The Evolution of Maternal Care in Pinnipeds

New findings raise questions about the evolution of maternal feeding strategies

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Species of the suborder Pinnipedia belong to three families (Phocidae—true seals; Otariidae—fur seals and sea lions; and Odobenidae—walruses) and are distinctive among mammals in that they are neither exclusively land dwelling nor exclusively ocean dwelling. Pinnipeds spend the majority of their time at sea foraging; however, with the exception of the walrus, they appear to require land (or sea ice) on which to give birth and nurse their young (Bonner 1984, Oftedal et al. 1987a). Consequently, nursing of young and foraging for food must be spatially and temporally separated. Although pinniped females and males aggregate during the breeding season, female pinnipeds, unlike many other carnivores, are the sole providers of nutritional resources to the young; there is no male assistance or extended social group that assists the female in acquiring the resources she needs to be able to produce the milk necessary to rear her young successfully. These circumstances have resulted in the evolution of unusual behavioral and physiological patterns of maternal care and lactation (often referred to as maternal or lactation strategy).

Provisioning of young is energetically the costliest component of reproduction and parental care in mammals (Clutton-Brock 1991, Gittleman and Thompson 1988, Oftedal et al. 1987a). This cost is borne by the female through the production of milk during lactation. Given that females maximize their reproductive success by rearing offspring that have a high probability of reproducing themselves, we might expect the suite of characteristics associated with maternal strategies to be under strong selection. In addition to being responsive to recent ecological pressures, maternal strategies also reflect attributes that are present by common ancestry (phylogenetic constraints).

Extensive research on maternal strategies has been done on pinnipeds. For some time the accepted view of maternal care among pinnipeds has been that there are three basic strategies, each characteristic of a separate family. In this article we reexamine this view by describing the basic characteristics of these strategies, reviewing new evidence that shows that the strategies are not necessarily family specific, and discussing the energetics and ecology of pinniped maternal care, which suggest that maternal body size may be more important than phylogeny in determining a maternal feeding strategy. Because several technological advances (e.g., electronic time-deep recorders, satellite-linked transmitters, and isotope dilution techniques) have played an instrumental role in this research, we also describe how they have contributed to our increased understanding of pinniped maternal strategies.

Taxonomy, natural history, and life history of pinnipeds

Mounting evidence from paleontological, morphological, and genetic data indicates that all pinnipeds evolved from a common carnivore ancestor approximately 25 million years ago and diverged into the current families by approximately 10 million years later (Arntson and Widegren 1986, Lento et al. 1995, Wyss 1988). The type of carnivore ancestor has not been resolved yet but may be ursid (bear)- or mustelid (otter)-like. Today, there are 18 phocid species, 14 otariids, and a single odobenid species (the walrus). Phylogenies based on the mito-
The otoriid and odobenids were placed in the same clade and separate from the phocids (Arnason et al. 1995, Lento et al. 1995). Although the phylogenies do not resolve whether phocids or otoriids diverged first from the common carnivore ancestor, morphological and biogeographical evidence suggests that otoriids were the first to diverge.

The phocids appear to include two subfamilies: the Monachinae and Phocinae. The latter comprises three groups—phocines, clysothorines, and erignathines (Figure 1; Perry et al. 1995). Among the otoriids there are at least two subfamilies, the Otariinae and Arctocephalinae, but there is not clear agreement on whether there should be additional subfamilies. For example, we show the northern fur seal as not belonging to the Arctocephalinae subfamily of otoriids (Figure 1) based on Lento et al. (1995), but earlier classifications placed the northern fur seal in the Arctocephalinae. A great deal of molecular systematics research is currently underway that should help to resolve the pinniped phylogeny in more detail.

In 1970, Bartholomew outlined how physiology, behavior, and ecology may have led to seasonal breeding aggregations in most pinniped species. Important components in his model were physical adaptations to the aquatic environment, large size and blubber stores to provide efficient thermoregulation in an aquatic environment (and probably secondarily allowing fasting during breeding), the need to return to land or ice to give birth and rear offspring, and the increased risk of predation from terrestrial predators resulting from limited mobility on land. In most extant species, females give birth in close proximity at traditional breeding sites once each year. The synchronized postpartum estrus and clustering of females favors male mating strategies that involve competing for territories encompassing preferred parturition sites or competing directly for groups of females to maximize the number of females mated.

Indeed, some of the most extreme examples of polygyny and male competition occur among pinnipeds (Boness et al. 1993). For example, the alpha male in a large colony of southern elephant seals may mate with 126 females in one season (McCann 1981), and a male northern fur seal holding a prime territory may have 150 or more females reside there during his tenure (Bartholomew and Hoel 1953). Many adult males are present at breeding colonies, but aside from a few studies that suggest that Galapagos sea lion males may protect young from sharks, there is no evidence that males contribute to rearing offspring (see Trillmich in press).

In all pinniped species, females usually give birth to one pup per year. The duration of maternal care varies from about three days to as long as three years (Bonner 1984, Bowen 1991, Oftredal et al. 1987a). The period between the independence of young and when they reproduce is relatively long (approximately four to six years for females and usually ten or more for males). The delay in reproduction among males is probably associated with extreme competition for mates and polygynous mating patterns. Males become sexually mature before they are socially competitive. Although pinnipeds are long-lived mammals, by giving birth to a single pup each year and, for some species, doing poorly in rearing their young the first time or two (Reiter et al. 1981, Sydeman et al. 1991), even the most successful females are likely to have a low reproductive output over their life span compared with males. For example, the most successful northern elephant seal females at Año Nuevo, California, wean only ten healthy pups in a lifetime, whereas the most successful males mate with as many as 121 females (Le Boeuf and Reiter 1988).

### Importance of technological advances

Any effort to understand the evolution of maternal strategies in mammals requires a knowledge of the behavior and energy requirements of mothers and offspring, the physiological characteristics of lactation, and the importance of ecological factors on maternal performance. The
inaccessibility of pinnipeds for behavioral observation when they are at sea, or even when on ice floes, makes them a special challenge for studying some aspects of maternal strategies. On the other hand, the ability to observe large aggregations and to mark and capture individual seals at traditional land-breeding colonies led to a flurry of studies of the energetics of lactation in the 1980s and 1990s, following the introduction of isotope dilution methods (Costa 1987, Oftedal and Iverson 1987) and advances in telemetry (DeLong et al. 1992, Gentry and Kooyman 1986), which enhanced our ability to investigate the energetics of reproduction and the aquatic behavior of pinnipeds.

Isotope dilution methods can be used to study several aspects of the physiology of free-ranging pinnipeds. These techniques involve administering a measured quantity of either a radioisotope (e.g., tritium) or stable isotope (e.g., deuterium oxide or O18) to an animal and subsequently measuring the concentration of the isotope in the body fluids (usually blood). Measurement of isotopes, when equilibrated with body fluids, provides an estimate of body water pool size, which, when combined with body mass and the concentration of water in lean tissues, can be used to estimate the fat and fat-free components of the body (Oftedal et al. 1993, Reilly and Fedak 1990). A knowledge of the amount of body fat an animal has gives a measure of the available energy stores that can be used to produce milk. In addition, measuring the subsequent change in isotope concentration in blood samples taken over time (days) since administration can be used to estimate average daily water intake (Oftedal and Iverson 1987). Under certain conditions, water intake can be used to estimate food intake, provided that the water content of the food source is known and that metabolic water can be estimated (Costa 1987). For example, when applied to suckling seal pups, these techniques yield accurate estimates of milk intake by the pup and milk yield of the mother (Costa et al. 1986, Iverson et al. 1993, Oftedal et al. 1987b, Tedman and Green 1987). Isotope methods can also be used to estimate average daily metabolic rate of free-ranging pinnipeds (Costa 1987).

Electronic microprocessors (e.g., time–depth recorders), radio transmitters, acoustic transmitters, and satellite-linked transmitters have dramatically improved our ability to study the behavior of pinnipeds. Radio transmitters, especially combined with automated data loggers, enable researchers to monitor for extended periods the presence or absence of individuals at a particular location (e.g., a haul-out site, where they breed, molt, or rest on land or ice) or to locate pinnipeds at sea by triangulation or direct aerial searching. Acoustic transmitters, like radio transmitters, emit a sound that can be tracked, but have the advantage over radio transmitters of being traceable underwater. The distance over which acoustic signals can be received, however, is limited compared with radio signals.

Another electronic instrument that has proven invaluable in studying pinnipeds at sea, the time–depth recorder, consists of a microprocessor that logs data from a pressure transducer, a temperature transducer, and a light-sensing diode. These sensors provide information on dive characteristics such as frequency, depth, duration, water temperature, and approximate location, respectively (DeLong et al. 1992). The location of pinnipeds at sea can be determined more precisely by satellite-linked transmitters than by time–depth recorders. Satellite-linked transmitters send both positional and diving information to polar-orbiting Argos satellites (e.g., McConnell et al. 1992). The analysis of individual dives and patterns of dives (Figure 2) as well as locations of dives have yielded extraordinary insights into foraging patterns of free-ranging pinnipeds.

**Pinniped maternal strategies**

Three maternal strategies have been described for pinnipeds, designated “aquatic nursing,” “fasting cycle,” and “fasting” strategies (Bonner 1984, Costa 1991, Gentry and Kooyman 1986, Oftedal et al. 1987a). The aquatic nursing strategy is most akin to that of many terrestrial mammals and the exclusively marine mammals (cetaceans and sirensians), in which young remain with their mothers wherever they go and nurse at sea as well as on ice (Fay 1982, Miller and Boness 1983). Relatively little information is available about this strategy, although, based on the walrus, the only pinniped exhibiting aquatic nursing, its basic features are as follows: females accumulate blubber stores before giving birth on ice floes;
after a few days of fasting, females take their calves with them when they leave the ice to forage and nurse them at sea (Figure 3), on ice, or on land; lactation lasts for two to three years, although after approximately five months calves will begin to feed on benthic organisms as well; and milk is low in fat compared to that of most other pinnipeds, although it is still high compared to that of most mammals.

The foraging cycle strategy is reminiscent of that found in mammals and birds that leave their young in “nests” while they forage. The major features of this strategy are as follows: females acquire a moderate store of energy in the form of blubber (subcutaneous fat) before they arrive at their traditional breeding sites; females fast for 5–11 days postpartum, using blubber stores to sustain lactation and maintenance energy needs during this “perinatal” period; females then alternate foraging trips to sea with visits to land to nurse their pups (Figure 4); the lactation period is relatively long, ranging from four months to three years; and milk is high in fat relative to that of terrestrial mammals, but generally lower than that of pinnipeds that use the fasting strategy. One important difference between pinnipeds that use the foraging cycle strategy and birds and mammals that use similar strategies is the length of time the mothers spend away from their offspring. Absences in most such pinnipeds of more than 2 days (and up to 13 days) is likely a function of the distance females travel to find food and of the amount of time required to replenish body stores of fat, the principal energy source for lactation (Costa and Gentry 1986).

The fasting strategy is uncommon in mammals and birds. It is characterized as follows: females arrive at breeding sites with large energy stores in the form of blubber; they fast throughout the entire period of lactation, using blubber stores to sustain lactation and maintenance energy needs; the lactation period is short, lasting from 4 to 50 days; and milk is extremely high in fat and energy.

Differences in strategy in relation to phylogeny

Until recently, it was widely accepted that each pinniped family exhibited a unique maternal strategy. The conventional view was that the odobenids used the aquatic nursing strategy, the otarids the foraging cycle strategy, and the phocids the fasting strategy (Bonner 1984, Costa 1991, Gentry and Kooymen 1986, Oftedal et al. 1987a). We now know that this view is overly simplistic and that these strategies are not family specific. Although aquatic nursing is presently known to exist only in odobenids, and fasting for an extensive fraction of lactation occurs only among phocids, a maternal foraging cycle is found in all otarids as well as in at least one, and probably several, phocids.

One phocid that clearly uses the maternal foraging strategy is the harbor seal (Figure 5). In a recent series of time–depth recorder studies on harbor seals at Sable Island, off the coast of Nova Scotia, Canada, we found that lactating females commenced trips to sea approximately six days after parturition (Figure 2; Boness et al. 1994, Bowen et al. 1992a). On average, they made seven foraging trips during the remainder of the 24-day lactation, with trips lasting seven hours. Both direct (stomach lavage) and indirect (changes in daily water intake of females from isotope dilution studies, and changes in the ratio of mass transfer from mother to pup over lactation) evidence indicate that females are feeding during these trips (Bowen et al. 1992a). Consistent with these findings, an independent study of harbor seals in Scotland, using animals with radio transmitters attached to their heads, reported periodic absences of lactating females from breeding sites and that the locations of these females at sea were the same as those where the seals are thought to feed at other times of the year (Thompson et al. 1994).

Several other characteristics of harbor seal maternal care resemble those of otarids rather than of phocids studied previously or are intermediate between the two (Table 1). For example, fat stores of harbor seal mothers at parturition amount to 21 kg on average, or approximately 24% of maternal mass (Bowen et al. 1992a). This percentage is comparable with that reported in otarids and much less than that found in other phocids. Harbor seal pups gain an average of 0.8 kg/d, a substantially higher growth rate than is seen in otarids, but low by comparison to the offspring of fasting phocid seals (Table 1). Lactation length in the harbor seal, on the other hand, is short as in other phocids, despite a maternal foraging cycle similar to that of otarids. Harbor seal females

Table 1. Aspects of the energetics of lactation and maternal energy investment in pinnipeds.

<table>
<thead>
<tr>
<th>Species</th>
<th>Maternal mass (kg)</th>
<th>Body fat (%)</th>
<th>Lactation length (d)</th>
<th>Milk fat (%)</th>
<th>Daily (MJ/d)</th>
<th>Total (MJ)</th>
<th>Per maternal metabolic mass (MJ/kg)^3</th>
<th>Pup mass gain (kg/d)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phocids</td>
<td></td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>Southern elephant seal</td>
<td>515</td>
<td>23</td>
<td>24</td>
<td>47</td>
<td>184</td>
<td>4414</td>
<td>41</td>
<td>3.3</td>
<td>Arnborn 1994, Peaker and Goode 1978</td>
</tr>
<tr>
<td>Northern elephant seal</td>
<td>504</td>
<td>40</td>
<td>27</td>
<td>54</td>
<td>98</td>
<td>2646</td>
<td>25</td>
<td>4</td>
<td>Costa et al. 1986</td>
</tr>
<tr>
<td>Weddell seal</td>
<td>447</td>
<td>—</td>
<td>53</td>
<td>48</td>
<td>74</td>
<td>3922</td>
<td>40</td>
<td>2</td>
<td>Tedman and Green 1987, Thomas and DeMaster 1983</td>
</tr>
<tr>
<td>Grey seal</td>
<td>207</td>
<td>34</td>
<td>16</td>
<td>60</td>
<td>95</td>
<td>1520</td>
<td>28</td>
<td>2.8</td>
<td>Bowen et al. 1992a, Fedak and Anderson 1982, Iversen et al. 1993</td>
</tr>
<tr>
<td>Harp seal</td>
<td>129</td>
<td>42</td>
<td>12</td>
<td>57</td>
<td>75</td>
<td>900</td>
<td>23</td>
<td>2.3</td>
<td>Kovacs et al. 1991, Ofstedal et al. 1996, Stewart 1986</td>
</tr>
<tr>
<td>Harbor seal</td>
<td>84</td>
<td>25</td>
<td>24</td>
<td>50</td>
<td>31</td>
<td>744</td>
<td>27^a</td>
<td>0.8</td>
<td>Bowen et al. 1992b, 1994^b</td>
</tr>
<tr>
<td>Otariids</td>
<td></td>
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<td></td>
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<td></td>
<td></td>
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<tr>
<td>Steller’s sea lion</td>
<td>273</td>
<td>—</td>
<td>330</td>
<td>24</td>
<td>21</td>
<td>6930</td>
<td>103</td>
<td>0.38</td>
<td>Costa 1991, Higgins et al. 1988</td>
</tr>
<tr>
<td>California sea lion</td>
<td>88</td>
<td>—</td>
<td>300</td>
<td>44</td>
<td>10</td>
<td>3050</td>
<td>106</td>
<td>0.13</td>
<td>Boness et al. 1991, Ofstedal et al. 1987a</td>
</tr>
<tr>
<td>Antarctic fur seal</td>
<td>39</td>
<td>22</td>
<td>117</td>
<td>42</td>
<td>11</td>
<td>1240</td>
<td>79</td>
<td>0.11</td>
<td>Costa 1991, Costa and Trillmich 1988</td>
</tr>
<tr>
<td>Northern fur seal</td>
<td>37</td>
<td>—</td>
<td>125</td>
<td>42</td>
<td>6</td>
<td>744</td>
<td>55</td>
<td>0.08</td>
<td>Costa and Gentry 1986</td>
</tr>
<tr>
<td>Galapagos fur seal</td>
<td>37</td>
<td>26</td>
<td>540</td>
<td>29</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>0.06</td>
<td>Costa and Trillmich 1988, Trillmich and Lechner 1986</td>
</tr>
</tbody>
</table>

^a Calculated using maternal mass of 91 kg at parturition because this was the mean mass of females for which milk energy was determined.

The energetics of maternal strategies

The foraging cycle and fasting strategies result in different quantities of total milk energy output and daily rates of offspring provisioning and growth during lactation (Table 1). Among those species exhibiting a fasting strategy, daily rates of total milk output are high. For example, at the extreme for fasting patterns, pack-ice-breeding hooded seals provide their young with 230 megajoules (MJ) per day, amounting to 1000 MJ during the four-day lactation period (Ofstedal et al. 1993). Another fasting species, the grey seal, provides 95 MJ per day and a total of 1520 MJ over a 16-day lactation period. In contrast, a foraging cycle species like the California sea lion provides only approximately 10 MJ per day of milk energy to its pup, but over the course of the nearly year-long lactation period females expend approximately 3050 MJ (Ofstedal et al. 1987b), or three times that of the hooded seal. When one standardizes these comparisons for differences in body mass among species (using maternal metabolic mass, which accounts for the allometric relationship between body mass and milk yield; Ofstedal et al. 1987a), it is still clear that on average fasting species have high daily milk energy output relative to foraging cycle species but lower total output over the course of lactation (Table 1).

Both total time spent nursing and the energy content of milk contribute to the variation in daily provisioning rates. Sea lions and fur seals, otariids that lactate for periods of four months to three years, suckle for approximately 1.5–2.5 hr/d when their mothers are on shore, but because females are at sea feeding more than half of the time, their overall suckling rate is much less than in fasting phocids (Ofstedal et al. 1987a) and in phocids exhibiting a foraging cycle because their foraging trips are much shorter than those typical of otariids. For example, the California sea lion suckles every 2.4 hours for a total daily duration of 1.8 hours, but this activity occurs only every third day, so that the average daily suckling rate over the three days is 0.6 hr/d. In the few otariid

species in which data are available, daily suckling duration appears to increase throughout lactation.

Phocids are variable in the daily duration of suckling (0.5–3.5 hr/day), but most exhibit an increase in duration over lactation (Bowen 1991, Oftedal et al. 1987a). Hooded seal females, with the unusually short lactation period, suckle once every 25 minutes for a daily suckling duration of 4.3 hours (Perry and Stenson 1992). Another phocid, the Antarctic Weddell seal, apparently also suckles for approximately four hours each day; however, it has a longer lactation period than the hooded seal, nearly five weeks (Bowen 1991, Oftedal et al. 1987a). One possible reason for the comparable suckling duration between Weddell and hooded seals is that Weddell seal pups spend more energy because they enter the water (which has a higher thermal conductivity than does air) and are much more active than hooded seal pups. If this is true, then one might ask why harbor seal pups, which also spend a considerable proportion of time active in the water, do not have high daily suckling durations.

Both phocids and otariids exhibit high levels of milk fat, although the reasons are likely to be different. Most phocid milks are more than 50% fat by late lactation. Hooded seal milk contains the highest amount of fat (61%; Table 1) and shows no change in fat content throughout lactation. The constant high fat content of hooded seal milk enables the mother to invest maximally in the pup over the extremely brief lactation. In phocid species with longer lactation, milk fat and energy content increase over lactation. These changes may represent the increasing energy demands of growing pups and the need for lactating females to conserve water (Iverson et al. 1993, Riedman and Ortiz 1979).

In contrast, otariid milks are lower in fat, although they are still high in fat compared with the milks of most terrestrial mammals. For example, California sea lion milk contains 32% fat early in lactation and 44% later (Oftedal et al. 1987b). High fat milks in otariids are needed to support the energy demands of fasting pups during their mothers' extended absences while foraging at sea. Like that of phocids, the milk of otariids may show significant increases in fat content over lactation, again, presumably, to meet growing offspring needs. Increasing energy requirements of older pups may also be reflected in the general tendency for foraging trips of otariid females to lengthen over lactation (Oftedal et al. 1987a). These longer trips may be necessary for females to replenish body stores used in milk production. In agreement with this idea, Antarctic fur seal pups grow most following long foraging trips by their mothers (Goldsworthy 1992).

Differences between phocids and otariids in the pattern and rate of milk energy delivery are reflected in both the rate and composition of offspring growth. Phocid pups grow between approximately 0.8–7.1 kg/d compared with only 0.06–0.38 kg/d in the few otariid species studied (Table 1). Relative to maternal metabolic mass, phocid pups gain mass at rates varying from 21–145 g/kg 0.75/d compared with only 3–5 g/kg 0.75/d in otariids. However, despite considerably slower growth rates, the long lactation periods of otariids result in pups that are larger at weaning relative to maternal mass (approximately 38%) than those of phocid species (28%; Bowen 1991).

Among phocids, offspring growth during lactation is primarily a gain in fat stores, with little increase in lean body (muscle and bone) mass, whereas among otariid offspring, growth over the longer lactation is in both fat stores and lean body mass. The so-called fattening of phocids is illustrated most dramatically in the hooded seal, in which fat deposition accounts for approximately 82% of total mass gain over lactation (Oftedal et al. 1993). Little is known about the fat content of weaned otariid pups, but Oftedal et al. (1987b) estimated that fat accounted for approximately 31% of the gain in body mass of three-month-old California sea lions, which are approximately one third of the way through the period of maternal care. These different patterns of pup growth are determined largely by daily energy intake; pups with the greatest daily
energy intake above maintenance costs gains relatively more fat than protein (Iverson et al. 1993).

Total gain in body mass of phocid pups is inversely related to the duration of lactation, when expressed relative to maternal metabolic mass (reviewed in Bowen 1991). This relationship most likely reflects a reduction in what Fedak and Anderson (1982) referred to as the female’s “metabolic overhead” (i.e., her nonmilk production costs) as lactation length becomes shorter. Although with a short lactation period, total energy expenditure by the mother is lowered (Table 1), a higher proportion of the female’s energy stores allocated to lactation can be transferred to the offspring. Over the 27-day lactation period of the northern elephant seal, for example, milk production accounts for 60% of total energy expenditure by the female (Costa et al. 1986). The total energy expenditure of hooded seal females over the four-day lactation period has not been measured, but it can be estimated. Hooded seal females lose approximately 38 kg over the lactation period, and of this loss, 80% is from the blubber layer (Bowen et al. 1987, Kovacs and Lavigne 1992). If we assume that fat catabolism accounts for 80% of mass loss, females use approximately 1233 MJ over the four days of lactation. Of this quantity, the average pup, gaining 7 kg/d, would consume approximately 1014 MJ (Ofstadal et al. 1993). Thus, approximately 82% of maternal expenditures are transferred to the hound seal pup, as compared with 60% in the northern elephant seal.

The different maternal strategies result in different patterns of mass change in lactating females. Because female phocids fast throughout lactation, they lose considerable mass. The magnitude of this loss is large in some species. For example, female grey seals lose approximately 40% of their initial body mass over the 16-day lactation period (Iverson et al. 1993). Similar loss in mass (40%) occurs in female northern elephant seals (Costa et al. 1986). There is little information on mass change in female otariids, but northern fur seal females lose approximately 20% of body mass during the initial perinatal fast. However, once they begin their foraging trips, they gain approximately 1.3% of their initial mass per day (Costa and Gentry 1986).

A possible reason why the harbor seal evolved a maternal foraging cycle similar to that of otariids, despite a short lactation period, may have to do with its small size and the energetic cost of lactation. The harbor seal is a small phocid, smaller than the other phocids that have been studied in detail. Female harbor seals average 84 kg at parturition, compared with 129–515 kg for the phocids previously studied (Table 1). Large-bodied phocid species, such as the grey seal, northern elephant seal, and hooded seal, which fast (Table 1), use approximately 84%, 58%, and 33%, respectively, of their stored fat over the entire lactation period (Bowen et al. 1987, Costa et al. 1986, Fedak and Anderson 1982). By comparison, harbor seals use 80% of their stored fat in only the first 19 days of the 24-day lactation period (Bowen et al. 1992a), despite the fact that they feed during at least part of this period (Bones et al. 1994). Given that such a large proportion of stores are exhausted even with feeding, it seems impossible that these small females could support all of lactation using only stored energy reserves.

The 84-kg harbor seal female is similar in size to most extant otariid females, which weigh less than 100 kg at parturition (the size of the apparent ancestral otariid; Table 1; Berta and Ray 1990). Five other phocid species are similar or smaller in body size than the harbor seal, and for one of these, the ringed seal, there is already some evidence suggesting a maternal foraging cycle (Hammill et al. 1991). Small body size may have contributed to the evolution of a maternal foraging cycle in phocids that have a short lactation.

The ecology of maternal strategies

The foraging cycle is broadly similar across otariids but shows interesting differences among closely related species. In an early attempt to explain this variation, Gentry and Kooyman (1986) noted that females of two subpolar species make long trips to sea followed by long periods on land, when pups receive large amounts of high-fat milk, and are weaned at approximately four months of age. In contrast, females of some tropical and subtropical species make frequent short trips to sea, spend short periods on land to nurse their pup with a relatively low-fat milk, and eventually wean their pup at one to three years of age. Little was known about temperate breeding species at the time that Gentry

October 1996

651
and Kooyman published their synthesis, but limited data suggested an intermediate pattern of maternal care. Gentry and Kooyman (1986) therefore proposed that fur seal maternal strategies follow a latitudinal gradient and argued that the patterns are driven primarily by differences in environmental seasonality and predictability of food resources. The high-latitude species have highly seasonal environments with predictable food resources, whereas low-latitude species are faced with little seasonality but unpredictable food resources arising from factors such as El Niño.

Gentry and Kooyman (1986), however, also noted that local distribution of food might affect the foraging cycle. Comparisons of closely related Arctocephaline species (see Lento et al. 1995), including some species not in Gentry and Kooyman’s analysis, indicate that lactation length appears to be negatively related to latitude, whereas maternal foraging trip length and milk fat content are not (Figure 6). For example, the Juan Fernández fur seal, a temperate breeding species found only in the Juan Fernández Archipelago off the coast of Chile, generally behaves more like subpolar species. The perinatal period (11.2 days), average length of foraging trips (12.2 days), and length of visits ashore to nurse pups (5.2 days) in this species are more extended than those in other otariids. Also, milk fat at comparable periods in early lactation (43%) is similar to the 47% and 40% observed in the subpolar northern fur seal (Costa and Gentry 1986) and Antarctic fur seal (Costa 1991), respectively. Along with these characteristics, which do not fit the predicted latitudinal trends, data from two time-depth recorders and satellite-linked transmitters show that Juan Fernández fur seals forage at distances of 450 km or more from the islands on which they give birth. Both the diving patterns of Juan Fernández fur seal females and fish ear bones (i.e., otoliths) found in the fur seal’s feces deposited on the breeding beaches point to foraging on fish species (myctophids) that are patchily distributed and most available at night when they migrate toward the sea surface. The patchy distribution of the myctophid fish probably necessitates the long distances Juan Fernández fur seal females travel to obtain adequate food to sustain lactation.

These data, along with those from other species, such as the Antarctic fur seal, suggest that the local distribution and abundance of prey species are likely to be the most important factors determining the length of foraging trips and attendance patterns. Foraging trip length, in turn, may have played an important role in the evolution of fat content of otariid milks. In the closely related Arctocephaline otariids, milk fat content is more strongly correlated with foraging trip duration than with lactation length (Figure 7). In species or populations in which females are absent from their pups for long periods, a higher fat milk appears to be needed to support pup growth because more body stores will have been used by the fasting pups during their mothers’ extended absence.

We know less about ecological influences on maternal strategies in phocids. Most phocids breed on either pack (free-floating) or fast (attached to land) ice, but some breed on land. Although several authors (Bonner 1984, Ofstad et al. 1987a), using cross-species comparisons, have claimed that the variation in lactation length (4–50 days) and hence the period of fasting, is related to breeding habitat, Trillmich (in press) has argued persuasively that because of a lack of phylogenetic independence and the small number of species involved in these analyses,
the evidence does not support the claims. In fact, the currently unresolved phylogenetic relationships among phocids and the small number of phocid species inhabiting the different habitat types make it impossible at present to test such hypotheses using a cross-species approach. However, we may gain some insight into habitat effects on lactation length from conducting carefully designed within-species studies of species, such as the grey seal, that have populations that breed in different habitat types. Although studies have already been conducted on populations of grey seals at pack-ice and land-breeding colonies, the studies were not designed with the idea of making comparisons of lactation length between habitats and thus did not control for factors that might confound a conclusion about possible habitat effects. For example, we know that maternal age can affect how long a female cares for her pup. Consequently, in a comparison of lactation length at two populations that differ in habitat, we must either specifically control for maternal age or sample a large number of females to remove any age bias.

Some likely influences on the evolution of phocid maternal strategies are, as others have suggested (Bowen et al. 1985, Smith and Hammill 1981), unstable pack ice and predation by species like the polar bear and arctic fox. Similar predation pressure probably also underlies the use of birth lars (snow and ice dens) in which young are born and nursed in two fast-ice northern phocids. None of the fast-ice phocids in the Southern Hemisphere, where there are no comparable on-ice predators, use birth lars. We clearly need more studies that are directly focused on habitat effects on maternal care and that adequately control for phylogenetic influences.

Conclusion

Pinnipeds exhibit three basic patterns of maternal care, but it is overly simplistic to view them as family-specific. A maternal foraging cycle, previously thought to occur only among otariids, which have a long lactation period, also occurs in some phocids with short lactation periods. Energetic and behavioral studies of the harbor seal, a phocid with a maternal foraging cycle, suggest that this behavior may have evolved in some phocids because of their small size. Additional studies are necessary to see how extensive this pattern is among phocids. It may be that a maternal foraging cycle has been selected for in small-bodied phocid species primarily because of the limitation that small size places on energy storage. The females of larger phocid species, not being so limited in this way, may exhibit facultative foraging during lactation, depending on the accessibility of food. The importance of seasonality and predictability of resources, as indicated by a latitudinal gradient, in shaping aspects of the otariid maternal foraging cycle strategy, appears to be less than previously hypothesized. Although length of lactation among otariids may be strongly related to seasonal and predictable resources, other characteristics, such as foraging trip length and rate of energy transfer, appear to be influenced more by location of food relative to the breeding grounds. With further studies to improve our understanding of the evolutionary relationships among pinnipeds, we will be better able to distinguish shared character states of common descent from recent ecological adaptations.

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