BEHAVIOUR OF PINNIPEDS

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Deane Renouf

Chapman and Hall
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Pinniped mating systems on land, ice and in the water: Emphasis on the Phocidae

Burney J. Le Boeuf

Dunnocks, Prunella modularis, are small brown passerines that exhibit an extremely variable mating system. The mating system of a population of 90 breeders, studied by Nicolas Davies and collaborators in the Cambridge University Botanic Garden, consists of several mating combinations (Davies, 1983, 1985; Davies and Lundberg, 1984, 1985). These can be viewed as different degrees of female monopolization by males varying in increasing order of male reproductive success (RS), from:

<table>
<thead>
<tr>
<th>Male RS</th>
<th>Female RS</th>
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<td>shared access to one female (polyandry)</td>
<td>sole access to several females (polygyny)</td>
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<tr>
<td>sole access to one female (monogamy)</td>
<td>shared access to several females (polygynandry)</td>
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Male RS increases to a high with polygyny; female RS increases to a high with polyandry. Clearly, there is sexual conflict. Males are selected to be polygynous (access to several mates); females polyandrous (shared male parental care). Davies and Lundberg (1984) show that the main factor influencing the ability of male dunnocks to monopolize females is female range size which, in turn, is determined by food distribution. Where food is sparse, female range is large and it is difficult for one male to monopolize a female (hence polyandry). When food is densely distributed, female ranges are smaller and it is easier for a male to defend a female alone (monogamy) or even to defend several females at once, either alone (polygyny) or with another male (polygynandry).

What does this bird tell us about mating systems in seals, sea lions, fur seals and walruses or in terrestrial mammals? Despite large
discrepancies in size, habitat, life styles and genetic relatedness, the following generalizations from this study of a hedge sparrow apply to pinnipeds.

1. Mating systems are not fixed attributes of populations or species (see also Lott, 1984). Mating systems are not inherited and they are not the same because of a common ancestor. Mating systems in birds and seals may be similar despite their distant relationship.

2. The two sexes are in conflict, being under selection pressure to seek different mating arrangements. Males maximize their RS by seeking more mates and females maximize their RS by successfully rearing young that have been produced and, when possible, obtaining as much assistance as possible from mates.

3. Female distribution determines to a great extent the degree to which males can obtain multiple mates, i.e. the degree of polygyny that develops.

4. The distribution of females results from the self-interest of individual females and is associated closely with resources necessary for producing and rearing the young (e.g. food distribution, nest or parturition sites). Female fecundity is limited by energetics.

5. The observed mating system reflects the outcome of sexual conflict and the arrangement that is advantageous to the sex with the momentary advantage. Which sex predominates and the mating system that results is determined by several interacting variables that set the stage for mating. These include phylogenetic inertia in reproductive physiology, physical factors such as weather, temperature and substrate, ecological factors such as predators and resources (food, nesting or parturition sites), and social factors such as the operational sex ratio, density and behaviour of the other sex.

In the cursory analysis and speculations that follow, I stress on the costs and benefits involved for each sex and the element of sexual conflict inherent in sexual reproduction between two genotypes. This approach provides a framework for understanding what we observe and enables us to make predictions for what we have not yet observed.

My aim is to compare pinniped mating systems, especially those of phocids, with those of terrestrial mammals without producing an exhaustive review. The literature on pinnipeds is of two kinds. We know a great deal about some species and virtually nothing about others. I summarize mating systems in well-studied terrestrial mammals and compare these systems to those observed in social pinnipeds. I speculate about possible mating systems in those pinnipeds about which we know little. In comparing pinnipeds with terrestrial mammals, I ask the questions: What do we expect to find? What do we observe? What are the principal determinants of what we observe? Do pinnipeds have unique features that influence the form
What do we expect in pinnipeds and other mammals? What are the consequences of mating in water or on land?

Mating systems have been defined and categorized in a number of ways (e.g. Crook, 1965; Selander, 1965, 1972). Agreement is not universal and this has led to confusion. All treatments emphasize the number of mates that one sex can accumulate. I follow Emlen and Oring (1977) in emphasizing ecological and behavioural potential to monopolize mates and the manner in which this is done. As they point out, the mating system of a population refers to the general behavioural strategy employed in obtaining mates. It encompasses features such as: (1) number of mates acquired; (2) manner of mate acquisition; (3) presence and characteristics of any pair bonds; and (4) patterns of parental care provided by each sex. Generally, three basic types are distinguished: polygyny, monogamy and polyandry. The forms that each takes varies considerably as well as the particular set of forces that shape the mating system. I exclude promiscuity (copulation with more than one member of the opposite sex) as a category because the RS of pinniped females does not vary with the number of sexual liaisons. Females are inseminated by only one male regardless of how often they copulate.

It is useful to distinguish degrees of polygyny, especially in comparing pinniped species. This can be done with measures of mating success such as the number of females with whom a male mates during a breeding season (variance in male mating success) or with a cruder estimate, the number of females with whom a male is associated during the breeding season (harem size; see, for example, Alexander et al., 1979). In this chapter, I define slight polygyny as the case when a male mates with 2–5 females, moderate polygyny refers to the case when a male mates with 6–15 females, and extreme polygyny obtains when a male mates with 16–100 or more females during a breeding season.

2.1 WHAT DO WE EXPECT IN PINNIPEDS AND OTHER MAMMALS?

The phylogenetic history of each animal group introduces bias and sets limits on the mating strategy of each sex. Mammals are predisposed to polygyny because of internal fertilization, gestation and lactation in the female. The unique mother-young relationship is critical for the survival and development of the young; the physiology of reproduction dictates a minor role for males in the care of offspring because males cannot nurse. Gestation and lactation saddle females with all or most of the parenting, commit her to a particular reproductive strategy and free the male to philander. Female mammals cannot produce and rear offspring at the rate that males can father
them. Consequently, females and males maximize their RS in quite different ways; females are limited by the number of young produced and raised, males are constrained by the number of females fertilized. Females are the limiting sex and males the limited sex (Trivers, 1972; Maynard Smith, 1977).

In contrast to mammals, the differences between the sexes among birds is small. After egg laying, males are equally adept at investing in the offspring as females. Consequently, the route to monogamy and polyandry is far easier in birds. Monogamy is found in over 90% of bird species, followed in frequency by polygyny and polyandry (Lack, 1968; Selander, 1972). However, recent studies on extra-pair copulation show that birds are not as monogamous as they appear (e.g. Burke et al., 1989; Westneat, 1987).

### 2.2 WHAT DO WE FIND IN MAMMALS?

Polygyny is the most commonly observed mating system in mammals (Trivers, 1972; Alcock, 1984). This includes most ungulates, rodents, primates and carnivores. Harem or female defence, where female groups are defended by a single male, is common. This is characteristic of patas monkeys, *Erythrocebus patas* (Hall, 1968), North American elk, *Cervus canadensis* (Altmann, 1956; Franklin et al., 1975), peccaries, *Pecari angulatus* (Sowls, 1974), horses, Equidae (Tyler, 1972), and some bats, Chiroptera (Bradbury and Vehrencamp, 1977). Equally prevalent is resource defence, where males defend habitat configurations in which females find better foraging or safety from predators, e.g. male pronghorn antelope defend areas containing water holes and high-quality grazing sites (Kitchen, 1974) and male marmots defend overwintering sites important for females (Downhower and Armitage, 1971). Male dominance polygyny (lekking), in which males display in traditional areas and females come to them to mate, is a rare form of polygyny in mammals that has been recorded in several African ungulates such as the Uganda kob (Leuthold, 1977). Lekking is much more common in birds (Payne, 1984). In many solitary species of rodents and felids, males leave their territories to find females in oestrus and the dominant males achieve the most copulations (Eisenberg, 1966).

Monogamy is rare, comprising only about 3% of all mammals (Kleiman, 1977). The exceptions include a number of terrestrial carnivores where males help feed pups and female RS is reduced without male parental investment, e.g. wolves, coyotes, foxes, African wild dogs, badgers, dwarf mongooses and several viverrids (MacDonald, 1983). Females in these groups prevent subordinate females from breeding, thus preserving monogamy. About 14% of
primate species, mostly nocturnal species that live in forests, are monogamous (Rutberg, 1983). Tamirins and marmosets, Callithricoidea, form social groups to defend territories but only the dominant male and dominant female breed; subordinates are prevented from breeding as in social carnivores (Rothe, 1975; Dawson, 1976). Males of these groups carry young (Clutton-Brock and Harvey, 1976). Monogamy occurs in a few ungulates that live in the open and rely on each other to detect predators (e.g. klipspringer (Oreotragus oreotragus), Kirk’s dik dik (Madoqua kirkii), oribi (Ourebia ourebia), southern reedbuck (Redunca) and among ungulates that live in dense cover or rely on concealment to escape predators (e.g. dik dik (M. phillipsi)). Monogamy is expected when both sexes must invest in offspring to ensure their survival and when environmental or social conditions discourage mate dissertation (Wittenberger, 1981).

2.2.1 Land-breeding pinnipeds

Extreme polygyny is characteristic of nearly all land-breeding pinnipeds (Nutting, 1891; Bertram, 1940; McLaren, 1967; Bartholomew, 1970; Stirling, 1975; Le Boeuf, 1986b). This includes all of the sea lions and fur seals, the two species of elephant seals, Mirounga, and the grey seal, Halichoerus grypus. This conclusion is inferred from behavioural observations (mating success) and the ratio of males to females on rookeries (e.g. Alexander et al., 1979). There are fewer sexually active males than fertilizable females at any given time during the breeding season, i.e. relatively few males monopolize mating. In northern elephant seals, M. angustirostris, the variance in lifetime reproductive success is estimated to be four times greater among males than females (Le Boeuf and Reiter, 1988), a measure reflecting the intensity of sexual selection acting on males (Wade and Arnold, 1980). Comparable figures are expected of northern fur seals, Callorhinus ursinus (Bartholomew and Hoel, 1953), and several other otariids because of their similar mating systems. The red deer (Cervus elephus) on Rhum, studied by Clutton-Brock et al., (1982) exhibit a similar degree of polygyny.

Female pinnipeds aggregate on beaches, rocky shelves, caves or flat areas on islands in groups numbering from a few individuals to over 1000 individuals. Mating occurs principally on land as opposed to in the water in most of these species. Polygyny takes two principal forms when viewed from the male perspective: (1) female or harem defence as in elephant seals (males fight for social status in a dominance hierarchy that confers priority of access to grouped females); and (2) resource defence - males compete for territories that include parturition sites and in some species, nursery sites, needed by females, e.g. Steller’s sea lion, Eumetopias jubatus, and northern fur
Pinniped mating systems: Phocidae

seals (Gentry, 1970; Bartholomew and Hoel, 1953). Resource defence polygyny takes on aspects of male dominance polygyny if one emphasizes the female's point of view, i.e. the female may be choosing among territories and male territorial holders determined by dominance relationships among males, e.g., California sea lions, *Zalophus californianus* (Heath, 1985; Heath and Francis, 1983). In either case, polygyny among most pinnipeds that breed on land is extreme.

Circumstantial evidence and behavioural observations suggest that two species, the walrus, *Odobenus rosmarus*, and Weddell seal, *Leptonychotes weddelli*, are moderately polygynous. Both mate in the water, which makes them difficult to observe and the hypothesis difficult to confirm. Female walruses in the Bearing Sea congregate in groups on ice floes. Males display in the water on the perimeter of these floes competing with each other to attract receptive females (Fay et al., 1984). This resembles the strategy of lekking birds, that of a male gaining multiple mates by attracting females to him (Payne, 1984). Leks are observed in birds and mammals when males cannot hold females directly or defend a resource needed by them (Bradbury, 1981). Atlantic walruses in the central Canadian High Arctic exhibit a mating system which more closely resembles female defence polygyny (Sjare, 1989). Male Weddell seals are thought to hold underwater territories (literally, maritories) near breathing holes used by females (Ray, 1967; Cline et al., 1971; Kaufman et al., 1975; Siniff et al., 1977; Wartzok et al., 1989). It is not clear whether males intercept and detain females moving through these areas or whether females shop for the most 'attractive' male on her way to forage, i.e. which sex is in control. A similar arrangement may occur in harp seals, *Phoca groenlandica*, near leads in the ice where females haul out.

### 2.2.2 Ice-breeding and water-breeding seals

Little is known about the remaining phocids that mate in the water or on ice. This category includes all of the pagophilic phocids: harp, ringed (*Phoca hispida*), ribbon (*P. fasciata*), bearded (*Erignathus barbatus*), hooded (*Cystophora cristata*), Baikal (*P. sibirica*), Caspian (*P. caspica*), and larga seal (*P. largha*) in the northern hemisphere and Ross (*Ommatophoca rossi*), leopard (*Hydrurga leptonyx*) and crabeater seal (*Lobodon carcinophagus*) in the southern hemisphere, plus the monk seals (*Monachus monachus* and *M. schauinslandi*) that mate in temperate waters and the harbour seal (*P. vitulina*), that mates in the water near land or ice. The spatial organization of most of these animals suggests slight polygyny or facultative monogamy, e.g. hooded seals (Kovacs, 1989). Females of species that breed on
The distribution of females and degree of polygyny

The distribution of females and degree of polygyny

pack ice are widely distributed from each other and appear in solitary pairs of a female and her pup, or in triads consisting of male, female and her pup, e.g. crabeaters, leopards, Ross, bearded and hooded seals. In some species [e.g. crabeaters, hooded seals], a male appears to attend a female and her pup on an ice floe until she becomes receptive and then departs after copulation, perhaps to attend another female (Siniff et al., 1979; Kovacs, 1989). It is not clear how males or females acquire mates or the extent to which some males obtain multiple mates. The monk seals and harbour seals copulate in the water and are more gregarious but little is known about their mating arrangements. The solitary distribution of females leads to the suspicion that slight polygyny occurs in all of these species. Defence of one female, monogamy, is expected to develop when resources required by females are not economically defensible and the sex ratio is skewed to excess males as in some shrimp, wood roaches, frogs in which males hold onto the female’s back, some migratory ducks and some songbirds (see Wittenberger, 1981 for review). But as is typical of mammals, the sex ratio in solitary seals is probably skewed the other way and females outnumber males (Rasmussen, 1952; Oitsland and Benjaminsen, 1975; Siniff et al., 1977; Helle, 1980) or it is equal (Smith, 1973a; Oritsland and Benjaminsen, 1975). In all likelihood, male seals of solitary species desert females after copulation then try to pair with another pre-oestrous female (see Kovacs, 1989). In this way, a male might copulate with 2-5 females and the mating system would be characterized as slightly polygynous. In seals, even when a male pairs with only one female or a few of them during a breeding season, there is no evidence that males invest in the offspring in any way as is the case in some primates and terrestrial carnivores.

2.3 WHAT DETERMINES THE DISTRIBUTION OF FEMALES AND THE DEGREE OF POLYGYNY?

In some birds and mammals the distribution of females (clumped or not clumped) is largely determined by food [or predators] and male distribution is determined by the distribution of females (Orians, 1969). For example, in long-billed marsh wrens, *Telmatodytes palustris*, females choose territories according to the richness of the food even if this means sharing a male with other females (Verner, 1964; Verner and Willson, 1966; Verner and Engelsen, 1970). Females choose to join other females on a rich territory defended by a male rather than mate alone with a male on an inferior territory. Here, clumping and the mating system (monogamy, bigamy, trigamy) is a function of food resources for the female; reproductive success
correlates with richness of the territory. Polygynous females on productive areas enjoy greater reproductive success than monogamous ones.

Macdonald (1983) argues that resource (particularly food) distribution is fundamental to the spacing and structure of social carnivores in that it sets limits to the group and territory size within which other combinations of selective pressures operate. Grouping in some terrestrial carnivores is associated with: (1) need for assistance in hunting and killing large prey (e.g. wolves that eat large dangerous quarry as opposed to red foxes that hunt singly and eat small food items); (2) need for defence against attacks by other predators. Mongooses live in packs for the increased vigilance provided against marauding predators and the potential for intimidating predators (Rasa, 1977). Opportunities to learn from the experiences of other group members, division of labour, care of the sick and several advantages associated with allopastoral care also play a role. Among less social carnivores, the spatial organization of females is determined by food distribution and that of males by the distribution of females, e.g., where several female territories are encompassed in one male territory (bobcat [Lynx rufus], wolverine [Gulo gulo], stoat [Mustela]).

Resources and avoidance of predators also make grouping advantageous in many well-studied ungulates and primates. Ungulates like wildebeest, Connchaetes taurinus, and gazelles, Gazella, that feed in the open, form groups for defence against large carnivores (Estes, 1967, Walther, 1965); hamadryas baboons (Papio hamadryas) form small groups for foraging and larger groups on hillsides at night for increased vigilance against predators (Kummer, 1968, 1971).

Among some pinnipeds, females appear to determine the general mating system in that polygyny varies with the degree of female clumping and oestrus synchrony (see Boness, this volume). Stirling (1975) summarized the relationship between size of female groups and substrate and ecological factors. Female clumping is associated with breeding on islands but not with breeding on ice, except where there is a need to maintain breathing holes (Weddell) or possibly to exploit a patchy resource (walrus). The hypothesis is that females clump on islands because of several advantages offered by terrain or substrate: (1) parturition sites and nurseries for rearing pups; (2) no terrestrial carnivore predators (a necessity when animals are adapted for swimming and not for running); and (3) proximity to food. The latter is necessary to cut commuting costs in lactating sea lions and fur seals that make feeding excursions from the rookery (Costa, this volume). Proximity to food may also help ease the transition of phocid young from reliance on mother's milk to feeding on their own. But islands are limited, especially in some parts of the Pacific, as are suitable beaches on islands, and females must group to get
The distribution of females and degree of polygyny

these benefits. There must also be additional factors causing clumping because females do not spread out from each other as much as they might even when space is abundant. Rather, they cluster tightly. This was evident when northern elephant seals began recolonizing San Miguel, San Nicolas and Año Nuevo Islands during the 1960s (Le Boeuf, 1972) and similar observations have been recorded for otariids (see Boness, this volume). Another factor in some species is that males intensify the clumping of females. In competing for females that gather loosely in one place, males of some species harass females by their repeated mating attempts and force them to clump closer together for self-protection. In northern elephant seals, a female that remains apart from a female group is accosted repeatedly by males and runs a higher risk of injury. Every breeding season, at least one out of every thousand females on the Año Nuevo rookery is killed by a male during a mating attempt (Le Boeuf, 1981; Le Boeuf & Mesnick, in press). In South American sea lions, *Otaria flavescens*, most females that give birth early in the season before a female group has formed become separated from their pups. One male claims the female and another the pup. They cannot approach each other and eventually, the pup dies from starvation (Campagna et al., 1988).

Female resources, such as food and parturition sites, coupled with lack of predation may determine initial distribution in island breeding pinnipeds as primary factors before other factors become important. However, we know little about where pinnipeds get food, its availability and the cost of getting it. Work in progress using time-depth recorders, doubly labelled water techniques to estimate energetic costs at sea, transmitters and satellite tracking to determine location of feeding in relation to bathometry and other variables, is promising (Davis et al., 1983; Gentry and Kooyman, 1986; Le Boeuf et al., 1986, 1988, 1989; Kooyman et al., 1982; Croxall et al., 1985; and see Chapter 6).

Pinnipeds are not found in large groups on expansive ice habitats (Smirnov, 1927; Burns, 1970; Fay, 1974; Burns et al., 1981; Stirling, 1975). The environmental potential for polygamy is low because females are not forced to clump and there is no need for them to clump together (Emlen and Oring, 1977). *A priori*, a female gets little from joining other females. Clutton-Brock and Harvey (1976), writing about mammals in general, state: ‘The advantages to a female of maintaining mating access to several males will in almost all circumstances, be less than the advantages to a male of maintaining mating access to several females’. Perhaps the most important impetus for not clumping on ice is that females find their food resources directly under it. Seals evolved on the ice edge; the waters under pack ice are evidently rich and continue to be exploited by several species. Females disperse widely to feed along the ice edge. There appears to
be no reason to avoid giving birth and copulating close to where feeding occurs. The female is supporting a fetus and it seems safe to assume that it is good to feed up to the point of giving birth. Under these circumstances, the onus is on the male to find females, which they do quite well. The fecundity rate is as high in females that breed in isolation on ice as it is in gregarious island-breeding pinnipeds: 85-94% in harp seals (Bowen et al., 1981), 85% in bearded seals (Burns, 1967, 1981; Burns and Eley, 1978), 80% in Weddell seals (Stirling, 1971), 80-95% in ringed seals (McLaren, 1958; Smith, 1973a) versus 85-94% in grey seals (Mansfield and Beck, 1977; Harwood and Prime, 1978), 82.5-88% in southern elephant seals (Mirounga leonina) (Laws, 1956, 1960), 95% in northern elephant seals (Le Boeuf, 1979) and 90% in northern fur seals (Lander, 1981; Smith and Polacheck, 1981). The leopard seal may have an exceptionally low pregnancy rate (Siniff, 1981), but this observation is based on little data. Evidently, male distribution follows that of females.

2.4 **DO THE UNIQUE FEATURES OF PINNIPEDS GIVE AN ADVANTAGE TO ONE SEX AND AFFECT THE FORM THAT MATING SYSTEMS TAKE?**

Pinnipeds differ from land mammals in having a body type adapted to swimming and diving and, for at least some, in being able to copulate in the water. The marine-adapted body makes them vulnerable to attack by fleet-footed terrestrial predators which may explain why most of them stay close to the safety of the water. In addition, their insulation against the cold marine environment makes them prone to overheating on land, making it prudent to remain close to haul-out points. These morphological features make grouping more likely on islands than on ice because there are few terrestrial predators on ice (polar bears in the Arctic are one exception) and overheating is no problem because temperatures are low (Bartholomew, 1970).

In what way does the water medium shape the social fabric of reproduction in pinnipeds? The pagophilic phocids that are widely distributed on ice are thought to copulate in the water (Oritsland, 1964; Stirling, 1975, 1983; Merdsoy et al., 1976). This conclusion is typically the result of not seeing copulation on ice, or from seeing it only rarely, e.g. harp seals (Kovacs, 1985). Indeed, many investigators that have studied these seals on ice for years have never seen a copulation above or below the water, (e.g. Don Bowen, John Burns, Kathy Frost, David Lavigne, Lloyd Lowry, and Ian Stirling, pers. comms). The only direct observation of copulation was in the underwater study of Merdsoy et al. (1976). For all the hours spent observing Weddell seals in the Antarctic, only one copulation, in the water,
has been recorded and reported [Cline et al., 1971]. Because of the aggressive courtship of males on ice floes, Siniff et al. (1979) concluded that the crabeater seal copulates on ice, but they never witnessed it. The capacity, if not the inclination, is there, for some seals will copulate on ice when conditions dictate, e.g. harp and hooded seals copulate above water when the ice freezes over [Oritsland, 1964; Sergeant, 1965; Popov, 1966]. When copulation has not been observed and it is not known whether mating occurs on the surface or under water, one can only speculate about mating systems. The circumstances on ice may bear little relationship to what is going on below in the water. Phrases that crop up in the literature such as 'mating takes place on ice', 'a monogamously breeding species', 'pairs last until mating', and 'appears polygynous', must be interpreted with caution.

Copulation usually occurs on land in pinnipeds that give birth on islands [Bartholomew, 1970; Stirling, 1975] however: (1) harbour seals and monk seals are an exception [Venables and Venables, 1957; Kenyon and Rice, 1959; Johnson and Johnson, 1978; Allen, 1984]; (2) California sea lions mate in the water in the high temperatures of the Gulf of California and predominantly on land at major rookeries in southern California [Peterson and Bartholomew, 1967; Heath and Francis, 1983; Heath, 1985]; (3) in all species, copulation in the water is possible and in many, occurs at low frequencies, e.g. less than 5% of copulations observed in northern elephant seals and northern fur seals [Le Boeuf, 1972; Bartholomew and Hoel, 1953].

Which sex determines where mating takes place and which benefits from mating on land or in the water? We lack data for mating on ice and in the water but a logical analysis by sex is instructive. A logical hypothesis derived from observations of terrestrial mammals is that females determine the location of copulation. Mating on land is advantageous to males seeking multiple mates but only occurs if females also benefit. When mating on land is not beneficial to females, mating will occur in the water because females can more readily determine whether copulation occurs and with whom.

Males increase their RS by obtaining multiple mates and, consequently, they are expected to take them where they find them. The more females aggregate, the easier the males' task. If females are grouped on land, a male will attempt to prevent other males from gaining access to them and he will copulate with as many as possible. This may involve fasting and never leaving his post, not being so aggressive as to cause females to run away or cross to another territory [cf. ungulates and birds on leks], defending his boundaries against other males, conserving energy and attracting the female to him, stealing females from adjacent males' territories or, more
infrequently, forcing copulation with an uncooperative female. Land
is the male's element for this strategy. As far as we know, females
do not group in the water [with exceptions like rafts of sea lions] and
the three-dimensional environment makes it easier for females to
escape.

Females require energy to produce and raise 'pups. Males do not
help in this regard; they contribute only a small quantity of sperm to
get the process started. Since a female's pup gets half of its genetic
complement from the male, it is advantageous for the female to
choose the 'best' sire. She should mate with a male of 'demonstrated
fitness', a male with 'superior genes' wherever she finds him or he
finds her (Selander, 1972; Trivers, 1972). The selection pressure is on
getting the best genes, and the location of mating should serve this
end for the female unless the decision is forced on her. I do not agree
with Stirling (1983) that the location of mating is a legacy of
ancestral forms and hence selectively neutral. Phylogenetic inertia
may explain parental investment patterns in mammals, and other
conservative deep-seated physiological designs, but location of
mating strikes me as a most malleable behaviour, one that each sex
might use to its advantage. For similar reasons, I part from Bartholo-
mew (1970) who has reasoned that terrestrial copulations are
explained by the fact that females stay on land until they come into
oestrus. Females of some species do and others do not [e.g. Zalophus,
Arctocephalus pusillus]. His conclusion implies that the female is a
passive vessel for endocrines that dictate her behaviour and that she
is not under selective pressure to mate where it is most advantageous
for her to do so.

On islands, female sea lions and fur seals select parturition sites
where males are defending territories. In a sense, males provide a
relatively undisturbed place for females to give birth and nurse.
These males are adults that have bested their rivals, which is an
indication of fitness. Females should mate with these males and do.
Similar logic holds for mating with high-ranking elephant seal males.
Male-male competition gives females information about which
males are most fit. Copulation on land versus water is incidental to
the main issue, which is that females should maximize their repro-
ductive success. On land, the interests of females and successful
males coincide. The 'victorious' males are eager to mate [being
selected to pass on their genes] and these are the best partners for
females who may be more apt to spread their genes if their male
progeny have similar traits as their fathers.

If males are not competing amongst themselves on land or ice, a
female does not benefit by mating out of the water. There is no a
priori reason for a female that gives birth alone on the ice to mate
with the first male that simply attends her. He may have a deleterious
gene that will strike him dead before he reaches his prime and that might be passed on to her offspring. At minimum, she should mate with an adult who has passed this test. It would be better still to let all males in the vicinity know that she is ready, cause them to compete on some arbitrary basis and mate with the winner. Inciting male-male competition is a common female strategy for identifying fit mates in many terrestrial mammals, birds and reptiles (Cox and Le Boeuf, 1977). The solitary female does not have much latitude for choice on ice. She may have more control in the water where she can get away from an unwanted suitor more easily, solicit specific males, incite several males to compete and mate with the winner, visit displaying males or males defending food-rich maritories. Logic predicts that the attending male will try to keep the female on ice or copulate with her before she goes into the water where there are other competing males. If mating occurs in the water, the behaviour of females is expected to influence the mating strategies of males.

2.5 WHAT ARE THE CONSEQUENCES OF MATING ON LAND VERSUS IN THE WATER?

Sexual size dimorphism with males being larger is a consequence of harem defence, resource defence and male dominance polygyny in terrestrial mammals and all pinnipeds breeding on land. This is because of sexual selection; great size gives males an edge in fighting, which leads to access to females. Phocids that live in close association with ice or breed aquatically lack sexual size dimorphism. This is not necessarily because polygyny does not exist in these species. Sexual selection may be intense among pinnipeds mating under water but, because of the different medium, the consequences are different and may not be reflected in size. We do not know the male mating strategies under water but size is probably not as important in winning fights as it is on land. For example, to defend an underwater territory, swimming speed, agility, or the ability to dive for long periods may be more crucial.

If attracting a female separates successful from unsuccessful males, loudness or persistence of calls may be selectively advantageous. Bearded seals, harp seals, Ross seals, Weddell seals, walruses and California sea lions are extremely vocal under water (Schell and Watkins, 1965; Ray and Schell, 1967; Schusterman, 1967; Poulter, 1968; Schusterman and Balliet, 1969; Ray et al., 1969; Ray, 1967; Mohl et al., 1975; Thomas, 1979; Ray, 1981). Sex differences in calls are evident in several species. For example, only the male bearded seals sing during the breeding season (Ray et al., 1969). Among Weddell seals, both sexes share a number of calls but trills, knocks,
cricket calls, ‘eeyoo and guttural glugs’ are unique to males (Thomas, 1979). The vocal component of male walruses’ soliciting females to approach them in the water has been noted (Schervill et al., 1966; Ray and Watkins, 1975; Sjare, 1989). One explanation for the extremely vocal behaviour of male California sea lions in air (Peterson and Bartholomew, 1969) and under water (Schusterman, 1967) comes from recent observations of oestrous females moving across territories to solicit a particular male (Heath, 1985). Incessant vocalizing in air and under water would be a way of getting the female’s attention as well as letting other males know that the territory is being patrolled. Auditory and visual displays may signal more than adulthood and readiness to mate: the behaviour may serve as an indicator of health and vigour. It takes energy to emit complex, high intensity calls or evolve elaborate colourful visual displays. Parasites may limit the extent of such signalling thereby providing females with a cue to male fitness. According to Hamilton and Zuk (1982), females would be favoured who could discriminate among males according to parasite load and damage. They present supportive evidence on some birds but no one has tested this hypothesis with seals. This may be one purpose of the elaborate, stereotyped bladder nose and blood-red septum displays of male hooded seals, (Berland, 1965] that are given in air and under water or the ribbon markings on ribbon seals that are darker in males than females (Burns, 1981).

Are females choosing among these singing and displaying seals under water? How do mating arrangements differ in seals that are migrating or borne passively on floating ice from those that are more stationary or that feed on the bottom like bearded seals? What are the optimal mating strategies for males under water? They might set up territories near places where females gather. They might intercept the females, hold them, attract them with sound, visual displays, or resources, or they could get to a female first and stay with her.

2.6 CONCLUSIONS

Mating systems in pinnipeds, like those of terrestrial mammals and birds, are determined by two classes of phenomena: phylogenetic inertia in parental investment pattern that sets limits on the reproductive strategies of each sex, and environmental variables that affect the optimal way for each sex to behave in order to maximize their reproductive success. The latter include physical variables like the substrate and temperature, ecological variables like food, predators and birthing sites, and social variables like density, the sex ratio and what the other sex is doing.

Pinnipeds follow the mammalian rule of polygyny more closely
than terrestrial mammals. Monogamy of the type seen in terrestrial carnivores, and primates, where males help females feed, protect or carry offspring, is absent. The mating system of pinnipeds is least like those of social canids –, animals with whom they share a recent common ancestor. Perhaps this is because food is distributed differently in the sea and may be less limiting, the prey are smaller than the predators, the female can rear her precocial young alone, and this frees males to pursue multiple matings. All pinniped species appear to be polygynous but the degree varies considerably from extreme to moderate to perhaps slight. Slight polygyny is suspected in pagophilic seals from their distribution patterns but mating is almost exclusively under water and, consequently, we are ignorant of the frequency and nature of mating arrangements. Most island breeding pinnipeds show a higher degree of polygyny than terrestrial mammals and birds, and in those pinnipeds that are sexually dimorphic the size discrepancy between the sexes exceeds that seen in terrestrial mammals.

The distribution of female pinnipeds, like that of terrestrial mammals, may be determined in a general way by resources and predators. The circumstances that lead to females aggregating are more varied among terrestrial mammals than among pinnipeds. Male mating strategies intensify female clumping in some pinnipeds. Male distribution follows female distribution.

Mating in the water may give an element of control to females that is lacking in their terrestrial counterparts. Aquatic mating selects for different male mating strategies and secondary sexual characteristics than those associated with terrestrial mating. Speculations about the underwater mating strategies and behaviour of pinnipeds need to be studied.

REFERENCES


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