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Maternal Effects on Offspring Size and Development in Pinnipeds

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INTRODUCTION

The rate and direction of trait evolution depend on the mechanisms by which parents transfer their characters to progeny (Schluter & Gustafsson 1993). Although the genetic basis for such transfer has received considerable attention, maternal effects or inherited environmental effects (Rossiter 1996) may also strongly influence the response of traits to selection (Kirkpatrick & Lande 1989). Kirkpatrick & Lande (1989) considered two classes of maternal effects: those that represent non-Mendelian phenotypic transmission, called maternal inheritance, and those in which offspring fitness is determined jointly by the value of its trait and some trait in the mother, called maternal selection. Examples of maternal inheritance include the amount or quality of nutrients provided to offspring by parents, while maternal selection includes parental defense of offspring against predators or conspecifics. Both maternal inheritance and maternal selection may operate simultaneously for an individual mother and her offspring, but need not.

Pinnipeds are aquatic members of the mammalian order Carnivora and are represented by three monophyletic lineages: the Otariidae (14 fur seals and sea lions), the Phocidae (18 true or earless seals), and the Odobenidae (the walrus). They exploit diverse habitats in most aquatic environments: estuaries, continental shelves, and the deep ocean in temperate, tropical, and both Arctic and Antarctic polar seas (Bowen et al. 2002). Pinnipeds have

often not been included in comparative ecological or evolutionary analyses of carnivores because they are aquatic mammals, and thus have evolved a number of morphological adaptations to exploit this medium. However, Bininda-Emonds et al. (2001) found little evidence that, as a group, pinnipeds should be considered separately from terrestrial carnivores in other functional traits such as physiology, life history, ecology, or behavior. In fact, pinnipeds share a suite of characters and many of the demographic features of other large-bodied mammals (Reiss 1989). They are large, long-lived, slow-growing mammals exhibiting delayed sexual maturity and reduced litter size, and females invest heavily in a single precocial offspring. Population abundance tends not to change dramatically from year to year, and numbers are most sensitive to changes in adult survival, followed by juvenile survival and fecundity (Eberhardt & Siniff 1977). Thus, what we learn from pinnipeds should contribute to our understanding of the ecological consequences of maternal effects in large mammals and perhaps other long-lived, large-bodied vertebrates.

As in many other mammals, pinniped females provide all of the nutrients required for dependent offspring through the provisioning of milk, while pinniped males provide no parental care. Therefore, male and female pinnipeds tend to maximize reproductive success in different ways; males by mating with many females to increase the number of offspring sired, and females by rearing a single, high-quality offspring. However, the potential for males to mate with many females depends on the competitive ability of males and the temporal and spatial distribution of receptive females, which can be influenced by resource distribution, the risk of predation, and the costs and benefits of group living (Boness et al. 2002). The diversity of mating systems exhibited by pinnipeds exposes lactating females to a wide range of densities and disturbances by conspecific adults, thus providing avenues for maternal effects.

LACTATION STRATEGIES

Parental care is an important component of reproduction in many animals (Clutton-Brock 1991). Thus, patterns of parental expenditure on offspring and the factors that influence that expenditure have long been of interest to ecologists (e.g., Trivers 1972; Gubernick & Klopfer 1981). Although parental care in pinnipeds can include offspring defense, the greatest component of parental care by far is the provisioning of milk to the offspring, which simplifies the study of parental reproductive expenditure in this group. Given the

high energetic cost and importance of lactation to maternal and offspring fitness (Millar 1977), characteristics of lactation and related reproductive traits are presumably under strong selection. However, understanding the factors that influence maternal reproductive effort in mammals is often complicated by communal rearing systems (Gittleman & Oftedal 1987), allomaternal care, multiple offspring litters, and postweaning maternal care. In pinnipeds, however, there is no paternal care or alloparental support (Boness & Bowen 1996) and maternal care of a single pup ends at weaning (Bowen 1991). The wide variation in lactation length, breeding habitat, and female body size, and the fact that maternal care occurs mainly through the provisioning of milk, make the Pinnipedia an interesting group in which to examine maternal effects on offspring.

Lactation in the pinnipeds is constrained by the spatial and temporal separation between giving birth on land or ice and acquiring nutrients for milk production at sea (Bartholomew 1970). Three basic lactation strategies have been recognized (e.g., Bonner 1984; Oftedal et al. 1987). The generally large-bodied phocid seals (family Phocidae) breed on both land and ice and have short lactation periods (4–50 days), during which the females of the larger species haul out onto the breeding substrate and fast until the pup is weaned. Until recently, this fasting strategy was believed to be typical of all phocid species (reviewed in Schulz & Bowen 2005). However, studies on harbor seals (*Phoca vitulina*) show that females of this relatively small-bodied species (body mass ~85 kg) cannot store sufficient energy to fuel both milk production and maternal metabolism over the course of lactation. Thus females must feed at sea for short periods almost daily throughout the lactation period (Boness et al. 1994; Bowen et al. 2001). In contrast, the generally smaller-bodied otariid species (family Otariidae; fur seals and sea lions) breed on land, exhibit long lactation periods (116–540 days), and a foraging-cycle strategy, during which females alternate feeding trips to sea (usually averaging ~7 days but up to 23 days in subantarctic fur seals; Georges & Guinet 2000) with suckling bouts on land. Finally, the large-bodied walrus (*Odobenus rosmarus*), the sole extant species of the family Odobenidae, exhibits a long lactation period and an aquatic nursing strategy in which offspring accompany foraging mothers and suckle at sea.

Maternal reproductive effort in pinnipeds is most likely influenced by the adaptive consequences of the spatio-temporal division between breeding and feeding as well as the thermoregulatory demands of living in the ocean. A number of factors have been advanced as influences in the evolution of lactation strategies in pinnipeds, and these factors operate as a complex adaptive

suite (Bartholomew 1970) involving multiple life-history, physiological, and behavioral traits of individuals as well as ecological factors, such as predation and breeding habitat (Schulz & Bowen 2005). Pinnipeds provide a good opportunity to examine maternal effects because they are long-lived and individual females can be studied over many reproductive events such that variation in offspring traits can be nested within females, thus largely removing the Mendelian genetic contribution to such variation.

The best-known maternal effects in pinnipeds involve maternal nutritional influences on offspring size and growth. Adult female pinnipeds are often large and store large quantities of energy in the form of blubber such that the nutrients allocated to offspring by mothers profoundly influences the growth, development, and survival of progeny. Because pinnipeds raise only single offspring, the potential trade-off between offspring number and size does not confound the interpretation of the expected response to selection. In addition to nutritional influences, other types of maternal effects are also known in pinnipeds. In this chapter, I review most of these effects beginning with the influence of timing and location of birth. With the few exceptions noted below, the data are taken from published papers. In cases where there were two studies of a particular maternal effect on the same species, I have included both in the tables if they were based on a reasonably large sample of individuals. Otherwise, I have selected the study with the largest sample size. Although studies involving < 25 mother-pup pairs may not provide good evidence of the existence or strength of a maternal effect, they were included if they represented the only data on that species.

EFFECTS OF TIMING AND LOCATION OF BIRTH

When and where offspring are born can have profound effects on offspring fitness (Emlen & Demong 1975; Rutberg 1987; Ims 1990). Within populations of most species of pinnipeds, offspring are born over a period of 3 to 12 weeks, but in several tropical or subtropical species births can occur in most months (King 1983; Boyd et al. 1999). Differences in the timing of births and the habitats used to give birth and rear offspring also occur among populations within species (Boyd 1991). For example, in the United Kingdom, grey seals (*Halichoerus grypus*) are born on land between late September and early December with births occurring progressively later as one moves clockwise from the southwest around the islands. In eastern Canada, grey seals are born on land and ice in December-January and in the Baltic Sea, they are born on ice in late February to early March. Thus both environmental and so-

cial factors may change over the course of the breeding season, favoring the offspring of females that give birth at one time vs. another—such changes are expected to affect postnatal traits such as growth rate and weaning mass (see also Mateo, this volume).

In several pinnipeds species there is evidence that both the location and timing of births are influenced by maternal traits, which in turn affect offspring phenotype and survival. For example, adult elephant seals are highly body-size dimorphic, with males often guarding harems of 20–100 females in colonies where the density of females increases over the course of the breeding season. Reiter et al. (1981) found that older northern elephant seal (*Mirounga angustirostris*) females arrived earlier in the breeding season and gave birth in higher-quality locations in the center of harems, where the risk of disturbance either by flooding of the beach during storms or by intermale aggression was significantly lower. Females giving birth on the periphery of a male's territory were younger on average and were more often separated from their pup and harassed by subordinate and subadult males. A presumed consequence of earlier birth dates was increased survivorship, as pups weaned early in the season were observed in greater numbers at both 7 months and 1 year after weaning (Reiter et al. 1978). Sydeman et al. (1991) also found that both date of arrival and date of parturition were significantly correlated with the age and experience of female northern elephant seals, but that reproductive experience and not age was responsible for the observed effects. The timing of parturition varied in a curvilinear way with arrival and parturition dates: later for inexperienced and very experienced females and earliest for females with intermediate levels of experience.

Birth location and timing of parturition also affect offspring phenotype in grey seals, another capital breeder (i.e., females that support maternal metabolism and milk production from nutrients stored prior to parturition and then fast during the lactation period). Grey seals are a body-size dimorphic species exhibiting a female-defense mating system in which males use several different tactics to secure matings (Lidgard et al. 2005). Females fast over the course of an 18-day lactation period (Iverson et al. 1993) and are mated several days before weaning their pups. Both female density and the operational adult sex ratio change markedly over the course of the breeding season (Boness et al. 1995). In the Farne Islands, Coulson & Hickling (1964) found that habitat selection by females affected pup growth rate. Pups born on the vegetated tops of islands gained mass at a rate 40% less (~2 kg/d) than those born on rocky shore sites. At North Rona, Pomeroy et al. (2001) showed that at low-lying birth locations close to sea access points, grey seal

pups grew more rapidly than elsewhere in the colony. This effect remained significant after controlling for maternal size and the efficiency of nutrient transfer to pups, indicating that the location of birth had consequences for pup development. With respect to the timing of births, Boness et al. (1995) found that grey seal females that gave birth before the peak of births at Sable Island, Canada, were disturbed less by males approaching and attempting to mate. By contrast, females spent 17 times more time rejecting males after the peak of births. Females that gave birth early also spent more time suckling, with the result that their pups grew faster and weighed 16% more than pups born late in the season, even after controlling for the effects of maternal postpartum mass (MPPM) on growth rate and weaning mass (see below). Among 49 females, maternal age had no significant effect on birth date, a finding also reported by Pomeroy et al. (1999) for grey seals at North Rona. However, unlike on Sable Island (Boness et al. 1995), heavier females gave birth earlier in the season on North Rona (Anderson & Fedak 1987; Pomeroy et al. 1999).

By contrast, birth date and location appear to have little effect on offspring phenotype in harbor seals (*Phoca vitulina*). This species gives birth in relatively small colonies where female density is moderate and, because mating occurs aquatically, males do not interact with lactating females on land. Unlike the larger phocid species, harbor seal females forage during lactation and both the timing and extent of foraging are inversely related to MPPM (Bowen et al. 2001). Neither MPPM nor the age of females giving birth varied over the course of the breeding season. The birth mass and relative birth mass (pup birth mass/MPPM) of pups were not correlated with birth date, and the mean birth dates of male and female pups did not differ significantly (Bowen et al. 1994; Ellis et al. 2000). Although there was no overall effect of age on birth dates, pups with lanugo (i.e., less developed pups covered with fetal pelage) were lighter and were born earlier in the breeding season to younger and lighter females (Ellis et al. 2000). Thus, there is some evidence that the timing of birth affects offspring size and stage of development in this species, but the effects are weak compared with other species.

The effects of birth date on offspring phenotype are also evident in fur seals and sea lions. In northern fur seals (*Callorhinus ursinus*), older, heavier females gave birth earlier than other females, but maternal age was a stronger determinant of birth date than MPPM (Boltnev & York 2001). Trites (1991) also found that the oldest northern fur seal females gave birth early in the season to larger pups and that primiparous females tended to give birth in midseason to smaller pups. Thus birth mass decreases throughout

the season as does maternal body size (Bigg 1986). Similar effects are found in Antarctic fur seals (*Arctocephalus gazella*), where birth mass decreases throughout the season along with a decrease in the length and mass of females (Boyd & McCann 1989; Lunn & Boyd 1993). However, maternal length accounted for almost twice as much of the variation in birth mass as did body mass. The authors speculated that larger, more experienced females were able to replenish reserves early and gave birth in prime sites when density in the colony was low. By contrast, in subantarctic fur seals (*Arctocephalus tropicalis*) larger females gave birth later in the season. Given that pup birth mass is positively correlated with maternal length in this species, birth mass increased over the course of the breeding season (Georges & Guinet 2000). In South American sea lions (*Otaria flavescens*), Campagna et al. (1992) found that mortality over the first month of life was higher in pups born early (32%) than those born during the peak of births (0.7%). Also, the mortality rate of pups born to solitary females was significantly higher than that in females that gave birth in harems. Pups born to solitary females were also lighter than similarly aged harem-born pups and were more likely to die (63%) than those born in harems (11%). Those pups died mostly from starvation and infanticide by males, which was rare in harems.

EFFECTS OF MATERNAL BEHAVIOR

Maternal behavior is likely an important source of maternal effects in pinnipeds, but has been less studied than other types of effects. In fur seals and sea lions, maternal foraging success during the lactation period largely determines the quantity of nutrients (i.e., milk) that females have available to provision their offspring. The relationships between the characteristics of maternal foraging and offspring traits are best studied in the Antarctic fur seal, where Lunn et al. (1994) showed that the average maternal foraging-trip duration in the current and previous year were negatively related to pup birth mass. Doidge & Croxall (1989) showed that the weaning mass of female pups was positively related to the time spent by the female onshore, indicating that females that spent less time foraging produced larger offspring. At Heard Island, another Antarctic fur seal colony, Goldsworthy (1995) also found that the rate of mass gain was positively related to the duration of preceding and subsequent maternal foraging trips, but the effect was observed only in male pups. In contrast, the rate of mass gain of female pups was positively related to the duration of maternal attendance. Differences in maternal condition did not explain these sex-specific effects

on offspring in this or other Antarctic fur seal populations (Costa et al. 1989; Doidge & Croxall 1989).

By contrast, Georges & Guinet (2000) found that subantarctic fur seal females in better condition before beginning to nurse had longer attendance periods. Pups whose mothers were large and performed short and regular foraging trips grew faster, and were heavier at weaning. Large mothers were also more efficient when foraging as reflected by maternal mass gain during foraging trips, a pattern also found in Antarctic fur seals (Boyd et al. 1991).

Among the generally smaller phocid species, in which females feed to some extent during lactation, there is evidence that smaller, and presumably younger, females (i.e., those below the median mass) were significantly more likely to become separated from their pup during storms than larger females (Boness et al. 1992). Time spent foraging in harbor seal females varied inversely with MPPM during late lactation; similarly, the proportion of daily energy expenditure fueled by food intake during lactation varied inversely with MPPM in late lactation, but not in early lactation (Bowen et al. 2001). There is also some evidence that in Weddell seals (*Leptonychotes weddellii*) the efficiency of energy transfer to pups is negatively correlated with MPPM, indicating that lighter mothers reduce their mass loss by feeding during lactation. However, the effects of variation in maternal foraging and attendance behavior on offspring traits are presumably small in this species, as only 13% of the variation in efficiency was explained by MPPM (Testa et al. 1989). This conclusion is supported by a recent study showing that MPPM was not related to the efficiency of nutrient transfer to Weddell seal pups (Wheatley et al. 2006).

Maternal dominance and aggressive behavior toward conspecifics provide another avenue for maternal effects. For example, older, more experienced northern elephant seal females were more aggressive and won more interactions with neighboring females; however, the relative importance of successful aggression, age, and experience could not be isolated because they were highly correlated (Sydeman et al. 1991).

EFFECTS OF MATERNAL AGE AND MASS ON SIZE AND GROWTH OF OFFSPRING

Offspring size is an important life-history trait because variation in initial body size of progeny can affect their subsequent growth and survival (Mousseau & Fox 1998). Although data are available for only a few species, there is increasing evidence that offspring size also affects growth and survival in

pinnipeds (see below) and is presumably positively correlated with adult size and reproductive performance. For example, in northern fur seals there is a positive relationship between body mass of males at ages 2–4 years and body mass at weaning (Baker et al. 1994). Nevertheless, the relationship between offspring size and fitness is virtually unstudied among pinnipeds.

Offspring size at weaning is largely determined by size at birth (a measure of prenatal energy investment of females), neonatal growth rate, and the duration of lactation (i.e., the quantity of nutrients and period of maternal provisioning). In pinnipeds, and particularly in members of the Phocidae, variation in offspring size and growth rate are expected to have a large non-Mendelian component as female energy stores (Pomeroy et al. 1999; Crocker et al. 2006) or access to food during lactation (e.g., Costa et al. 1989) can differ significantly from one reproductive event to another, and those differences can directly affect offspring phenotype through the quantity of milk provided. Also, pinnipeds are long-lived species (20–40 years) that continue to grow well after their first reproductive event (McLaren 1993), providing successful females with the opportunity to improve skills or enhance resources that increase the probability of successfully rearing offspring. Thus, in addition to the timing and location of birth and behavioral traits, we should expect MPPM, body condition, age, and breeding experience to affect the phenotype of pinniped offspring.

Offspring Size at Birth

The effects of maternal traits on offspring size at birth have been studied in both otariid and phocid species. The two most commonly measured maternal traits are MPPM and age. In the 10 species for which there are data, pup birth mass was positively related to MPPM, with two exceptions, the harp seal (*Phoca groenlandica*) and hooded seal (*Cystophora cristata*, Table 6-1). In these species, the relatively small sample may limit our ability to detect the effect. In most species, the effect of MPPM on pup birth mass is characterized by a linear relationship indicating that heavier females give birth to larger pups. Nevertheless, there are considerable differences among species in the amount of variation in birth mass that is explained by MPPM (Table 6-1). Explained variation averages $19.7\% \pm 4.8$ SE in the 3 otariid species and $20.3\% \pm 5.9$ in the 5 phocid species (24.6% if harp and hooded seals are excluded because of small sample sizes), providing no evidence of a difference between families (t-tests, $p = 0.84$ and 0.56 , respectively).

In several species (northern fur seals, harbor seals, and southern elephant seals), there is evidence that pup birth mass initially increases with an

Table 6-1. Nature and strength of relationship between mean maternal postpartum body mass (MPPM) and mean pup mass in pinnipeds. R^2 and number of mother-pup pairs given in square brackets.

Species	MPPM		Relationship with pup trait				Sources
	(kg) ^a	Lactation time (d) ^a	Birth mass	Rate mass gain	Weaning mass		
Antarctic fur seal	39	116	+ [25%, 47]; + [18%, 45] _m	+ ^b [34% _m , 38; 58% _f , 41]	Nonsignificant [d, 63]	1, 2, 3, 4	
Northern fur seal	41	118	+, asymptotic [10%, 250]	N/A	N/A	5	
Subantarctic fur seal	50	300	+ ^b [24%, 86]	+ ^b	N/A	6	
Harbor seal	85	24	+, curvilinear [20%, 244]	+ [19%, 100]	+ [26%, 100]	7, 8	
Harp seal	139	12	nonsignificant [13]	N/A	nonsignificant [49]	9	
Grey seal	190	17	+ [23%, 251]	+ [28%, 16], + [49% ^c , 97]	+ [44%, 228]	10, 11, 12	
Hooded seal	236	4	nonsignificant [19]	+ ^c [40%, 26]	+ [58%, 15]	13	
Weddell seal	447	50	+ [76%, 54]	+ ^c [94%, 10]	+ [d, 47]	14, 15	
Northern elephant seal	488	26	+ [38%, 27]	+ [42%, 27]	+ [44%, 27]	16	
Southern elephant seal	529	24	+ asymptotic [37, 30% _m , 80, 71 _m]; + [36%, 38]	+ [77%, 26]	+ [61%, 38]; + [52% _m , 66% _f , 53, 90 _f]	17, 18, 19	

^a based on largest sample size from Schulz & Bowen (2004); ^b maternal body length; ^m male; ^f female; ^c maternal mass loss; ^d not reported; N/A = not available.

Sources: 1. Costa et al. 1988; 2. Boyd & McCann 1989; 3. Doidge & Crossall 1989; 4. Guinet et al. 2000; 5. Boltnev & York 2001; 6. Georges & Guinet 2000; 7. Ellis et al. 2000; 8. Bowen et al. 2001; 9. R. Stewart (pers comm.); 10. Bowen et al. 2006; 11. Pomeroy et al. 1999; 12. Mellish et al. 1999; 13. Kovacs & Lavigne 1992; 14. Tedman & Green 1987; 15. Wheatley et al. 2006; 16. Deutsch et al. 1994; 17. Arnborn et al. 1994; 18. Carlini 1998; 19. Arnborn et al. 1993.

increase in MPPM and then levels off despite further increases in MPPM. However, the relationships are quite different in these three species. In northern fur seals and southern elephant seals, MPPM has little effect on pup birth mass except in the lightest females, whereas in the harbor seal there is a linear relationship with MPPM over most of the range of female masses and only in the heaviest females does the effect disappear (Ellis et al. 2000). With so few species having been studied, the significance of these differing patterns among species is unclear.

The effect of maternal age on pup birth mass has been reported in only seven species (Table 6-2). In contrast to the effect of MPPM, maternal age generally has a nonlinear relationship with pup birth mass and in two species, northern fur seals and grey seals, there is evidence of a quadratic or dome-shaped relationship such that the oldest females give birth to lighter pups than intermediate-aged females (Figure 6-1) providing evidence for senescence. The effect of maternal age on pup birth mass appears to be significantly greater among phocids ($41.3\% \pm 6.7$ SE) than among otariids (mean = $5.3\% \pm 0.7$, t-test with unequal variances, $p = 0.03$), but firm conclusions must await data on more species.

Given that maternal age and MPPM are correlated during part of the female's life, understanding the relative effects of age and size requires that these traits be studied simultaneously within the same females. Boltnev & York (2001) studied the relationships between MPPM, age, and pup birth mass in northern fur seals. They found that MPPM was positively correlated with pup birth mass in females less than the median mass, but not for females greater than the median mass. Female body mass alone explained about 17% of the observed variability in pup mass at birth. Female age also had significant linear and quadratic effects on birth mass in both male and female pups. The best fitting model, which included pup sex, female age, and mass and parturition date, explained 33% of the variation in pup birth mass, with age and MPPM accounting for 43% and 7% of the variation, respectively. When pup mass was modeled as a logistic function of MPPM and a quadratic function of maternal age (as indicated by the data), the best model again explained about a third of the variability in birth mass. However, the importance of maternal traits was quite different, with maternal age accounting for only 18% and MPPM accounting for 32% of the explained variation. This analysis underscores the difficulty in determining the relative effects of such correlated maternal traits.

The relative influence of maternal age and mass on pup size at birth has been studied in several phocid species. Northern and southern elephant

Table 6-2. Effects of maternal age and breeding experience on offspring mass in pinnipeds. R^2 and number of mother-pup pairs given in square brackets.

Species	Age range (yr)	Relationship with pup trait				Sources
		Birth mass	Rate mass gain	Weaning mass		
Antarctic fur seal	3-14	+, asymptotic [4-5%, 1037]; inconsistent	nonsignificant [100]	+ [14%, 29]		1, 2, 3
Northern fur seal	3-23	+ ^a [43.56]; quadratic [6%; 250]	N/A	N/A		4, 5
Harbor seal	4-16	+, asymptotic [54%, 75]	+ ^b [14%, 68]; nonsignificant ^c	nonsignificant [74]		6, 7, 8
Harp seal	4-25	nonsignificant [13]	N/A	domed [9.3%, 49]		9
Grey seal	4-42	domed [39%, 251]	quadratic [24%, 228]	domed [51%, 228]		10, 11
Weddell seal	^d	nonsignificant when MPPM entered into the model	N/A	nonsignificant when MPPM entered into the model		12
Northern elephant seal	3-13+	+ [31%, 41]	+, curvilinear [17%, 39]	+ curvilinear [31%, 63]		13, 14
Southern elephant seal	4-22	N/A	nonsignificant when MPPM entered into the model	nonsignificant when MPPM entered into the model		15

^a fetal mass; ^b through midlactation; ^c through entire lactation period; ^d not reported; N/A = not available.

Sources: 1. Lunn et al. 1994; 2. Lunn & Boyd 1993; 3. Lunn et al. 1993; 4. Trites 1991; 5. Boltnev & York 2001; 6. Ellis et al. 2000; 7. Bowen et al. 2001; 8. Bowen et al. 2003; 9. R. Stewart (pers. comm.); 10. Bowen et al. 2006; 11. Bowen et al. (unpublished); 12. Wheatley et al. 2006; 13. Sydeman et al. 1991; 14. Deutsch et al. 1994; 15. Arnborn et al. 1997.

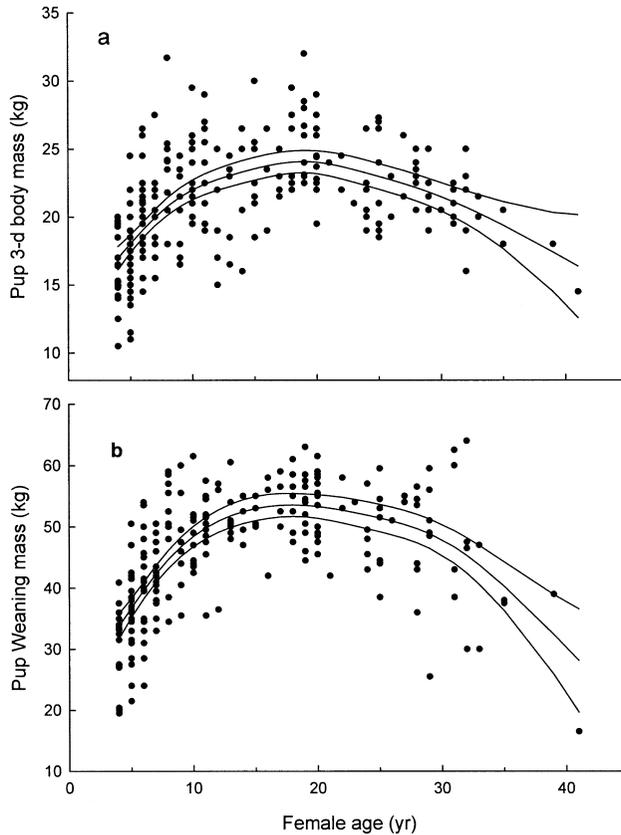


Figure 6-1. Age-related changes in (a) pup 3-day and (b) weaning mass in grey seals (after Bowen et al. 2006). Curves represent fitted values and 95% pointwise confidence limits from generalized additive models. Each symbol represents an independent mother-offspring pair.

seals are the two largest phocid species and mothers provision pups on an energy-rich milk for approximately one month. In both species, pup birth mass was positively correlated with MPPM (McCann et al. 1989; Deutsch et al. 1994) and with maternal age in the northern species, but maternal age had no significant effect on birth mass after adjusting for MPPM (Deutsch et al. 1994). Similarly, Arnborn et al. (1994) showed that heavier southern elephant seal mothers (up to ~550 kg) gave birth to heavier pups, but that there was little relationship between pup birth mass and MPPM in females > 550 kg. Maternal age was not a significant variable when MPPM was included in the model. There is also evidence that MPPM affects the sex ratio of southern elephant seal pups, in that small females (i.e., < ~350 kg) gave birth only

to female pups and the sex ratio of pups increased rapidly in females up to about 425 kg, with no detectable increase thereafter (Arnbom et al. 1994). Maternal age had no significant effect on sex ratio once MPPM was entered into the analysis. By contrast, maternal age explained a significant amount of the variation in pup birth mass of grey seals after statistically controlling for the effects of MPPM (Bowen et al. 2006).

The harbor seal is a relatively small species (MPPM = 85 kg) in which most females must forage during lactation to support the energetic cost of milk production (Boness et al. 1994; Thompson et al. 1994; Bowen et al. 2001). In this species, older mothers bore heavier pups even after controlling for the effects of MPPM on birth mass (31% explained variation), but this was not true for heavier mothers after controlling for the effect of maternal age (Ellis et al. 2000). Thus age, and not body mass, appears to be the primary influence on pup birth mass in this species. Ellis et al. (2000) also used PATH analysis to simultaneously examine the effects of maternal mass and age on pup birth mass in harbor seals. They constructed an overall model using females of all ages and separate models for three age classes representing different levels of reproductive experience. In the overall model, the strongest effects were of maternal age (path coefficient = 0.79) and mass (0.15) on birth mass, but age was several times as important as mass. In the separate age class models, only the model for the youngest females (4–6 years) had interaction strengths similar to the overall model. For older females (7–10 years) only negative relationships between birth date and maternal mass on percentage lanugo (i.e., fetal pelage) were significant, and in the oldest females (11–16) none of the paths was significant. Thus, the significant effects of maternal age, but also of MPPM, on pup birth mass were limited to the youngest females indicating an asymptotic relationship between these traits and pup birth size.

Offspring Growth Rate and Weaning Mass

The rate at which females allocate nutrients to their offspring affects both the rate of offspring growth during lactation and offspring size at weaning. Therefore, factors influencing the provisioning rates of offspring by females have received considerable attention, but again only in a handful of pinniped species. Evidence for the effects of MPPM on pup growth rate and weaning mass comes largely from phocid species. To a great extent this simply reflects the greater difficulty in conducting studies on fur seals and seal lions with their long periods of lactation (often > 1 yr). However, even among the phocid species there is a bias toward research on larger species. Neverthe-

less, as predicted, there are positive relationships between pup growth rate and weaning mass and MPPM in all 6 phocid species studied to date, accounting for an average of 51.7% and 48.7% of the variance, respectively (Table 6-1). There are no reported studies on otariids, but two studies found a positive relationship between pup growth rate and maternal length (Table 6-1), suggesting that MPPM might have been a significant factor had it been measured. Only in the Antarctic fur seal are there data on the relationship between weaning mass and MPPM; in this species, MPPM was not a significant factor (Doidge & Croxall 1989).

The effects of maternal age on pup growth rate and weaning mass are less evident, having been found in only five (1 otariid and 4 phocids) of the 7 species studied (Table 6-2). Furthermore, the results are inconsistent among species. In the case of pup growth rate, only in grey seals and northern elephant seals was there evidence for an effect of maternal age, accounting for 24% and 17% of variance, respectively. In both species the relationship was curvilinear, but in grey seals a quadratic relationship best fit the data, again providing evidence of senescent decline. In harbor seals, there was a positive relation between pup growth rate and maternal age through mid-lactation, but this relationship was no longer significant at weaning (Bowen et al. 2001). In the only otariid studied, maternal age did not account for a significant fraction of the variability in pup growth rate (Table 6-2). Maternal age accounted for an average of 26.3% of the variability in weaning mass among the four species for which there is evidence for an age effect (Table 6-2). Age was not a significant factor after MPPM was included in the model for harbor seals, southern elephant seals, and Weddell seals (Bowen et al. 2001; Arnborn et al. 1997; Wheatley et al. 2006).

Milk Energy Intake

Studies on the energetics of lactation can provide an understanding of some of the mechanisms underlying maternal effects on growth and development. In the case of phocids, this is due to the positive correlations between MPPM and maternal age and milk energy output within species (e.g., Iverson et al. 1993; Mellish et al. 1999; Crocker et al. 2001).

Milk energy output over all or a portion of lactation has been estimated in 14 species, including 9 phocids, although most studies are based on small numbers of females or cover only a small fraction of the lactation period (reviewed in Schulz & Bowen 2004). Nevertheless, in several species the relationships among female traits, milk energy output, and offspring growth and weaning mass are well understood. One example is the grey seal (Iver-

son et al. 1993; Mellish et al. 1999). In this species, isotope dilution studies have shown that females at the beginning of lactation vary considerably in total body fat and protein content, but that the ratio of fat to protein is independent of MPPM. This indicates that larger females have absolutely more stored resources to allocate to offspring, but not relatively more. Females produce an energy-rich milk comprising ~60% fat through mid to late lactation. However, the fat content of the milk of individual females ranges from about 45% to 65% (Iverson et al. 1993). Furthermore, differences in milk composition appear to persist among years within females, suggesting that they have a strong genetic basis (Lang et al. 2001). Females expend almost 50% of their fat reserves over the course of lactation, resulting in a loss of 31.4% of MPPM over 17 days. MPPM accounts for about 32–53% of the variability in total milk output. Daily milk energy intake accounts for 85% of the variability in the daily rate of mass gained by pups. Lactation length is positively related to MPPM, with the heaviest females lactating for almost twice as long as the smallest females. Thus, the best predictor of pup weaning mass was total milk energy intake (i.e., daily intake \times lactation length), explaining 88.4% of the variability. Pups of larger females are not only heavier at weaning but are relatively fatter than lighter pups, and this is presumably one of the factors resulting in improved survival of larger pups (see Hall et al. 2001; 2002). Similar relationships between maternal traits and pup growth rate and weaning mass are also evident in other phocid species: elephant seals (Fedak et al. 1996; Crocker et al. 2001), Weddell seals (Tedman & Green 1987; Wheatley et al. 2006), hooded seals (Bowen et al. 1987; Oftedal et al. 1993), and harp seals (Oftedal et al. 1996).

EFFECTS OF PARITY

Reproductive experience is imperfectly correlated with maternal age. Thus, it is useful to examine the effect of parity on maternal lactation performance and offspring traits. In northern fur seals, primiparous females are lighter and shorter than multiparous females and carry smaller fetuses that multiparous females (corrected for age and sampling date; Trites 1991). However, differences in fetal body mass were not entirely accounted for by differences in female body size, suggesting that physiological changes resulting from having given birth (perhaps leading to improvement in fetal nutrition) were involved. In harbor seals, primiparous females gave birth to significantly lighter pups than multiparous females, even after controlling for the effects of maternal age on birth mass (Ellis et al. 2000). In grey seals, pup birth mass

was positively related to increasing reproductive experience over the first three parities, even after the effects of MPPM had been statistically removed (Bowen et al. 2006). In contrast, parity had little effect on pup weaning mass in grey seals, when MPPM was included in the analysis.

Age at primiparity had no effect on birth mass or weaning success in Antarctic fur seals (Lunn et al. 1994). Similarly, in primiparous grey seals and harbor seals, age at primiparity had no significant effect on pup birth mass (Bowen et al. 2006; Ellis et al. 2000). Pup weaning mass did increase with age at primiparity in grey seals, but the effect of age became nonsignificant once MPPM was included in the analysis (Bowen et al. 2006).

THE RELATION BETWEEN MATERNAL/OFFSPRING TRAITS AND OFFSPRING SURVIVAL

Maternal effects need not necessarily be adaptive. For example, the maternal transmission of parasites or toxins may have negative effects on offspring (Clark & Galef 1995). However, many maternal effects are presumed to be adaptive, and in some cases, there is evidence that this is indeed the case. For example, in northern elephant seals, a higher proportion of female pups born early in the season survived to reproduce and gave birth for the first time at an earlier age than female pups born during the peak or late season (Reiter et al. 1981), presumably because early-born females were larger. There is also evidence from several species linking offspring traits, particularly size and growth rate, with improved survival (see Table 6-3), suggesting that we can also expect to find that higher-quality offspring will indeed have greater reproductive success.

The most convincing evidence that maternal effects improve survival comes from studies of the larger phocid species because these species are accessible during lactation and juveniles return to relatively few haul-out sites, where they can be resighted. Effects on survival can be partitioned into those occurring prior to weaning and those occurring after weaning (Table 6-3). Reiter & Le Boeuf (1991) found that reproductive success (i.e., the proportion weaned, a measure of preweaning survival) increased with maternal age, with prime northern elephant seal females (6+ years) on Año Nuevo about twice as likely to be successful as young females. The differences between the two groups of females were greatest during years of bad weather or when the density of harems was high, suggesting that these effects are modified by environmental and social factors. Working on the Faral-

Table 6-3. Effects of maternal and offspring phenotype on offspring survival.

Species	Effect on offspring survival		Sources
	Preweaning	Postweaning	
Antarctic fur seal	+, related to maternal foraging trip duration and with female pup growth rate	N/A	1
Northern fur seal	+, greater pup birth mass and length	+, greater late lactation male body mass	2, 3, 4
Subantarctic fur seal	+, greater pup birth mass	N/A	5
Harbor seal	N/A	nonlinear, asymptotic function of late autumn body mass	6
Grey seal	quadratic function of maternal age	+, greater weaning mass and body condition and lower immunoglobulin levels	7, 8, 9
Weddell seal	+, greater maternal age, multiparous > primiparous females	+, maternal age and experience	10
Northern elephant sea	+, maternal age	+, greater pup length, no effect of pup mass	11, 12, 13
Southern elephant seal	N/A	+, nonlinear function greater pup weaning mass	14

N/A = not available.

Sources: 1. Boyd et al. 1995; 2. Boltnev et al. 1998; 3. Baker & Fowler 1992; 4. Baker et al. 1994; 5. Mison-Jooste 1999; 6. Harding et al. 2005; 7. Bowen et al. 2006; 8. Hall et al. 2001; 9. Hall et al. 2002; 10. Hastings & Testa 1998; 11. Reiter et al. 1978; 12. Sydeman et al. 1991; 13. Le Boeuf et al. 1994; 14. McMahon et al. 2003.

lon Islands, Sydeman et al. (1991) showed that weaning success in northern elephant seal females increased from 3–7 years of age and then leveled off. However, after statistically controlling for previous reproductive experience, weaning success increased linearly throughout the life of a female. In Weddell seals at McMurdo Sound, Antarctica, Hastings & Testa (1998) found that pup preweaning mortality was significantly higher for primiparous females (7.1%) than multiparous females (3.2%). However, there was no effect of female parity on pup preweaning survival among multiparous females ($n =$

228 females and 627 pups) indicating that the effect was limited to first-time breeders. In grey seals breeding on Sable Island, Canada, the proportion of females successfully weaning offspring increased with maternal age and mass from ages 4–7 years, varied without trend from age ~8–33 years, and then declined sharply in the oldest females (Bowen et al. 2006). As most 6- and 7-year-old grey seal females were multiparous, the improvement in pup preweaning survival was not limited to those born to primiparous females, as in Weddell seals.

Although there is strong evidence for the effects of maternal traits on offspring size and development (Tables 6-1 & 6-2), there are few studies that directly link maternal traits with postweaning survival of offspring. Nevertheless, there is increasing indirect evidence that maternal traits can be expected to influence offspring survival. Hall et al. (2001) found that the probability of postweaning survival to age 1 year in grey seals increased with body condition at weaning, which in turn is affected by maternal condition (Pomeroy et al. 1999). Regardless of the body condition of pups or the time of year, survival of female pups was estimated to be 3.4 times as great as that of males, although the reason for this difference was unknown. Furthermore, regardless of sex, a 1-standard-deviation increase in body condition of pups was estimated to increase survival by 1.4 times. In a subsequent study at another colony, both body condition and a measure of pup immune function, serum gammaglobulin (IgG), were assessed (Hall et al. 2002). Again, increased body mass or condition of grey seal pups was positively related to survival, but higher postweaning circulating levels of IgG decreased the probability of survival. It was not known if this was because some individuals had naturally higher IgG levels or because levels were higher due to antigenic challenge. In Hawaiian monk seals (*Monachus schauinslandi*), the probability of survival from weaning to age 2 years at French Frigate Shoals was significantly related to offspring size at weaning for 1984–1987 cohorts and to measures of physical condition for the 1990–1994 cohorts (Craig & Ragen 1999). Again, the effect of offspring traits on survival was modified by environmental variation, as there was no relationship between survival of the 1988–1989 cohorts and size at weaning and the relationships differed at another breeding colony. At both study sites, the nature of the relationships between offspring traits and survival also changed over time.

In Weddell seals, although the survival of pups to 1 year of age did not vary with maternal age and parity, survival to age 6 increased with age of the mother (Hastings & Testa 1998). Annual survival of pups to all ages also increased with the body length of the mother and increased with maternal

length for male offspring, but not for females. In small mothers, survival was higher for female offspring than male offspring, whereas in large mothers survival was higher for male pups than female pups during both the first and subsequent years.

In the two largest phocid species, there is conflicting evidence regarding the effect of offspring size on survival. Le Boeuf et al. (1994) found no relationship between survival to ages 1 and 2 years and weaning mass in northern elephant seals; however, there was a positive relationship between survival and length to age 1, but not to age 2. However, these estimates were made during a period of rapid population growth. Thus, the inconsistent and relatively weak effects of offspring traits on survival could reflect the presumably favorable conditions experienced by these juveniles. By contrast, in two colonies of southern elephant seals, one larger and declining (Macquarie Island) and one that had recently stabilized (Marion Island), McMahan et al. (2003) found that pups that survived were significantly heavier at weaning than those that did not survive. Survival rates differed between the two colonies, and the functional form of the relationship with weaning mass also differed. At Macquarie Island first-year survival was a polynomial function of weaning mass, whereas at Marion Island survival was best described by an exponential function of weaning mass.

Harding et al. (2005) also found that the relationship between winter survival rate of harbor seals pups and their autumn body mass was a nonlinear, asymptotic function. They calculated that increasing thermal stress with decreasing body size and low winter temperatures may result in a negative energy balance resulting in increased mortality in smaller pups. This is consistent with the finding that food intake and changes in body condition in harbor seals over the first month postweaning were a function of their body mass at weaning (Muelbert et al. 2003). Heavier pups were relatively fatter than lighter pups and therefore had significantly greater total body energy. Furthermore, the temporal pattern and composition of mass loss differed between heavier and lighter pups, with lighter pups mobilizing their blubber stores earlier than heavier pups.

Less is known about the links between maternal and offspring traits and offspring survival in otariids. In Antarctic fur seals, pup preweaning mortality was positively related to the foraging trip duration of mothers during lactation, but negatively related to growth rate in female pups only (Boyd et al. 1995). In northern fur seals, larger pups at birth survived significantly better to 40 days postpartum (i.e., ~33% of lactation) than smaller pups (Boltnnev et al. 1998). High birth mass was also associated with reduced newborn

mortality throughout the pupping season in Cape fur seals (*Arctocephalus tropicalis*; Mison-Jooste 1999).

The effect of offspring traits on postweaning survival in otariids is known only in the northern fur seal. On St. Paul Island, Alaska, males that survived at least two years were heavier than the mean for their cohort as pups (Baker & Fowler 1992). This effect was not evident in female pups, but the sample was too small to draw firm conclusions. In a follow-up study on cohorts born in the late 1980s and early 1990s, when pup body masses were considerably higher than during the 1960s, Baker et al. (1994) found that larger-than-average males still survived better than smaller individuals, but the difference was less evident during this period of more favorable conditions (i.e., heavier pups) compared to the 1960s.

FACTORS AFFECTING THE EXPRESSION OF MATERNAL EFFECTS

The expression of maternal effects is to some extent contingent on features of both parent and offspring environments (e.g., Riska et al. 1985; Bernardo 1996; Rossiter 1996). Environmental factors such as colony density and weather can affect the ability of mothers to maintain contact with their offspring. In northern elephant seals, the proportion of pups separated from their mothers varied from -24 to 57% at the crowded Point Harem colony over a 4-year period. Adult and subadult males caused about half of the separations with weather as a cofactor. Twenty-eight percent of separations were caused by pups wandering away from their mothers. Although separations were often short, a high proportion (48–66%) of orphaned pups (i.e., those separated for > 2 days) died, underscoring the importance of female vigilance (Reidman & Le Boeuf 1982). Density effects can also be important within season. Northern elephant seal females that arrived earlier and were more successful in female interactions were more likely to successfully wean their offspring than other females. These effects were again mediated by colony density, with females that pupped in areas of lower density being more successful (Ribic 1988). Sydeman et al. (1991) showed that weaning success in younger females declined over the breeding season even after adjusting for breeding experience, presumably because they were negatively affected by increased colony density. However, the weaning success of older females did not change. Similarly, as noted above, grey seal females that gave birth early in the breeding season, when colony density and male harassment were lower, produced heavier pups (Boness et al. 1995).

Given the high cost of lactation in mammals, interannual variability in

access to food seems an obvious avenue to influence the expression of maternal effects on offspring traits. Antarctic fur seal females feed mainly on krill (*Euphausia superba*) during the breeding season and respond strongly to interannual variation in krill abundance, which is patchily distributed. During 1990–1991, a year of low krill abundance, female fur seals spent significantly greater effort, both in terms of time and activity while foraging, than usual (Boyd et al. 1994). Despite this greater foraging effort (estimated at one-third to one-half greater than normal), mothers were unable to meet the energy demands of lactation, resulting in lower pup growth rates and increased pup mortality (Lunn & Boyd 1993; Lunn et al. 1994).

There is evidence that environmental variability also affects foraging success, body condition, and offspring size and survival in several phocid species. During strong El Niño events, the daily rate of mass gained by adult female northern elephant seals was only 33% of that during weak or non-El Niño years and females returned to the breeding colony with significantly lower fat stores and reduced natality (Crocker et al. 2006). At decadal scales, less extreme variability in the foraging success and energy storage of adult northern elephant seal females had direct consequences for pup weaning mass, with reduced maternal mass gain resulting in lighter pups (Le Boeuf & Crocker 2005).

Another Pacific pinniped species, the Hawaiian monk seal, appears to benefit from strong El Niño events. Antonelis et al. (2003) found that after accounting for temporal trends from 1983 to 2001, the girths of pups were 3.7 cm (3.5%) and 2.7 cm (2.5%) greater during El Niño years at French Frigate Shoals and Laysan Island, respectively. Average pup weaning masses were significantly greater during El Niño years at French Frigate Shoals (+2.6 kg or 4.0%), but were not significantly different at Laysan Island (+1.8 kg). Pups born at French Frigate Shoals during El Niño years also survived significantly better, but this effect was not detected at Laysan Island. Given the life history of the species, the authors reasonably speculated that the increase in pup weaning mass was likely associated with increases in the abundance of available monk-seal prey that would enhance female foraging success during gestation, improve her body condition, and thereby increase the energy transfer to her offspring from milk.

CONCLUSIONS

Although relatively few species have been studied, there is evidence that offspring phenotype in pinnipeds is influenced by both maternal inheritance

and maternal selection. Pinniped offspring are affected by maternal decisions about the timing and location of birth, the foraging ability of mothers, and the ability of mothers to defend and maintain contact with dependent offspring. Larger, older, and in some cases more experienced females give birth to larger pups, which then grow faster during lactation and are heavier at weaning. There is also compelling evidence from a number of species that offspring size at weaning increases the postweaning survival of offspring for one or more years and to the age of first reproduction. These results have implications for life-history theory predictions about the trade-off between maternal growth and reproductive expenditure over the life of a female, as a critical assumption is that the amount of resources allocated to offspring affects fitness.

The expression of maternal effects on offspring phenotype in pinnipeds is clearly influenced by maternal and offspring environments. These include changes in colony density within and among breeding seasons, social structure, and variation in the availability of food either prior to, in the case of most phocids, or both prior to and during the period of offspring provisioning, in the smaller phocids and otariids. These environmental factors modify the expression of maternal effects to the extent that in some contexts they may not be evident, for example, at low density or high food availability. Thus, future studies should measure relevant environmental factors to provide an ecological context in which to interpret findings.

There are somewhat conflicting results on the relative importance of maternal postpartum mass (MPPM), age, and reproductive experience on offspring traits in pinnipeds. This is partly due to the positive correlation among these maternal traits, making it more difficult to tease out the independent effects. However, other factors also potentially limit inferences, including small sample size, the range of MPPM and age included in analyses, environmental conditions, and the demography of the study population. Furthermore, only 30% of pinniped species have been studied, and even within the better-studied Phocidae, there is a bias toward the larger, more accessible species. Therefore, a comparative analysis of frequency and relative importance of maternal effects in pinnipeds is premature.

Offspring phenotype is the product of its genes, the environment in which those genes are expressed, the gene-environment interaction, and maternal effects. Parental environment often plays a large role in the magnitude and nature of the maternal effects. The attributes of the parental environment are often a permanent feature of the species' environment, suggesting their importance as ecological and evolutionary forces (Rossiter 1996). However,

identifying the strength of maternal effects (reviewed in Rossiter 1996) requires that other influences on phenotype be accounted for. Quantitative genetics provides several approaches to estimate the relative contribution of genes and the environment to trait variation (e.g., Schluter & Gustafsson 1993). Breeding designs to estimate maternal effects may be straightforward for many taxa, but are impractical if not impossible for large, long-lived mammals such as pinnipeds and other marine mammals. Cross-fostering may be possible in some species, such as the Hawaiian monk seal in which females often suckle pups other than their own (although in practice these experiments could not be performed on such a critically endangered species); however, in most species, females do not foster. Therefore, in the absence of breeding experiments, we must be cautious in reaching conclusions about both the nature and strength of maternal effects in pinnipeds. One approach would be to make better use of long-term studies of the reproductive performance of individuals over time, thereby largely controlling for maternal nuclear gene contribution to offspring, although the contribution of sires will still partly confound interpretation.

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