave generally can do so. The males of some species, however [e.g., northern fur seal and the South American and Australian (*Neophoca cinerea*) sea lion], are able to prevent females from leaving their territories by threats, herding, and sometimes physical aggression leading to injury.



Figure 3 A Steller sea lion (*Eumetopias jubatus*) territory. Adult males defend resource-based territories that encompass female parturition and thermoregulatory sites. Females choose among males in a surprisingly consistent way. As a result, some males holding territories never or rarely mate, while a few males mate with many females. Photograph by Sarah L. Mesnick.

The importance of male courtship displays in otariids is not well understood. For example, it is not known whether male displays, such as the incessant barking of male California sea lions, function as threat displays directed at other males, as courtship displays to attract females, or both. Alternative male mating strategies are widespread and generally thought to be practiced by subadult or subordinate males. These include gang raids by groups of non-territorial males to abduct or mate with females in the main breeding territories (observed in South American and Australian sea lions), males stealing females from the territories of their neighbors (kleptogyny; northern fur seals) or males trying to sneak copulations or mate at sea (several species). How successful these strategies are in inseminating females is generally not known. In Antarctic fur seals (*Actocephalus gazella*), a large DNA-based paternity study found that females who pupped on the study beach in the year of conception almost certainly conceived to territorial males and males did not appear either to sneak copulations or mate aquatically, although probability of paternity was strongly influenced by maternal state at conception (females who come to the beach but do not pup appear less likely to conceive with males from that beach) and the authors could not entirely preclude the possibility that a few males might employ alternative strategies (Hoffman *et al.*, 2003).

Female mating strategies are less well understood than male mating strategies but several lines of evidence, including genetic studies, suggest that females exercise more choice among males than previously suspected. Female otariids choose which territory to haul out in and usually, but not always, move freely in and out of a male's territory. Estrus occurs within 1–2 weeks postpartum in all but one species (California sea lion, about 21–27 days). When it is time to mate, a female may leave the male's territory in which she gave birth and mate with another male. This behavior has been observed in California sea lions, South American fur seals, and between the territories of sympatric Antarctic fur seals (Goldsworthy *et al.*, 1999).

Climate, rookery topography and the intensity of male herding and harassment influence the ability of females to exercise mate choice. In hot climates, females have more opportunity for mate choice due to their frequent thermoregulatory movements between their birthing site and the water. In contrast, in colder climes, intense male herding restricts female choice and may injure females. Female northern fur seals are thought to successfully reduce the risk of injury from males by forming dense aggregations and competing for central locations within these groups, which minimizes contact with males, and by acting submissive around males. In this species, females do not appear to choose males directly. Rather, by gathering on traditional mating grounds, the result is that males fight for access for these sites, and females subsequently mate with the winners of these contests. Female otariids may also directly solicit and initiate copulation from males. In Steller sea lions, e.g., a female gains the sexual attention of a male by laterally swinging her neck, dragging her hindquarters and sinuous movements of her body against his body. While females tend to direct most solicitation behavior toward the older “proven” territorial males, the extent of female choice remains unclear. Multiple mating is known in 30% of otariids studied (Boness *et al.*, 1993) and suggests an important and variable role for sperm competition and mate choice across species.

2. *Phocids* Most phocid females are thought to fast during a short and concentrated lactation period and are generally thought not to return to sea to feed until after weaning their pup. However, smaller individuals of some species may supplement fat stores by foraging to sustain lactation (Bowen *et al.*, 2001). Many species

live in high latitudes, and a number of species give birth on ice. Females of most phocids are spatially dispersed during lactation; they may be solitary or occur in small-to-moderate-sized well-spaced colonies. In 16 of 19 species, the majority of mating takes place in the water near or after the end of lactation (Boness *et al.*, 2002). As a consequence, males have less opportunity to defend and mate with multiple females. Aquatically mating phocids are less polygynous and less sexually dimorphic than terrestrially mating phocids or otariids.

For most species, the breeding season is relatively short and, in species that breed on ice, mating takes place when temperatures are well below freezing. Reverse sexual dimorphism, with females larger than males, occurs in several species. Large female size may help a mother provide greater quantities of fat-rich milk to her pup and protects her from low polar temperatures. Small size in males is also thought to facilitate agility underwater where males may defend aquatic territories, display, and mate with females. Nevertheless, aquatically mating species are considered to be slightly or moderately polygynous. Mating takes place within a few days of the weaning of the pup.

A common feature of the behavior of aquatically mating phocids is the production by males of simple or complex underwater vocalizations and stereotypical dive displays during the breeding season (Van Parijs *et al.*, 2003). These vocalizations are thought to be used predominantly in male–male competition and are also likely to play a role in attracting females. “Eerie but melodious” songs have been described for male bearded seals (*Erignathus barbatus*) and trills, knocks, buzzes, and chirps for male Weddell seals (*Leptonychotes weddellii*). Harbor seal (*Phoca vitulina*) males produce broadband growls. Hooded seals males make numerous sounds underwater and also produce sounds in air as they inflate and deflate their hood and red nasal sac. The number and diversity of underwater vocalizations is correlated with various social and environmental factors, including mating system, female gregariousness and predation intensity, and is geographically variable (Stirling and Thomas, 2003). In leopard seals (*Hydrurga leptonyx*), both males and females produce underwater broadcast calls thought to serve in mate attraction.

In aquatically mating phocids, there is considerable variability in male mating strategies displayed by each species as well as plasticity within and between populations. In some species, such as crabeater seals (*Lobodon carcinophagus*), spotted seals (*Phoca largha*), and hooded seals, males directly defend the lactating female and her immediate vicinity, a strategy akin to roving and mate guarding of a single female or small group of females. A typical group consists of a female and her pup and an adult male who may have to wait before the female comes into estrus and is receptive to mating. Presumably, the male will mate with the female when she enters the water after weaning her pup. This strategy can be described as sequential female defense polygyny since the male may leave after mating to search for another receptive female. Other males may surround these triads and may compete with the attending male for access to the female, typically with threats and sometimes bloody fights.

In other species, males defend aquatic territories (called “maritories”) off the beach or ice where females haul out to raise their pups. Males spend considerable time in these territories giving underwater vocal and visual displays and may mate with any receptive female that enters the territory. This characterizes the behavior of Weddell, harp, bearded, and harbor seals, although there is considerable variation within and between breeding colonies. In the geographically wide-spread harbor seal, colonies occur in diverse habitats and males adjust their mating strategies depending on the topography. Some males defend adjacent discrete territories offshore from female

haulout areas, others defend territories near female foraging areas or along route to foraging areas, and still others do not defend territories but display in the vicinity of female haulouts. Studies from all habitats observe that males perform stereotypic vocal and dive displays during the period the females is in estrus and raise the possibility of a lek-type mating system in which females select males (Boness *et al.*, 2006).

The northern and southern (*Mirounga leonina*) elephant seal and some populations of the gray seal (*Haliocoeris grypus*) are unusual among phocids in that mating takes place on land. These species exhibit forms of female defense polygyny. Harassment by subordinate males is widespread, costly to females, and may be an important factor contributing to spatial and temporal synchrony among breeding females (Le Boeuf and Mesnick, 1990, Boness *et al.*, 1995). In all the three terrestrially breeding species, males that are unable to maintain control over access to females may attempt to “sneak” copulations or capture, sometimes aggressively, and mate with females as they leave the colony.

In elephant seals, males use visual and acoustic threats as well as physical fighting to compete for dominance in a social hierarchy that confers access to females (Le Boeuf, 1974). Female elephant seals may exercise mate choice by competing for central positions in harems where dominant males reside and by inciting male–male competition and subsequently mating with the winner of these battles. Polygyny in elephant seals is among the most extreme recorded in all mammals; lifetime reproductive success of most males is nil or low. Many die before reaching breeding age and higher-ranking males prevent many of those that survive from breeding. DNA paternity analyses confirm that the proportion of pups sired by alpha males is consistent with that expected from observed mating success in southern elephant seals but show that behavioral observations overestimate the success of some northern elephant seal alpha males (Hoelzel *et al.*, 1999). The relatively lower success of northern elephant seal males may be due in part to the behavior of the northern elephant seal females which copulate more frequently than southern females and may mate during departure from the harem, the greater success of non-alpha males, and/or reduced virility of specific alpha males.

Mating behavior among the geographically wide-spread populations of the gray seal is difficult to categorize because of their varied habitat and social organization. Gray seal females typically do not cluster as tightly and are more mobile in the colony than elephant seal females. Males exhibit state-dependent reproductive strategies, a primary mating tactic involving prolonged female defense and three alternative strategies have been identified (Lidgard *et al.*, 2004). Although males exhibiting the primary strategy achieve the greatest mating success, males that exhibit alternative tactics have been shown to achieve some success. At North Rona, Scotland, genetic studies show that over 80% of assigned paternities agree with behavioral observations in which a female in estrus mates with the local dominant male. However, about 10–20% of females do not have their pups sired by local males and may instead seek preferred sires outside the local male’s range or mate with unobserved males, during their departure, or at sea (Twiss *et al.*, 2006). Among gray seal colonies, North Rona has a relatively stable social organization; a lower correlation between observational and genetic measures of success would be expected in colonies with a more fluid social structure and increased female mobility (Pemberton *et al.*, 1992).

3. *Walrus (Odobenus rosmarus)* Walruses have the most elaborate courtship displays of all pinnipeds. Walruses show marked sexual size dimorphism and are thought to be strongly polygynous. Atlantic

walruses (*O. r. rosmarus*) in the Canadian High Arctic exhibit a mating system that resembles female defense polygyny in which males appear to monopolize access to female herds. Pacific walruses (*O. r. divergens*) in the Bering Sea may have a lek-like mating system. Groups of males cluster around females, which form dense aggregations on pack ice. Males are aggressive toward one another and produce intricate visual and vocal displays, consisting of barks, whistles, growls, and underwater bell-like sounds. The massive tusks of the male walrus appear to play an important role as a symbol of rank used to threaten other males and as a visual signal to females who may choose among males partly by the size of their tusks.

B. Cetaceans

1. *Odontocetes* In contrast to pinnipeds, which are relatively sedentary and clustered during the breeding season, female odontocetes are mobile and dispersed. This has two important consequences for male mating strategies: males have less opportunity to control access to aggregated females and less assurance of paternity. It is not surprising, therefore, that the basic mating strategy of male odontocetes appears to be one of searching for receptive females and spending little time with them other than to mate. It is likely that mate guarding, or monopolization of females long enough to increase assurance of paternity and to reduce extra pair copulations, also occurs, although the phenomenon has been noted only in bottlenose dolphins and Dall’s porpoise.

Female mating strategies in odontocetes are little understood. Given their mobility and three-dimensional habitat, it is generally thought that females are able to exercise choice by out-maneuvering males or by rolling belly-up. Observational and hormonal evidence suggests that females of several species copulate frequently both during and outside the breeding season and may be polyestrous. Frequent copulation may function to ensure fertilization, induce sperm competition, obscure paternity, and help to establish social bonds with potential future partners. In many odontocete species, sexual behavior is an important component of nonreproductive social interactions and often has little to do with fertilization, making it difficult to infer mating strategies from incomplete observations. An example is the intriguing “wuzzling” behavior of Hawaiian spinner dolphins (*Stenella longirostris longirostris*). Wuzzling refers to the interweaving, caressing, and copulating dolphins of both sexes and all ages and is especially common in the summer months, when many females come into estrus. Is the behavior social? Sexual? Or both?

We know little about mating systems in the vast majority of odontocetes. However, there are substantial data on bottlenose dolphins, sperm whales, and killer whales. A mating strategy of female defense or sequential defense polygyny has been suggested for two species of bottlenose dolphin. In Indian Ocean bottlenose dolphins in Shark Bay, Australia, males in pairs or trios cooperate to form temporary consortships with individual females, often through aggressive herding (Connor *et al.*, 1996). “Second-order alliances,” teams of pairs or trios, attack other alliances in contests over female consorts. In common bottlenose dolphins in Sarasota Bay, Florida, individual males and members of long-term male associations form temporary consortships with females without obvious aggressive herding (Wells *et al.*, 1999). The extent to which this sequential female defense strategy is successful is uncertain; individual females are polyestrous and associate with several males during the season in which they conceive. These behaviors may facilitate female mate choice, promote sperm competition, and obscure paternity. In Moray Firth, Scotland, common

bottlenose dolphin males apparently do not form alliances or aggressively herd females, although single males may accompany groups of females throughout the breeding season. Among these three sites, the level of male bonding may be inversely related to male body size and the degree of sexual dimorphism (Tolley *et al.*, 1995). In Shark Bay, individuals are small in size, not noticeably dimorphic and alliance formation enables males to gain and maintain access to females. In Moray Firth, males are larger than females and can do this on their own.

Most sperm whales in the Galápagos Islands appear to rove between groups of females searching for potential mates. One or more large males may attend a group of females (sometimes simultaneously) for short periods of time ranging from a few minutes to several hours (Fig. 4). Rather than males herding female groups, females were observed to alter course and speed so that they could join a large male hundreds of meters away. Males did not interact aggressively with each other within female groups, despite several accounts in the literature of males fighting outside of groups. Given the apparent roving strategy of males, the role of the tremendously large nose of the male sperm whale and its possible use as a sound generating organ remains unclear. The loud clicks may function in male–male competition or advertisement to attract females.

Pods of resident killer whales in the Pacific Northwest are frequently observed associating with one another in the summer months when prey (and observer) abundance is high. In these multi-pod

groups, there is much sexual activity amongst all pod members, young, and old alike. Since no dispersal of either sex occurs from resident pods, it is thought that mating takes place during these encounters. Considering that the entire pod engages in these ceremonies, it is likely that the function of multi-pod encounters is both sexual and social. Similarly, genetic analyses of long-finned pilot whales captured in a Faroese fishery indicate that males remain in their natal groups but do not mate within them (Amos *et al.*, 1993). Young were sired by males not captured with the group, implying that pilot whales must mate when two or more groups meet or when adult males pay brief visits to other groups.

Very little is known about mating systems in the remaining species of toothed whales. However, we can infer something about the mating strategies of these species from the type and degree of sexual dimorphism and its association with other characteristics such as body scarring and relative testis size (see article on Sexual Dimorphism). For example, relative testis size ranges nearly two orders of magnitude among odontocete species, from less than 0.05% [several Mesoplodon species, the franciscana (*Pontoporia blainillei*), the baiji (*Lipotes vexillifer*), and sperm whale] to nearly 5% [harbor porpoise and dusky dolphin (*Lagenorhynchus obscurus*)] of body weight. These data suggest the importance of sperm competition in several odontocete species, and especially among some of the delphinids and porpoises. The importance of mate choice competition, attempts to entice and attract females through elaborate visual or acoustic displays, is suggested by differences between the sexes in vocalizations and exaggerated visual signals such as the post-anal hump or enlarged dorsal fins. At present, sexually dimorphic acoustic signals are known only in sperm whales. However, because odontocetes produce a wide range of sounds, acoustic displays are likely to occur in several other species as well. The importance of contest competition for access to mates is suggested by sexual dimorphism in size, weaponry (teeth and tusks) and the presence of scarring of conspecific origin (tooth rake marks). Sperm whales, the beaked whales, and bottlenose whale (*Hyperoodon* spp.) exhibit these traits.

2. *Mysticetes* Among the mysticetes, substantial data on breeding behavior exist only for the humpback (*Megaptera novaeangliae*), right (*Eubalaena* spp.), and gray (*Eschrichtius robustus*) whales. Even in these species, little is known about female behavior. The humpback whale has been studied most intensively. Male humpbacks adopt one or more of the three primary strategies: display by singing long, complex songs; direct competition with other males for females in “competitive groups;” and escort of females, including those with newborn calves. It is possible that males escorting females are waiting for mating opportunities or are guarding females after copulation. Two secondary strategies, roving and sneaking, have also been suggested.

Female humpbacks sometimes aggressively reject subadult males and they may incite competition among males. Although molecular analysis of paternity has shown that females are mated by different males between years (Clapham and Palsbøll, 1997), it is unknown whether females mate multiply within a given breeding season. Singing by male humpbacks is an intriguing phenomenon, since songs change over time yet all members of a population sing essentially the same song at any one time. Singing by humpback males may serve to attract females, signal status to other males, or both. Additional suggestions for the function of song include a means to synchronize estrus and a basis for organizing males during breeding season (Darling *et al.*, 2006). Whether the aggregation and displaying



Figure 4 Adult male sperm whales (*Physeter macrocephalus*) rove among female groups searching for receptive individuals and staying with each group for only a few hours at a time. Dominica. © Flip Nicklin (Minden Pictures).

of humpback whales at specific sites constitutes a lek also remains controversial (see article on Song).

Little else is known about the mating systems of baleenopterid whales. Blue (*Balaenoptera musculus*), fin (*B. physalus*), Bryde's (*B. edeni*), and minke (*B. acutorostrata*) whales have patterned calls, termed songs, which are geographically variable and thought to function in mating, although the mechanism is unclear. Species recognition, male–male competition, and female choice are possibilities. In the Gulf of California, male fin whales may sing while guarding feeding territories (Croll *et al.*, 2002).

Right whales show sexual activity throughout the year, although calving is strongly seasonal. Since the gestation period is 1 year and there is no evidence of diapause, mating leading to conception presumably occurs primarily in the winter. The function of sexual activity during other seasons is unknown. Observations of multiple male right whales mating with single females, together with the huge (1 ton!) testes, strongly suggest that sperm competition is a principal mating strategy in this species, and also probably in bowhead (*Balaena mysticetus*) and gray whales (Brownell and Ralls, 1986). The level of aggression in male–male interactions in these species is low compared to that observed in humpback whales, an observation that is also consistent with the predominance of sperm competition as a mating strategy.

C. Sirenians, Sea Otters (*Enhydra lutris*) and Polar Bears (*Ursus maritimus*)

Male manatees (genus *Trichechus*) and dugongs (*Dugong dugong*) tend to be solitary and search for potential mates by roaming over large areas that include the home ranges of several females. Groups of males sometimes follow and try to mate with a single female, forming a “mating herd.” In both manatee and dugongs, males in these herds threaten and fight with each other but it is still unknown whether this behavior is a form of scramble competition or is more akin to a type of lekking. In Shark Bay, Australia, dugongs associate in a more classical kind of lekking, with several males patrolling exclusive areas and engaging in activities usually indicative of both male competition and mate attraction, including acoustic signaling. In both manatees and dugongs, the mating season extends over several months and sexual dimorphism is slight. Interbirth intervals are at least 2 years and may be as much as 5 years in some cases.

Female sea otters typically give birth annually. Births generally peak in the spring, although females in warmer areas may give birth in any month. Adult males are larger than females. Male sea otters establish territories that contain food resources and sheltered resting places and usually overlap the home ranges of one or more females. Males may defend territories seasonally or all year. Other males congregate in groups outside of the areas occupied by territorial males. Courtship and mating, as are typical for many mustelid species, is physically aggressive and females may be injured or killed by males. Copulation occurs with both the male and female on their backs near the water's surface and the male grasps the female's head or jaws, including the nose, in his own jaws. Recently mated females typically have red, swollen noses. After mating, the pair may stay together for a few days in which they feed, groom, play, and rest in close company.

Polar bears are highly sexually dimorphic and polygynous; adult males may be over twice as heavy as adult females. Females have extensive home ranges and males are forced to travel over large areas when searching for mates. Males apparently fight among themselves for access to females. Specific courtship behaviors are lacking or are as yet undescribed. The largest and strongest males apparently do most of the

mating while other males sometimes wait in the distance. Polar bears are notable among marine mammals in that they are the only species in which females give birth to multiple young (1–2 is the most common litter size and rarely 3–4). The interbirth interval is about 3 years.

IV. Mating System Studies and the Future

Our knowledge of marine mammal mating systems has increased dramatically in recent years due to technological advances in the use of molecular markers, animal-borne cameras and underwater acoustic recording devices which provide new insights and make it possible to investigate previously inaccessible behaviors and species. Long-term field studies continue to be sources of deepening understanding and new analytical methods such as social network studies and investigations of genetic kinship will likely reveal more complex patterns of social structuring than is currently known. Female mating strategies, including the role of multiple mating and the importance of cryptic female choice are gaining increasing attention. As our understanding of the physiology of female receptivity grows, we will be better able to interpret both female and male mating behavior. At the same time, our increasing ability to hear and see underwater will enable us to tap into the little known realm of underwater acoustic and visual displays.

See Also the Following Articles

Breeding Sites ■ Courtship Behavior ■ Estrus and Estrous Behavior ■ Song ■ Reproductive Behavior ■ Sexual Dimorphism ■ Territorial Behavior

References

- Amos, B., Schlötterer, C., and Tautz, D. (1993). Social structure of pilot whales revealed by analytical DNA profiling. *Science* **260**, 670–672.
- Boness, D. J., Bowen, W. D., and Francis, J. M. (1993). Implications of DNA fingerprinting for mating systems and reproductive strategies of pinnipeds. *Symp. Zool. Soc., Lond.* **66**, 61–93.
- Boness, D. J., Bowen, W. D., and Iverson, S. J. (1995). Does male harassment of females contribute to reproductive synchrony in the grey seal by affecting maternal performance? *Behav. Ecol. Sociobiol.* **36**, 1–10.
- Boness, D., Clapham, P. J., and Mesnick, S. L. (2002). Life history and reproductive strategies. In “Marine Mammals: An Evolutionary Approach” (R. Hoelzel, ed.), pp. 278–324. Blackwell Science, Ltd.
- Boness, D. J., Bowen, W. D., Buhleier, B. M., and Marshall, G. J. (2006). Mating tactics and mating systems of an aquatic-mating pinniped: The harbor seal. *Phoca vitulina*. *Behav. Ecol. Sociobiol.* **61**, 119–130.
- Bowen, W. D., Iverson, S. J., Boness, D. J., and Oftedal, O. T. (2001). Energetics of lactation in harbour seals: Effect of body mass on sources and level of energy allocated to offspring. *Funct. Ecol.* **15**, 325–334.
- Brownell, R. L., and Ralls, K. (1986). Potential for sperm competition in baleen whales. In “Behaviour of Whales in Relation to Management. Special Issue 8 (G. P. Donovan, ed.), p. 97–112. Reports of the International Whaling Commission, Cambridge.
- Clapham, P. J., and Palsbøll, P. J. (1997). Molecular analysis of paternity shows promiscuous mating in female humpback whales (*Megaptera novaeangliae*, Borowski). *Proc. Roy. Soc. Lond.* **264**, 95–98.
- Clutton-Brock, T. H. (1989). Mammalian mating systems. *Proc. Roy. Soc. Lond.* **236**, 339–372.
- Clutton-Brock, T. (2007). Sexual selection in males and females. *Science* **318**, 1882–1885.
- Connor, R. C., Richards, A. F., Smolker, R. A., and Mann, J. (1996). Patterns of female attractiveness in Indian Ocean bottlenose dolphins. *Behavior* **133**, 37–69.

- Cox, C. R., and Le Boeuf, B. J. (1977). Female incitation of male competition: A mechanism in sexual selection. *Am. Nat.* **111**, 317–335.
- Croll, D. A., Clark, C. W., Acevedo, A., Tershy, B., Flores, S., Gedamke, J., and Urbán-Ramírez, J. (2002). Only male fin whales sing loud songs. *Nature* **417**, 809–810.
- Danilewicz, D., Claver, J. A., Perez Carrera, A. L., Secchi, E. R., and Fontoura, N. F. (2004). Reproductive biology of male franciscanas (*Pontoporia blainvillei*) (Mammalia: Cetacea) from Rio Grande do Sul, southern Brazil. *Fish. Bull.* **102**, 581–592.
- Darling, J. D., Jones, M. E., and Nicklin, C. P. (2006). Humpback whale songs: Do they organize males during the breeding season? *Behavior* **143**, 1051–1101.
- Gentry, R. L. (1998). “Behavior and Ecology of the Northern Fur Seal.” Princeton University Press, Princeton.
- Goldsworthy, S. D., Boness, D. J., and Fleischer, R. C. (1999). Mate choice among sympatric fur seals: Female preference for conphenotypic males. *Behav. Ecol. Sociobiol.* **45**, 253–267.
- Heath, C. B. (1989). The behavioral ecology of the California sea lion. Ph.D. Thesis. University of California, Santa Cruz.
- Hoelzel, A. R., Le Boeuf, B. J., Reiter, J., and Campagna, C. (1999). Alpha-male paternity in elephant seals. *Behav. Ecol. Sociobiol.* **46**, 298–306.
- Hoffman, J. I., Boyd, I. L., and Amos, W. (2003). Male reproductive strategy and the important of maternal status in the Antarctic fur seal. *Arctocephalus gazella*. *Evolution* **57**, 1917–1930.
- Le Boeuf, B. J. (1974). Male-male competition and reproductive success in elephant seals. *Am. Zool.* **14**, 163–176.
- Le Boeuf, B. J., and Mesnick, S. L. (1990). Sexual behavior of male northern elephant seals: I. Lethal injuries to adult females. *Behaviour* **116**, 143–162.
- Lidgard, D. C., Boness, D. J., Bowen, W. D., McMillan, J. I., and Fleischer, R. C. (2004). The rate of fertilization in male mating tactics of the polygynous grey seal. *Mol. Ecol.* **13**, 3543–3548.
- Mays, H. L., and Hill, G. E. (2004). Choosing mates: Good genes versus genes that are a good fit. *Trends Ecol. Evol.* **19**, 554–559.
- Mesnick, S. L., and Hill, G.E. (1997). Sexual Alliances: Evidence and Evolutionary Implications. In “Feminism and Evolutionary Biology: Boundaries, Intersections and Frontiers” (P. A. Gowaty, ed.), pp. 207–260. Chapman and Hall, New York.
- Pemberton, J. M., Albon, S. D., Guinness, F. E., Clutton-Brock, T. H., and Dover, G. A. (2002). Behavioral estimates of male mating success tested by DNA fingerprinting in a polygynous mammal. *Behav. Ecol.* **3**, 66–75.
- Roughgarden, J., Oishi, M., and Akçay, E. (2007). Reproductive social behavior: Cooperative games to replace sexual selection. *Science* **311**, 965–969.
- Stirling, I., and Thomas, J. A. (2003). Relationships between underwater vocalizations and mating systems in phocid seals. *Aq. Mamm.* **29**, 227–247.
- Tolley, K. A., Read, A. J., Wells, R. S., Urian, K. W., Scott, M. D., Irvine, A. B., and Hohn, A. A. (1995). Sexual dimorphism in wild bottlenose dolphins (*Tursiops truncatus*) from Sarasota, Florida. *J. Mammal.* **74**, 1190–1198.
- Trivers, R. L. (1972). Parental investment and sexual selection. In “Sexual Selection and the Descent of Man, 1871–1971” (B. Campbell, ed.), pp. 136–179. Aldine, Chicago.
- Twiss, S. D., Poland, V. F., Graves, J. A., and Pomeroy, P. P. (2006). Finding fathers: Spatio-temporal analysis of paternity assignment in grey seals (*Halichoerus grypus*). *Mol. Ecol.* **15**, 1939–1953.
- Van Parijs, S. M., Lydersen, C., and Kovacs, K. M. (2003). Vocalizations and movements suggest alternative mating tactics in male bearded seals. *Anim. Behav.* **65**, 273–283.
- Wells, R. S., Scott, M. D., and Irvine, A. B. (1987). The social structure of free-ranging bottlenose dolphins. *Curr. Mammal.* **1**, 247–305.
- Wells, R. S., Boness, D. J., and Rathbun, G. B. (1999). Behavior. In “The Biology of Marine Mammals” (J. E. Reynolds, III, and S. Rommell, eds), p. 324–422. Smithsonian Institution Press, Washington, DC.

Melon-Headed Whale

Peponocephala electra

WAYNE L. PERRYMAN

I. Characteristics and Taxonomy

The melon-headed whale is one of a group of small, dark-colored whales that are often referred to as “blackfish.” It is mostly dark gray in color with a faint darker gray dorsal cape that is narrow at the head and dips downward below the tall, falcate dorsal fin (Fig. 1). A faint light band extends from the blowhole to the apex of the melon. A distinct dark eye patch, which broadens as it extends from the eye to the melon, is often present and gives this small whale the appearance of wearing a mask. The lips are often white, and white or light gray areas are common in the throat region and stretching along the ventral surface from the leading edge of the umbilicus to the anus. At sea, this species is difficult to distinguish from the pygmy killer whale (*Feresa attenuata*). It differs externally from the pygmy killer whale by having a more pointed or triangular head and sharply pointed pectoral fins. Both of these characters are difficult to recognize at sea unless these small whales are seen from above. Experienced observers often rely more on behavioral than on physical characters to separate these two blackfish in the field. In stranded specimens, the melon-headed whale can be distinguished from all other blackfish by its high tooth count, 20–26 per row, compared to generally less than 15 teeth per row for pygmy killer whales.

Asymptotic length for males (2.52 m) is greater than for females (2.43 m), and males also have comparatively longer flippers, taller dorsal fins, broader tail flukes, and are more robust (Best and Shaughnessy, 1981; Miyazaki *et al.*, 1998). In addition, some males exhibit a pronounced ventral keel that is found posterior to the anus. The longest specimen reported was a 2.78-m female that stranded in Brazil (Lodi *et al.*, 1990); a 2.64-m male that stranded in Japan weighing 228 kg is the heaviest specimen reported (Miyazaki *et al.*, 1998).

The skull of the melon-headed whale is typically delphinid in shape, with the exception of a very broad rostrum and deep antorbital notches. It is similar to the skull of the common bottlenose dolphin (*Tursiops truncatus*), but the teeth of the melon-headed whale are



Figure 1 Melon-headed whales underwater.