CHAPTER 11

PROTECTION AND ABUSE OF YOUNG IN PINNIPEDS

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ABSTRACT

The aim of this paper is to describe nurturing and abusive behavior to young in selected species of two families of pinnipeds, the phocids and otariids, attempt to explain the phenomena observed from a functional or proximal perspective, and compare the behaviors seen in pinnipeds to those observed in other large mammals. We focus on the most thoroughly studied species, such as the elephant seals, Mirounga angustirostris, and M. leonina, and the southern sea lion, Otaria byronia, and incorporate observations from other species when possible.

I. NATURAL HISTORY OVERVIEW

A brief review of the social systems and context in which young pinnipeds are produced and reared helps in understanding the treatment of young by adults of both sexes.

All 15 species of eared seals or, Otariidae, the sea lions and fur seals, are polygynous and sexually dimorphic with males being larger than females (King, 1983; Riedman, 1990). Adult males of all species are territorial, defending terrestrial or aquatic areas containing females and their pups...
against other males. All mating and nursing of young occurs on territories. Non-territorial males, most of whom are younger, group together in the general vicinity of territories. The 19 species of phocids, or true seals, vary from moderate polygyny to extreme polygyny, from reversed dimorphism with the female being larger, to monomorphism, to extreme sexual dimorphism with males being larger. Breeding on pack or fast ice is associated with small “family” groups (a female and her pup attended by a male), monomorphism, and a low level of polygyny. In the more social and polygynous species, such as elephant seals, males compete in dominance hierarchies. As a rule, nursing females are less often disturbed by male behavior in territories than when males compete in a dominance hierarchy. In the former, only one male moves among the females and their pups, while in the latter male traffic is great and a threat to female and pup safety. The walrus, Odobenus rosmarus, breeds in small social groups on floating ice (Fay 1982). Males are larger than females and the species appears to be moderately polygynous; the mating system around an ice floe where estrous females gather resembles a lek. Males make vocal and visual displays in the water to attract estrous females.

With respect to protection and nurturance, the mother does everything and the males do nothing in all species. Females give birth to a single pup annually in all species except the walrus, and the Australian sea lion, Neophoca cinerea, where the time between births exceeds one year (Marlow, 1975). Gestation lasts less than a year in all species except the walrus; gestation in this species lasts 15-16 months (Fay, 1982).

There are many differences in the lactation pattern of phocids and otariids (Costa, 1990; see Table 1) and these have important implications for pup health and safety. Lactation is distributed from four months to over a year among the eared seals (Gentry et al., 1986). After giving birth, a female nurses her pup for about one week then goes to sea to feed for 2-7 days. For the next few months the mother alternates nursing the pup on land for about two days with feeding trips to sea that last less than seven days. When the pup is about four months old, the pair may leave the rookery and forage together until the following year when most females wean their pups just before giving birth again. In some species (Galapagos fur seal, Arctocephalus galapagoensis, Gentry et al., 1986, and Steller sea lion, Eumetopias jubatus, Pitcher and Calkins, 1981), intermittent suckling may last up to three years. In contrast, lactation is concentrated into a brief period among phocids, lasting only four days in hooded seals, Cystophora cristata, and up to six weeks in weddell seals, Leptonychotes weddelli, and the Hawaiian monk seals, Monachus schauinslandi. The brevity of the nursing period of phocids is made possible by fasting. In several well
Table 1. Differences in the nursing pattern and maternal behavior of seals (phocids) and sea lions (otariids). Source: see references in text.

<table>
<thead>
<tr>
<th></th>
<th>Seals</th>
<th>Sea Lions</th>
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<tr>
<td><strong>Nursing</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Periodicity</td>
<td>Concentrated</td>
<td>Distributed</td>
</tr>
<tr>
<td></td>
<td>(nurse daily while fasting)</td>
<td>(nurse 2 days, forage 2–7 days)</td>
</tr>
<tr>
<td>Duration</td>
<td>4–45 days</td>
<td>4 mo. to 1 year</td>
</tr>
<tr>
<td>Weaning</td>
<td>abrupt</td>
<td>gradual</td>
</tr>
<tr>
<td>Pup recognition</td>
<td>poor</td>
<td>good</td>
</tr>
<tr>
<td>Adoption</td>
<td>common</td>
<td>rare</td>
</tr>
<tr>
<td>Milk stealing</td>
<td>common</td>
<td>rare</td>
</tr>
</tbody>
</table>

studied species, females fast completely while nursing, remaining on land with their pups feeding them daily from body reserves (Le Boeuf et al., 1972; Reiter et al., 1981).

Because phocids are capable of storing all energy that is required for the entire lactation period and otariids must feed during the lactation interval, mother-pup behavior in the two families differs. Phocid mothers remain near their pups and provide protection for them until weaning. On dangerous shifting pack ice, the best thing a hooded seal mother can do is to provide her pup with fat-rich milk and wean it quickly before the ice breaks up and endangers them. Elephant seal pups that become separated from their mothers during the 4-week nursing period may starve because reunions are unlikely due to the crowded conditions in many harems and the fact that individual recognition is poorly developed in both the mother and the pup (Petrinovich, 1974). Without a source of milk, the neonate dies. It may steal milk from other mothers but this is dangerous. Since all milk is derived from the mother’s body stores (Ortiz et al., 1984; Costa et al., 1986), a mother that allows an alien pup to suckle is “taking food out of the mouth” of her own pup. Most females viciously attack alien milk thieves (Le Boeuf and Briggs, 1977). Weaning is abrupt in most phocids. When the mother leaves, the pup is approximately 50% fat and in good physical condition but it is inexperienced socially, and alone, it must learn to cope with the environment and to make a living at sea.

In eared seals, the pup is left alone and is vulnerable when the mother goes to sea to feed; this becomes increasingly less important as the pup
matures. When the mother returns from a feeding trip, she calls and singles out her own pup from the rest. The keen recognition of the mothers for their own pups nearly eliminates milk stealing in these animals. Because the mother alternates feeding with nursing, she can modulate nutrient transfer according to her food intake. For example, in some species the mother transfers more milk to sons than daughters (Costa and Gentry, 1986), a behavior consistent with some predictions from sex ratio theory (e.g. Trivers and Willard, 1973; Maynard Smith, 1980; Le Boeuf et al., 1989). In the fall, mothers and pups depart the rookery together. It is assumed that the mother provides some protection to her pup from predators and perhaps, helps the pup to feed on its own. In any case, weaning is gradual and the pup begins to feed on its own months before it is weaned from mother’s milk.

II. PROTECTING AND NURTURING BEHAVIOR

In all social pinnipeds, one of the greatest threats to a pup is from neighboring females. Consequently, mothers spend much time protecting their pups against perceived threats. In most species, the movement of an individual female elicits threat vocalizations from neighbors. In Steller sea lions, mothers seek out a reasonably flat surface on the rocks out of the surf zone to give birth, but not too far away from the sea because surf spray provides relief from high temperatures (Gentry, 1970). These sites are in short supply and females compete aggressively for them. They vigorously attempt to keep other females at a distance shortly after birth. With time since parturition, they become increasingly tolerable of female neighbors. In elephant seals, the threat of a neighboring female to a mother’s pup is constant and real (Le Boeuf et al., 1972; Reiter et al., 1981; McCann, 1982). At any moment a neighbor may turn and bite her pup; bites to the head and nose may be severe and fatal. The older the mother, the larger her size, and the better she is at defending her pup; pups of the most aggressive mothers are least frequently injured (Christenson and Le Boeuf, 1978). The main concern of the elephant seal mother is to keep her pup near her and to adopt the suckling position when the pup calls to signal its hunger. Good mothers are responsive to the pup at all times. They call to their pups if they stray and they pursue them. Mothers are nearly helpless when a stampeding male tramples, crushes and comes to rest on her pup. Nevertheless, a female will bite and vocally threaten the offending bull, a behavior that has little effect on him and appears to be no more than a nuisance to him.
One of the most interesting nurturing behaviors in pinnipeds involves the permanent adoption or temporary fostering of an orphan or a neighboring pup (Riedman, 1982). This phenomenon is most widespread in the elephant seals, grey seals, Weddells seals, Hawaiian monk seals, and the walrus, all species that breed in moderate to large groups where mother-pup separations are frequent and give many opportunities for adoption (Riedman, 1990). D. Boness (pers. comm.) estimates that 25–75% of female grey seals engage in some form of fostering in certain rookeries. In one study of Weddell seals, 7.8 percent of the females in the sample nursed pups different from the ones with which they were first seen (Stirling, 1975). Among monk seals breeding in the Hawaiian leeward islands, the majority of mothers foster alien pups at some time (Johnson and Johnson, 1978, 1984; Alcorn, 1984; Boness, 1989). Fostering behavior has also been observed in eared seals, especially the Australian sea lion, and the Antarctic fur seal, A. gazella, but it is rare, perhaps owing to the fact that females have little difficulty recognizing their own pups.

Studies of northern elephant seals at Año Nuevo Island, California (Reiter et al., 1981; Riedman and Le Boeuf, 1982; Riedman, 1983), have revealed a variety of forms that fostering can take (Table II). Most cases of adoption involve females that have recently lost their own pups. Approximately 50% of these adopt a single pup and treat it as they would their own pup for the remainder of the nursing period, about 3–4 weeks. In most cases, the adopted orphan closely resembles the foster mother’s own lost pup in age. Just about every other possible combination occurs between a female that has lost her pup and an adoptee but in small frequencies. A female may adopt two pups, usually one in addition to her own, despite the fact that all but the largest females (Fedak et al., 1989) have only sufficient resources to feed one pup and wean it at the mean weaning mass (126 kg for females and 137 kg for males, Le Boeuf et al., 1989). A few females attract a crowd of 5–6 orphans by allowing all of them to nurse at will. In an apparent case of mistaken identity, some females aggressively compete to nurse a neighbor’s pup. After a few days of this, the neighbor usually acquiesces and the two females take turns nursing the pup. On occasion, a female who has just lost her pup will adopt as her own a pup that has just been weaned.

The key variable that affects the incidence of adoption and fostering among elephant seals in a given breeding season is the degree of mother-pup separation (Le Boeuf and Briggs, 1977). The latter varies as a function of the interaction of tides, storms and high surf, crowding, and whether the harem site offers high ground from which mothers and pup can retreat from high water. The frequency of permanent adoptions and temporary
fostering is a function of the number of orphans in the rookery. Since young females are most likely to lose their pups, it is young females that most frequently adopt and foster orphans. These chaotic times offer some pups the opportunity to obtain more milk than they would from their mothers alone. Pups that are nursed by two mothers reach a weaning mass that is twice that of normal weaned pups (Reiter, et al., 1978).

Among all pinnipeds, the incidence of fostering is highest among species where mother-pup separation is most frequent. This statement is supported by data from northern and southern elephant seals, grey seals (Anderson, 1979), Weddell seals (Kaufman et al., 1975), the walrus (Fay, 1982), and even in a few species of otariids (McCann, 1987). One exception to the rule is the Hawaiian monk seal, a species that breeds in small numbers on broad, sandy beaches where the possibility of mother-pup separation due to crowding is remote. Nevertheless, the incidence of fostering can be as high as 87% (Boness, 1989).

Aside from having the opportunity to foster pups, what explanations for the behavior have been used? On the proximal level, some instances of fostering behavior appear to be due to "reproductive errors", a situation where the female misdirects maternal behavior to an alien pup she mistakes for her own (Le Boeuf and Briggs, 1977). Two functional explanations address the benefits a female may derive by adopting. One pertains specifically to elephant seals and involves the continuance of the regular

Table II  The number of females exhibiting various types of fostering behavior on the Point Beach harem of Ano Nuevo Island during three breeding seasons. The number of adoption cases is in parentheses. Adapted from Riedman and Le Boeuf (1982).

<table>
<thead>
<tr>
<th>Fostering behavior</th>
<th>Frequency</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>1977</td>
</tr>
<tr>
<td>Female loses her own pup, then:</td>
<td></td>
</tr>
<tr>
<td>Adopts single pup</td>
<td>10</td>
</tr>
<tr>
<td>Adopts two pups</td>
<td>0</td>
</tr>
<tr>
<td>Adopts weaned pup</td>
<td>1</td>
</tr>
<tr>
<td>Adopts orphan with another female</td>
<td>(2)</td>
</tr>
<tr>
<td>Shares care of pup with its mother</td>
<td>5</td>
</tr>
<tr>
<td>Female nurses her own pup, and:</td>
<td></td>
</tr>
<tr>
<td>Adopts single pup</td>
<td>3</td>
</tr>
<tr>
<td>Adopts two pups</td>
<td>1(3)</td>
</tr>
</tbody>
</table>
reproductive cycle after losing a pup (Le Boeuf et al., 1972). It was observed that females that lost their pups and did not nurse, did not copulate and may have missed giving birth the following year. Hence, lactation may be necessary to induce ovulation. Females that lose a pup and adopt or nurse alien pups come into estrus, copulate, and give birth the next year. It is possible to test this hypothesis but it is difficult. The second explanation, which addresses adoption in general, is that a foster mother increases her inclusive fitness if she adopts a genetically related pup. As yet, there is no evidence that this is the case but it is now possible to test this hypothesis using “DNA fingerprinting” (Jeffries et al., 1985). Lastly, it is possible that females receive no benefit from fostering. Since phocids like elephant seals feed pups from body stores laid down during months at sea before parturition, and they are set to spend about one month on land whether they nurse or not, it matters little that they invest this energy in another pup. The cost is “prepaid” and at the end of lactation the female makes up the lost of body reserves quickly (Le Boeuf et al., 1989).

III. ABUSE OF YOUNG

The incidence of pup abuse is highest in social species where individuals form large groups during the breeding season. A variety of forms of pup abuse have been observed.

The dangerous plight of the walrus mother is unique. As nursing mothers migrate with their pups they haul periodically to rest along with other walruses. The consequences of bringing calves ashore into a mixed herd of walruses are severe. The female and her pup must climb over or around other bodies to find a resting place. Walruses jab with their formidable tusks to protect their place and can cause lethal injury to an adult or pup. Taggart (1987) writes that of 30 walruses which were observed jabbing calves, 14 were adult females, 12 were adult males, and 4 were immature animals. Of the 14 females that jabbed calves, two were nursing their own calves. He notes that on one day during his study the entire group of walruses departed the study site (Punuk Island). Left behind were 119 fresh dead walruses. Of these, 40% were calves, neonates and suckling pups. In elephant seals, breeding age males and nursing females account for 60–95% of the pup deaths on the rookery prior to weaning (Le Boeuf et al., 1972; Le Boeuf and Briggs 1977). The pup mortality rate prior to weaning at the Año Nuevo rookery in California varied from 13–26% of pups born over a nine-year period.

Mother-pup separation leading to the trauma-starvation syndrome is a key factor in pup abuse in elephant seals (Le Boeuf and Briggs, 1977).
The main causes of mother-pup separation are the movement of bulls in the harem, weather and tidal conditions (Le Boeuf and Condit, 1983). About 16% of separations per year are due to the behavior of the mothers (Riedman and Le Boeuf, 1982). Some females abandon their pups soon after parturition or confuse it with a pup nearby. Young females, in particular, become embroiled in fights with neighbors and when they are over their pups are gone or are injured. Most orphans occur within a few days after birth. If pups do not reunite with their mothers, or fail to get adopted, they wander about the harem and steal milk from nursing females or starve. "Good" mothers, vigilant and protective of their limited resources which they reserve for their own pups, kill over half of the orphans produced. These wary females give a variety of responses to milk thieves that escalate from vocal threat, nipping the nose, head, or rump, to vicious biting, shaking and throwing the pup. When one female bites an orphan, neighboring females may join in, and in a frenzy, compete to bite, shake and toss the victim and kill it on the spot. More frequently the pup is seriously injured. Once injured, the orphan is less apt to reunite with its mother, less adept at stealing milk, and therefore, is more apt to sustain additional injuries. The downward spiral is rapid and by the mean age of 14 days the pup is dead. During its last few days, the orphaned pup may have a score of injuries ranging from a broken jaw to internal bleeding. It may be blind due to edematous swelling of wounds about the head and it is starving. Barely able to move, it tries to suckle anything: weaned pups, the penile opening of a sleeping male, the eye sockets of a decomposing sea lion carcass. Western gulls begin to peck at its eyes. Even the successful milk thieves that survive to weaning age bear numerous scars and weigh less than pups weaned by their mothers.

The other main source of injury and death to suckling elephant seal pups is being run over by bulls (Le Boeuf and Briggs, 1977). In their effort to obtain mates and exert dominance over each other, males crash through the harem, impervious to young pups in their path. Both the pursuer and the pursued move over pups rather than around them. Pups less than one week old are most vulnerable to being trampled and injured seriously; the itinerant orphans are more than twice as vulnerable as filial pups that remain near their mother's side. Pups trampled by bulls die of internal injuries (ruptured organs and osseous trauma) whereas pups bitten by females die of head wounds and lacerations, complicated by infection and starvation. Adult males do not bite neonates.

Similar behavior has been observed in other social phocids. Most deaths on the rookery in southern elephant seals and grey seals (Bonner and Hickling, 1971; Anderson et al., 1979) are due to starvation resulting from
permanent separation from the mother and injuries caused by adult males and females.

Neonate abuse is far less prevalent among the eared seals than among phocids (e.g., several species of fur seals, the Steller sea lion, and the southern sea lion) and females rarely injure pups. However, there are exceptional circumstances and species. It is common for females of several species (e.g., the California sea lion, *Zalophus californianus*, C. Heath, pers. comm.) to become aggressive to other females and pups in the area just before and after giving birth. Among northern fur seals, females will occasionally dispute over a pup, pull it in opposite directions and injure it, but this is rare (Bartholomew, 1959, Francis, 1987). A significant exception to the rule that female sea lions do not fatally injure pups occurs in the Australian sea lion, *Neophoca cinerea*. Adult females and males at Kangaroo Island, Australia, are responsible for most neonate deaths on the rookery. Females have an unusually low tolerance for strange pups and will attack, bite and toss them (Marlow, 1972). The results of these attacks vary from slight to serious with some of them leading to death. As in elephant seals, the females that are most aggressive to strange pups are the best mothers, being extremely solicitous of their own pups and guarding them carefully. Marlow (1975) reports that out of 20 attacks on pups that involved serious shaking and tossing, 11 were performed by females, the rest were performed by males. Also unusual in this species is the report that some females, having just lost their pups, will abduct and adopt strange pups. Males, are an even more dangerous threat to pups than females (Marlow, 1972, 1975; Higgins and Tedman, 1990). They injure and abuse pups in three ways: 1) In their constant effort to herd females, males cause substantial mother-pup separation (Marlow, 1975). 2) Like females, males will attack, bite and toss pups; Marlow (1975) observed that males were responsible for nine of 20 attacks on pups; Higgins and Tedman (1990) documented four pup deaths due to males. 3) Bulls also attempt to copulate with small pups which may result in lethal injuries (see also Hooker's sea lion, *Phocarctos hookeri*, Marlow, 1975).

The context in which male southern sea lions in Uruguay (Vaz-Ferreira, 1975) and Patagonia, Argentina (Campagna et al., 1988a), abuse, injure and kill neonates is most unusual. The largest males defend territories and females along the high tide line along beaches (Campagna et al., 1988a, 1988b). Two to three times daily during the peak of the breeding season, adult and subadult males without territories or females raid the breeding unit *en masse*, the adult raiders attempt to secure females or to carry one out. Younger, pubertal subadult males abduct pups that are left behind in the melee and confusion, or who wander about searching for
their mothers following a raid (Campagna et al., 1988b). With the pup held in his jaws, the male retreats from the breeding group, comes to a stop and drops the pup (Figure 1). Sometimes it is allowed to escape and return to the breeding females. More often, the male drops the pup and ignores it so long as it does not wander. If it starts to escape, he pins it down on the substrate or grabs it in his jaws, shakes it from side to side and tosses it into the air. Pups are injured and sometimes killed in this manner. Males may alternate this behavior with sexual mounts including pelvic thrusting (in 9% of abductions). However, intromission has never been observed. In some cases, the abductor takes the pup far out into shallow water, often with several males in pursuit. The males compete to control the pup, grabbing it, biting it, tossing it and repeatedly submerging it. Some of these episodes last up to 30 min and in some cases the pup was not seen again and it was assumed that it drowned. The behavior of controlling, blocking, biting and tossing pups is analogous to the behaviors that adult males direct to breeding females. One gets the impression that the subadults are treating the pups like prospective mates.

The incidence of pup abductions in southern sea lions at Punta Norte, Argentina, is quite high. During four breeding seasons, 21% of 400 pups born were seized by subadult males; 57% of the seized pups were held captive for 10 min to 2 hrs. It was estimated that 5.6% of the pups seized died of bite wounds to the head and neck; 50% taken to the water were drowned.

**Weanlings and Juveniles**

Because sea lion and fur seal pups are not weaned for a year or more, and after this time they come and go from rookeries at a different time than breeding males, there is little opportunity for males to interact with newly weaned pups. In contrast, among the elephant seals, weaned pups begin to emerge from harems towards the end of the breeding season when estrous females are on the decline and returning to sea, and most of the breeding age males are still present (Figure 2). Weanlings remain on the rookery for 2 1/2 months before going to sea for the first time (Reiter et al., 1978). In this context, males mount weanlings, attempt to mate with them, and in the process, injure and kill some of them. Weekly surveys of weanlings during three breeding seasons (Rose et al., 1991) revealed that by the third week in March, 34–50% of the pups sampled (250–400) showed signs of having been mounted by a male (Figure 2). Mounting of weanlings declined after this date because the males returned to sea. Signs of mounting were caused by neck bites and ranged from missing
Figure 1  A subadult male southern sea lion at Punta Norte, Patagonia, Argentina, abducts a suckling pup (a), a behavior which resembles that of an adult male abducting an estrous female (b).
Figure 2 The percentage of weanlings on the rookery bearing evidence of having been mounted by males (tooth marks, injuries or scars) as reflected by successive samples during the breeding season (right axis). The relative frequency (percentage of total that were present) of the total number of adult females and weanlings on the rookery as a function of date in the breeding season (left axis). Adapted from Rose, Deutsch and Le Boeuf (1991).
fur, scraps, and surface cuts to shallow gashes and puncture wounds to deep gashes, exposing the blubber, and profuse bleeding (Figure 3). Two weanlings were observed being killed directly by males mounting them. The age group that most frequently mounted weanlings were 6 year old pubertal males, a group that rarely copulated with females because they were denied access to them. Adult males rarely mounted weanlings. Males that mounted weanlings did not distinguish between the sexes.

IV. EXPLANATIONS FOR ABUSE OF YOUNG AND COMPARISONS WITH OTHER ANIMALS

It is evident from this brief survey that adult male and adult female pinnipeds abuse, injure and kill young under certain circumstances. The circumstances and incidence vary greatly between the two major families in the suborder and are linked to different life history patterns. There is also considerable variation between species in the same family. Nevertheless, abuse of young can be put into three general categories: trampling and crushing, attacking and biting, and sexual assault. Female abuse falls into two categories: 1) females bite strange pups to protect a space around their own pup or to protect resources intended for their own pup, and 2) abandoning young.

Explanations at both the ultimate and proximate level are summarized. Male trampling and crushing of young occurs in species where males are large relative to pups and male movements are frequent in the vicinity of neonates. Abuse of this type is most obvious in the elephant seals. Le Boeuf and Briggs (1977) argue that pups are trampled because breeding males are selected to maximize their reproductive success. It is to a male's advantage to run over a neonate, rather than avoid it, if this means he is more effective in chasing competitors away from females and evading dominant males, and in the end, inseminates more females by this tactic. The fact that the neonate is not likely to be his own, since it was sired during the previous breeding season, makes this argument even more plausible.

Males attacking and biting pups alone, such as occurs in the Australian sea lion, is difficult to explain. Higgins and Tedman (1990) state that misdirected aggression is likely and that pups may be seen as a threat to territorial males. Pup killing by any means might be construed as spiteful behavior that evolved because it decreases the reproductive success of others at a low cost to the actor (Trivers, 1985). Young males, who do most of the killing, are not apt to be killing a pup they sired because they are young and sexually inexperienced. However, it is unclear how a male would benefit
Figure 3  A subadult male northern elephant seal (six years of age) bites and mounts a newly weaned pup on the neck (a). Neckbites during male mounting attempts leave evidence of this behavior in the form of depressions in the pelage, skin scrapes, and open wounds (b).
from spiteful killing because, while reducing the fitness of others, he would also be benefiting many other unaffected individuals, diluting or eliminating his potential relative gain from interference competition (Campagna et al., 1988b).

Males of a number of species respond sexually to neonates, weanlings or juveniles by attempting to mate with them. This behavior has been observed in southern sea lions, Australian sea lions, Hooker's sea lion, northern fur seals, and the two species of elephant seals. This behavior may simply reflect strong selection for high libido in males of these species. Regarding the behavior of southern sea lion males, Campagna et al., (1988b) concluded that the resulting infanticide was of no adaptive value to the perpetrators and that the behavior was a low-cost byproduct of pups being treated as adult females. Males with little or no sexual experience, and a high motivation to mate, generalize their sexual behavior from unobtainable estrous females (protected by territorial males) to the more easily obtained but unsuitable pups. Males do not get obvious, immediate reproductive benefits from seizing, holding and mounting pups but, they gain experience which might make them more effective with adult females later on. A similar explanation applies to male elephant seals mounting weanlings and juveniles (Rose et al., 1991). Sexually inexperienced, sexually mature subadult males are the major perpetrators, and the incidence of the behavior is highest at the end of the breeding season just after the last adult females have left the rookery.

Females biting strange pups is best understood in terms of the mother protecting her own young or a resource (milk) destined for her own young. This stems in large part from the tradeoff of breeding socially. The benefits of group living, such as breeding with a male of demonstrated fitness (Trivers, 1985) or relying on others to signal the approach of predators, are offset by problems such as competition for birthing sites and milk stealing by alien pups. Selfish, aggressive mothers do the best job of rearing their own young by punishing those that threaten their pups or their resources. In northern elephant seals, size and dominance increase with age so it is the prime-age and oldest females that best protect their offspring and injure those of others (Reiter et al., 1981). It is the pups of the youngest females, who get orphaned or wander, that are most often injured and killed.

The abandonment of pups is also a function of age in elephant seals (Le Boeuf et al., 1972; Reiter et al., 1981). Young primiparous females sometimes give birth and never turn around to face the pup but merely orphan it at birth. This seems to be largely a matter of inexperience. Abandonment in this species and in others is often difficult to distinguish from pup “misplacement” and misidentification. Bad weather, crowding,
aggressive female neighbors, and fighting or courting males in the vicinity at the time of parturition can confuse even experienced mothers (Le Boeuf and Briggs, 1977; see Coulson and Hickling, 1964 re Grey seals). For example, if a young elephant seal mother is separated from her pup shortly after birth by a dominant aggressive female, she may not be able to reach her pup for hours or days. By that time, she may not recognize it. Along similar lines, a mother southern sea lion and her pup may be separated shortly after birth (Campagna et al., 1988a). One adult male holds the female and five meters away, another male holds the pup. The mother cannot go to the pup because she is bitten and tossed back to where the male can guard her. The same is true of the pup. In about five days the pup dies of starvation.

This brief review summarizes positive and negative treatment of young by adults in some pinnipeds. Too few species have been studied intensively from this perspective. We have emphasized social species that breed on islands in temperate zones because they have been well studied. Far less is known of the natural history of most phocids that breed on pack and fast ice at low circumpolar latitudes. Moreover, and this is the most telling irony, most information we have about the treatment of young refers to terrestrial behavior. We know woefully little about behavioral interactions at sea where these marine mammals forage and spend much of their time. For example, adult female northern elephant seals spend only 16% of the year on land; the rest of the time they are at sea.

Are the pinnipeds unique in the behaviors displayed to young? No, in our opinion, no new behavior patterns, particularly with respect to abuse of young, emerge. Males injure and kill young in much the same way and for the same reasons, or lack of reasons, in many terrestrial species (Hausfater and Hrdy, 1984). Treating pups as a sexual stimulus is widespread among mammals. Females killing the young of other females occurs in a variety of terrestrial mammals, e.g. wolves, African hunting dogs, prairie dogs, ground squirrels (Sherman, 1981). The abandonment of young by primiparous mothers has been documented extensively in a number of mammals, including humans.

Some explanations for abuse of infants and for infanticide in terrestrial mammals do not apply to pinnipeds. For example, infants are not used as "passports" to gain access to resources or as "agonistic buffers" to turn off the aggression of an adversary as has been observed in some primates (Hrdy, 1976; Strum, 1984). Pinnipeds do not cannibalize pups as some other infanticidal mammals do (Struhsaker, 1977; Hoogland, 1985; Takahata, 1985). Killing pups does not cause the mother to resume ovulating sooner, an explanation for infanticide in African lions and hanuman lan-
gurs (Hrdy, 1974, 1977; Packer and Pusey, 1982, 1983), and in any case, the killer is not more apt to mate with the mother. In elephant seals, at least, females whose pups are killed from any cause do not have a higher probability of weaning a pup in the next breeding season (Le Boeuf, et al., 1989), as occurs in prairie dogs, Cynomis ludovicianus (Hoogland, 1985).

One question that emerges from this exercise is why is there such variation in abusive treatment of young by adults from one species to the next? Why is it that southern sea lions of both sexes are so abusive to their young and the other four sea lion species are not? Why are elephant seals so different from harbor seals, Weddell seals and harp seals? Is it because of the spotty research coverage with some species being well known and others virtually unstudied? We suspect that there is no simple answer to this question. Life history patterns are important in some cases. For example, some phocids like elephant seals fast while nursing and hence, mothers are strongly selected to prevent milk thievery. Others, like harbor seals, Phoca vitulina, do not appear to fast during lactation. Crowding, weather and individual variables, like the age and history of adults involved, influence the frequency of pup harassment but the degree to which these are important remains to be determined.

REFERENCES


