

THE EVOLUTION OF LACTATION STRATEGIES IN PINNIPEDS: A PHYLOGENETIC ANALYSIS

TYLER M. SCHULZ^{1,3} AND W. DON BOWEN²

¹*Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada*

²*Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia B2Y 4A2, Canada*

Abstract. Pinnipeds are a diverse group of aquatic carnivores that exhibit wide variation in body size, milk composition, lactation strategies, and the length of maternal care. We used 12 pinniped life-history and ecological traits to test hypotheses concerning the influence of phylogeny, maternal body size, breeding substrate, and other factors on the evolution of lactation strategies. We used independent contrasts to account for phylogenetic effects on correlations between traits. Our findings indicate that the negative relationships between maternal mass and lactation length and between maternal mass and the percentage of time spent at sea by females during lactation are not recent adaptations, but likely a result of phylogenetic history and an evolutionary grade shift in lactation length, which occurred when the phocids diverged from the otariids. Differences in body size between the ancestral phocid and otariid impacted their foraging strategies and metabolic rates, which subsequently influenced lactation strategies. The fat-storage abilities of large phocids may have allowed them to exploit remote and patchy prey resources and thereby reduce time spent feeding during lactation. We also suggest that an early divergence in the mammary gland structure of phocids and otariids is a fundamental influence on pinniped lactation strategies. Although estimates are lacking for several key species, body size appears to have little adaptive influence on the lactation length of extant species. Instead, an abbreviated lactation period seems to be adaptive in minimizing the relative milk energy expended over lactation, although it may have initially evolved to reduce maternal overhead, especially in ancestral fasting phocids. Subsequently, a brief lactation in phocids was also selected through the effects of terrestrial predation, the instability of breeding on pack-ice, and the energy benefits of increasing milk energy output.

Key words: adaptation; lactation; life-history; maternal; phylogeny; pinnipeds.

INTRODUCTION

Parental care is an important component of reproduction in many animals (Clutton-Brock 1991). Thus patterns of parental investment and the factors that influence it have long been of interest to ecologists (e.g., Trivers 1972, Gubernick and Klopfer 1981). Although parental care can include offspring defense, feeding, and grooming, in mammals the greatest component of parental care by far is the provisioning of milk to the offspring, which simplifies the study of parental investment 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 (Boness and Bowen 1996), and hence are likely to be correlated. Still, understanding the factors that influence maternal reproductive effort in some mammalian groups is complicated by communal behaviour (Gittleman and Oftedal 1987), allomaternal care, multiple offspring litters, and postweaning maternal care.

In pinnipeds, however, there is no paternal care or alloparental support (Boness and Bowen 1996), and maternal care of a single pup ends at weaning (see Plate 1). The wide variation in lactation length, breeding habitat, and female body size, and the fact that maternal care occurs mainly through the provision of milk make the Pinnipedia an interesting group in which to examine the factors that influence maternal reproductive effort in mammals.

Lactation in the Pinnipedia (order Carnivora) is constrained by the spatial and temporal separation between giving birth on land or ice and acquiring nutrients for milk production at sea. Three basic lactation strategies have been recognized, and until relatively recently, each was thought to have evolved in a different family (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 d), 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. In contrast, the generally smaller-bodied otariid species (family Otariidae; fur seals and sea lions) breed on land, exhibit long lactation periods (116–540 d), and a foraging-

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³ E-mail: tmschulz@dal.ca

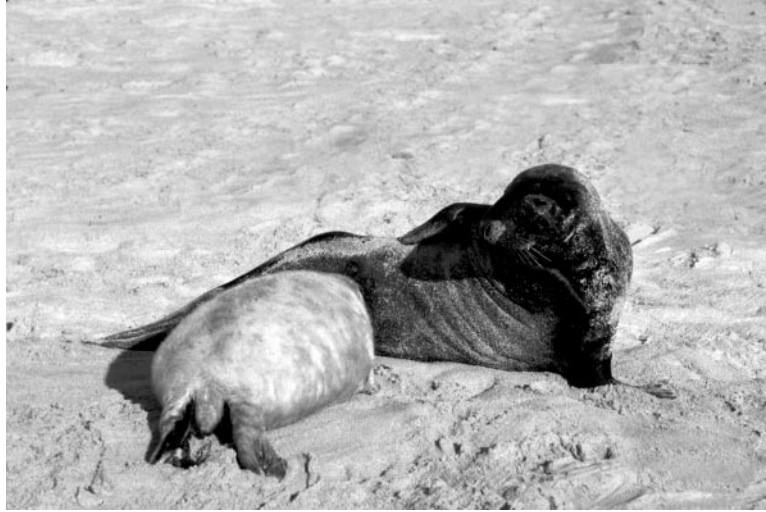


PLATE. 1. Grey seal (*Halichoerus grypus*) female and her suckling pup near the end of lactation at Sable Island, Nova Scotia. Photo credit: S. J. Iverson.

cycle strategy, during which females alternate feeding trips to sea with suckling bouts on land without the typical mammalian regression and involution of the mammary gland (Oftedal et al. 1987). 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 during which offspring accompany foraging mothers and suckle at sea. The observation that each family had apparently evolved a different lactation strategy implied that evolutionary history was the primary influence of lactation behavior. However, variation in lactation length, provisioning strategy, breeding substrate, and body size prompted researchers to advance adaptive hypotheses concerning the evolution of pinniped lactation strategies. Our growing understanding of the evolutionary relationships among pinnipeds, coupled with recent studies indicating that factors other than phylogeny may have been important in the evolution of lactation strategies (e.g., Boness and Bowen 1996, Lydersen and Kovacs 1999), suggests that the relative roles of phylogeny and ecology should be re-evaluated.

To date, evidence in support of these hypotheses has come from cross-species comparisons that treat species as independent observations. However, because species are descended in a hierarchical manner from common ancestors, they cannot be considered independent observations in statistical analyses (Felsenstein 1985, Harvey and Pagel 1991). In contrast, the independent contrasts method transforms species data such that they become largely independent and identically distributed (Felsenstein 1985). As a result, this method has become a widely used tool for removing phylogenetic similarity from interspecific comparisons, thereby permitting more credible tests of adaptive hypotheses. We used independent contrasts to re-examine hypotheses that had been advanced to account for correlations among

traits associated with lactation (Table 1). Both cross-species and phylogenetic correlations between life-history traits were conducted to determine the validity of conclusions from previous nonphylogenetic analyses (Ricklefs and Starck 1996).

The hypotheses

Although maternal reproductive effort in terrestrial mammals can be affected by diet, litter size, and the nature of parental care (Gittleman and Oftedal 1987), maternal 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. Although we tested the influence of these factors separately or in pairs, it is important to appreciate that they do not operate in isolation, but rather 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. These multiple factors have rarely been accounted for in previous analyses.

Maternal body size is thought to have strongly influenced the evolution of pinniped lactation strategies through its effects on a number of traits (Table 1). Most female phocids are both larger and have greater adipose stores per kilogram of body mass than female otariids (Costa 1991a). Thus, the body-size hypothesis predicts that large body size coupled with large fat reserves and low mass-specific metabolic rate allows large phocid females to rely solely on previously stored energy throughout lactation. By forgoing the time-consuming costs of foraging, large phocids are able to transfer the milk energy necessary to ensure pup survival in an abbreviated lactation period. In contrast, the smaller

TABLE 1. The correlations between life-history traits that were tested to evaluate the broad adaptive hypotheses outlined in the text.

Hypothesis and independent variable	Dependent variable	Expected relationship
Body-size hypothesis		
Maternal mass	lactation length	negative
	percentage of time spent at sea	negative
	total milk energy output	positive
	daily milk energy output	positive
	neonatal mass	positive
	weaning mass	positive
Breeding-substrate hypothesis		
Substrate stability	lactation length	positive
Maternal-overhead hypothesis		
Lactation length	percentage of maternal energy devoted to maternal overhead	positive
Milk-energy-costs hypothesis		
Lactation length	total milk energy output per metabolic mass	none/positive
Energy-transfer hypothesis		
Lactation length	daily milk energy output per metabolic mass	negative
	average percentage milk fat	negative
	pup growth rate	negative
Average percentage milk fat	pup growth rate	positive
	daily milk energy output	positive
Seasonal-productivity hypothesis		
Latitude	lactation length	negative
	percentage of time spent at sea	negative
Thermoregulation hypothesis		
Latitude	maternal mass	positive
	neonatal mass	positive
	average percentage milk fat	positive
Neonatal mass	daily milk energy output	positive
Additional correlations		
Neonatal mass	weaning mass	positive

Note: Sources for previously advanced or tested hypotheses are given in the *Introduction*.

body size of some phocids (e.g., the harbor seal, *Phoca vitulina*) and most otariids limits them to a foraging-cycle strategy. Alternatively, because of increased absolute metabolic costs of maintenance, large pinnipeds may not ordinarily be able to sustain the high energetic costs of both lactation and foraging during lactation unless access to rich local prey resources is available (Boyd 1998). This idea builds on the prey-proximity hypothesis (Costa 1993), which suggests that the fasting strategy of some phocids is an adaptation to feeding on patchy, highly dispersed, or distant prey resources, whereas otariids are adapted to local, rich, and predictable prey resources.

The breeding-substrate-stability hypothesis (Stirling 1975, 1983; Table 1) has been advanced to explain the short lactation periods in phocids. As unstable pack-ice can break up in strong winds and waves, resulting in the premature separation of mothers and pups or in death by crushing (Stirling 1975, Bonner 1984), the abbreviation of lactation may be an adaptation to ensure that the pup is weaned prior to the break-up of pack-ice (McLaren 1958, Bowen et al. 1985).

Another explanation for the abbreviation of lactation is the maternal-overhead hypothesis (Fedak and Anderson 1982), whereby shortening the duration of lactation increases the fraction of maternal energy stores that can be transferred to the pup, as total maternal overhead costs (i.e., the total energy devoted to maintaining maternal metabolism during the lactation period) are reduced. Under this hypothesis, it is predicted that the percentage of total energy expenditure spent on maternal maintenance metabolism should be positively correlated with lactation length (Table 1). Because of the high energetic costs of provisioning milk to offspring, the maternal-overhead hypothesis also predicts that there will be an inverse correlation between lactation length and maternal body size.

The milk-energy-costs hypothesis (Table 1) proposes that an abbreviation of the lactation period is an adaptation to reduce the relative cost of total milk energy output incurred by the female (Ofteidal et al. 1987). However, Costa (1991a) argued that the ability of pinnipeds to store and transfer energy in the form of milk allows females to compensate for differences in the

length of lactation without significantly altering total energy investment. This argument infers that there should be no correlation between lactation length and total milk energy output per metabolic mass (Costa 1991a). Under what we term the energy-transfer hypothesis, an abbreviated lactation period is expected to be associated with high rates of pup growth as well as high-fat milk and high rates of daily milk energy output per metabolic mass (Bonner 1984, Bowen et al. 1985, Oftedal et al. 1987, 1996, Costa 1991b, Oftedal and Iverson 1995; Table 1).

Although the abbreviated lactation period of phocids might be explained by unstable breeding substrates and the high energetic costs of lactation, Gentry et al. (1986) explained the variation in lactation length in fur seals by the seasonal-productivity hypothesis. According to this hypothesis, high latitudes are associated with marked seasonality and highly productive oceanic environments, which would select for a relatively short lactation period and a reduction in the amount of time spent at sea foraging (Table 1). In contrast, the longer lactation periods of species at low latitudes may reflect the lower productivity of prey and the unpredictability of food arising from factors such as El Niño (Gentry et al. 1986).

Finally, the thermoregulation hypothesis predicts that pinnipeds in colder climates will be morphologically and behaviorally adapted to conserve body heat. Therefore, species at high latitudes, which experience cold climates, should have large adult and neonatal body size to reduce their surface area:volume ratio (Table 1). Additionally, mammalian species at high latitudes are expected to have high-energy milk to meet the energetic needs of thermoregulation of their offspring (Jenness and Sloan 1970). Because of the increased energetic needs of large pups, mammalian species with large neonates are hypothesized to provide more energy on a daily basis to their young than species with smaller offspring (Gittleman and Oftedal 1987; Table 1).

In addition, to evaluate previous conclusions concerning allometric relationships (see Kovacs and Lavigne 1986, 1992), we estimated the regression slopes between maternal mass, neonatal birth mass, and weaning mass.

METHODS

Data sources

We collated 12 life-history, physiological, behavioral, and ecological variables of pinnipeds in a previous study (Schulz and Bowen 2004). Of those 12 variables, 11 were used here to test the adaptive hypotheses described above. In order to evaluate the maternal-overhead hypothesis, we also calculated the percentage of total maternal energy expenditure spent on maternal maintenance metabolism during lactation (Appendix). In testing both the influence of body size

on lactation strategy and the seasonal-productivity hypothesis, we used percentage of lactation that females spent at sea as a proxy for the foraging effort expended during lactation. Trait estimates were evaluated for their quality based on a number of criteria including sample size, methodology, and proportion of lactation covered by the study (see Schulz and Bowen 2004). The highest quality estimates available for each species were averaged for each variable (Appendix). Poor quality estimates were only removed from correlations that were highly influenced by the less dependable data. Therefore, unless otherwise stated, all available estimates were used in the analyses to increase sample size and statistical power. Although all available species estimates were used to test the hypotheses outlined in Table 1, some correlations were also conducted within specific groups (e.g., otariids and phocids) to allow the testing of particular hypotheses and permit comparison with previous findings (e.g., Kovacs and Lavigne 1992).

Phylogeny

We used the pinniped subsection of the composite Carnivora phylogeny (Fig. 1) presented in Bininda-Emonds et al. (1999). This super-tree combines phylogenies from all published sources. Although we acknowledge that this super-tree contains ambiguities and soft polytomies (branch-points with more than two descendant branches), it is perhaps the best phylogeny for this analysis, as it incorporates all the available phylogenetic information and utilizes many independent lines of evidence, including molecular, morphological, and fossil support. However, given the debate over the placement of the walrus within the phylogeny (Berta and Wyss 1994, Arnason et al. 1995, Lento et al. 1995) and the suggestion that ambiguously placed species should be omitted so as to prevent incorrect results (Symonds 2002), we conducted analyses with and without the walrus.

Cross-species analyses

Cross-species analyses were carried out using ordinary least-squares (OLS) and reduced-major-axis (RMA) regressions (Rayner 1985). Although previous studies of pinnipeds have typically used OLS regression, this method fails to consider error associated with the independent variable, such that the resulting slopes may be underestimated (Pagel and Harvey 1988, Nunn and Barton 2000). Because RMA regression incorporates error in both the dependent and independent variables, it should provide more reliable estimates of regression slopes in cases where the independent variable was measured with error (e.g., body mass). Where the numerical value of the slope was of interest (e.g., hypotheses about the relationship between traits and maternal mass or neonatal mass), the RMA estimate of the slope was considered more appropriate. When the numerical value of the slope was not of interest, OLS

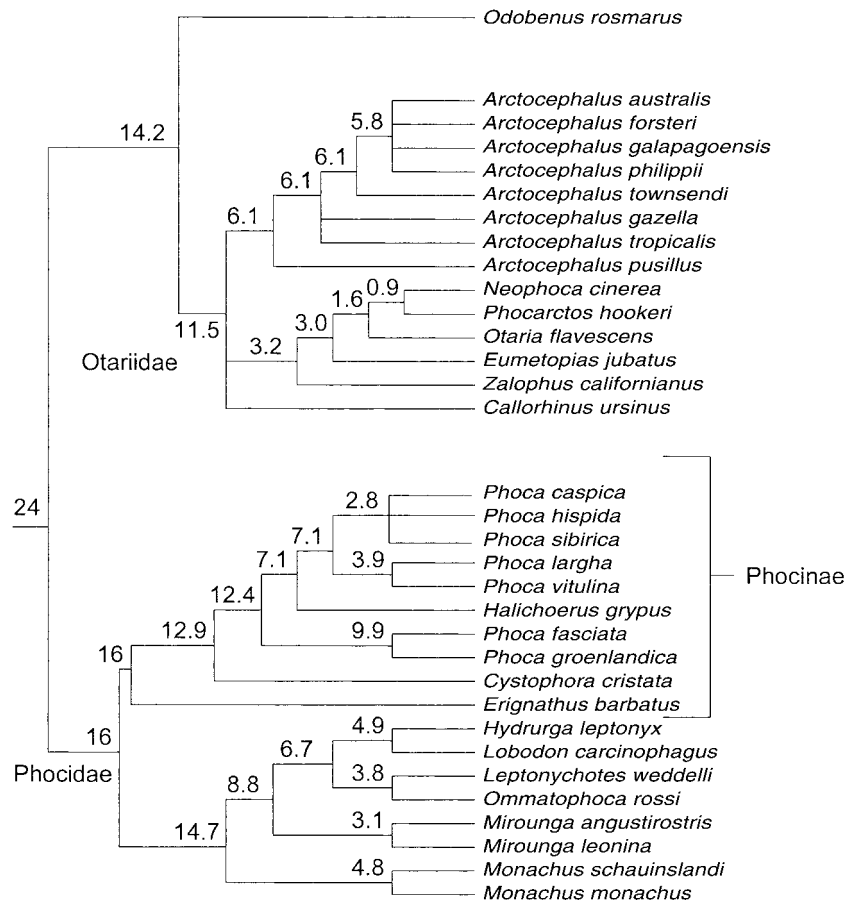


FIG. 1. The composite phylogeny for the pinnipeds as given in Bininda-Emonds et al. (1999). The date of divergence (in units of 10^6 yr BP) for each node is found immediately to the left of the node. Branch lengths are not drawn to scale.

and RMA regressions gave qualitatively similar results, since the correlation coefficient is consistent between both methods. The effect of body size was removed by using the residuals of the OLS regression of each variable against maternal mass in subsequent analyses. Whereas the RMA model is useful in accounting for error in the x -axis, OLS regression is used to calculate the size-free residuals, as it is the only line-fitting method that creates residuals that are completely uncorrelated with the x variable (Pagel and Harvey 1988). The size-corrected residuals were then regressed against each other to test the hypotheses after removing the influence of body size (Garland et al. 1992). The statistical software programs SPSS 10.0 (1999) and S-PLUS 4.5 (1998) were used to conduct these analyses.

To test the hypothesis that large pinniped species give birth to relatively smaller young, the slopes of the OLS and RMA regressions of \log_{10} neonatal mass vs. \log_{10} maternal mass were tested under the null hypothesis that the slope was equal to 1.0. We tested this hypothesis in four groups of species: all pinnipeds, phocids only, otariids only, and otariids plus the walrus

to compare our findings with the conclusions of Kovacs and Lavigne (1986, 1992).

We used cross-species Analyses of Covariance (ANCOVA) to test the breeding-substrate-stability hypothesis while controlling statistically for the effect of maternal postpartum mass (MPPM). In this analysis, both land and land fast-ice were considered stable substrates, whereas pack-ice was considered an unstable substrate. Preliminary tests revealed that inclusion of the walrus in these analyses resulted in a significant interaction term, thus violating the assumption of equal slopes. Subsequently, analyses were performed without the walrus and also within only the Phocidae. We also used cross-species ANCOVA to test for differences in lactation length between the Phocidae and Otariidae with MPPM as the covariate.

Prior to conducting both cross-species and phylogenetic analyses, MPPM, neonatal mass, lactation length, weaning mass, pup growth rate, total milk energy output, total milk energy output per metabolic mass, daily milk energy output and daily milk energy output per metabolic mass were \log_{10} -transformed. Spe-

cies estimates were squared to normalize breeding latitude and the percentage of time spent at sea during lactation (referred to hereafter as time at sea).

Phylogenetic analyses

We corrected for phylogenetic nonindependence using Felsenstein's (1985) method of independent contrasts. Contrasts for each variable were generated using PDTREE (Garland et al. 1993) and standardized (divided by the squared root of the branch lengths) so that they received equal weighting in the subsequent statistical analyses (Garland et al. 1992). PDTREE was also used to plot the absolute value of the standardized contrasts against their standard deviations to determine whether adequate standardization had been achieved. Branch length transformations were performed if there was any significant linear or nonlinear trend in the plot, indicating that the contrasts had not been adequately standardized (Garland et al. 1992). Scatterplots were used to look for clade differences in the means of the absolute values of the standardized contrasts, which might indicate differences between clades in the average rates of evolution (Garland 1992). There was no clear evidence of different rates of character evolution between the otariid/odobenid and phocid clades. OLS regression and RMA lines-of-best-fit were forced through the origin as required by phylogenetic independent contrasts analysis (Felsenstein 1985, Garland et al. 1992).

To account for phylogenetic effects in ANCOVA, the test statistics previously calculated using cross-species analyses were compared to phylogenetically corrected critical values. We used PDSIMUL (Garland et al. 1993) to conduct a Monte Carlo simulation of lactation length and maternal mass along the specified tree (Bininda-Emonds et al. 1999) to generate empirical null distributions of F statistics (see Garland et al. 1993). We performed 1000 simulations under a gradual Brownian motion model with zero correlation between the two traits (as used by Martins and Garland 1991) with values restricted to biologically realistic ranges. We used limits of 1 and 600 days for lactation length, as one day is the shortest lactation length possible and 600 days is slightly longer than that of the otariid with the longest lactation, the South American sea lion (*Otaria flavescens*). We used limits of 20 and 800 kg for maternal mass, as 20 kg is slightly less than the average female mass of the smallest extant fur seal, the Galapagos fur seal (*Arctocephalus galapagoensis*), and 800 kg is the approximate mass of the largest pinniped female, the Pacific walrus (*Odobenus rosmarus divergens*). Final values were set to equal the observed mean values of lactation length and maternal mass (158.8 d and 165.0 kg, respectively) for the 32 species analyzed. For analyses of relationships within the Phocidae family, final values were set at 27.9 d and 232.4 kg for lactation length and maternal mass, respectively.

All of these values were \log_{10} -transformed before conducting simulations.

PDANOVA (Garland et al. 1993) was used to obtain the null distributions of F statistics. We then used SPSS 10.0 to read in the ASCII file of F statistics and compute the critical value of the test statistic ($\alpha = 0.05$) from the 95th percentile of the null distribution of F statistics (see Garland et al. 1993, Ferguson et al. 1996, Brashares et al. 2000). If the F statistic for the real data set was greater than this critical value, the relationship was considered significant.

RESULTS

Removal of the walrus from the statistical analyses resulted in only a few qualitative differences, which are discussed below.

Body-size hypothesis

As predicted under the body-size hypothesis, based on cross-species data MPPM was negatively correlated with lactation length (Fig. 2A) and time at sea, and positively correlated with daily milk energy output, neonatal mass (Fig. 2B), and weaning mass (Table 2). The phenotypic similarity among species within the two major families (i.e., otariids and phocids) is clear from the plot of lactation length against MPPM (Fig. 2A). The clustering of data points within families demonstrates the lack of independence among species estimates and indicates an evolutionary grade shift or early divergence in lactation length between phocids and otariids. Although MPPM was not significantly correlated with total milk energy output for the pinnipeds as a whole, there was a significant positive correlation within the Phocidae.

After accounting for the phylogenetic relationships among species, MPPM remained significantly correlated with neonatal mass (Fig. 2D), weaning mass, and daily milk energy output. However, MPPM was no longer significantly correlated with lactation length (Fig. 2C) or time at sea using all species, or total milk energy output within the Phocidae (Table 2). In contrast, when all available pinniped estimates were used, there was a significant positive correlation between MPPM and total milk energy output, which was not significant in the cross-species analysis.

Breeding-substrate hypothesis

Cross-species ANCOVA results supported the breeding-substrate-stability hypothesis in that species that breed on stable substrates (i.e., land or fast-ice) had longer lactation lengths, adjusted for maternal mass, than those that breed on unstable substrates (i.e., pack-ice) ($F = 21.04$, $F_c = 4.17$, $df = 1, 30$, $P < 0.001$). Within Phocidae, lactation length, adjusted for maternal mass, differed significantly with breeding substrate stability ($F = 5.96$, $F_c = 4.54$, $df = 1, 15$, $P = 0.027$). Cross-species analysis also confirmed previous conclusions that, when adjusted for body mass, lactation

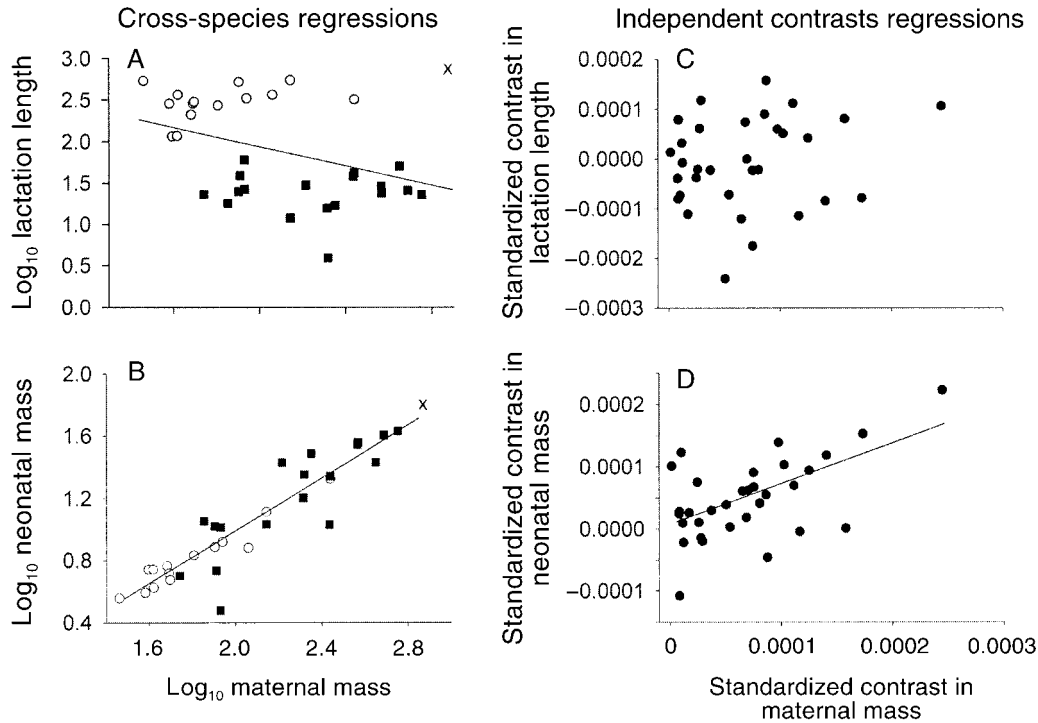


FIG. 2. (A) Log-log plot of lactation length in relation to maternal mass for the 33 species of pinnipeds. The least-squares linear regression line is from conventional analysis ($b = -0.576$, $r = -0.370$). The family of each species is indicated as Phocidae (solid squares), Otariidae (open circles), and Odobenidae (\times symbols). (B) Log-log plot of neonatal mass in relation to maternal mass. The least-squares linear regression line is from conventional analysis ($b = 0.861$, $r = 0.926$). The family of each species is indicated by symbols as in panel (A). (C) Plot of the standardized independent contrasts in \log_{10} lactation length in relation to \log_{10} maternal mass. The least-squares linear regression line is from phylogenetic analyses ($b = 0.061$, $r = 0.059$). (D) Plot of the standardized independent contrasts in \log_{10} neonatal mass in relation to \log_{10} maternal mass. The least-squares linear regression line is from phylogenetic analyses ($b = 0.678$, $r = 0.751$).

duration is longer in the otariids than in the phocids ($F = 104.00$, $F_c = 4.18$, $df = 1, 29$, $P < 0.001$).

Evidence for the substrate-stability hypothesis remained statistically significant after accounting for phylogeny. Within the pinnipeds as a whole (excluding the walrus), lactation length, adjusted for maternal mass, still differed significantly among breeding substrates ($F = 21.04$, $F_c = 10.90$, $df = 1, 30$, $P < 0.05$). Within the Phocidae, lactation length, adjusted for maternal mass, also differed significantly with substrate stability ($F = 5.97$, $F_c = 5.08$, $df = 1, 15$, $P < 0.05$). After accounting for phylogeny and maternal mass, otariids still had significantly longer lactation periods than phocids ($F = 104.00$, $F_c = 52.94$, $df = 1, 29$, $P < 0.05$), suggesting that the differences are the result of selection.

Maternal-overhead hypothesis

As predicted by the maternal-overhead hypothesis, there was a significant positive correlation between cross-species estimates of lactation length and the percentage of maternal expenditures devoted to maternal overhead, which persisted after removing the influence of body size (Table 2, Fig. 3). To account for phylogeny, we cubed branch lengths to adequately standardize

the independent contrasts (see Garland et al. 1992). After correcting for shared ancestry the relationship was no longer significant (Table 2).

Milk-energy-costs hypothesis

In support of this hypothesis, there was a significant positive cross-species correlation between lactation length and total milk energy output per metabolic mass, which remained significant after correcting for phylogenetic relationships (Table 2).

Energy-transfer-hypothesis

Using cross-species estimates, there was a significant negative correlation between lactation length and daily milk energy output per metabolic mass, average percent milk fat, and pup growth rate (Table 2). Daily milk energy output was positively correlated with pup growth rate. Similarly, there was a significant positive correlation between average percent milk fat and pup growth rate, but only after removing the influence of maternal mass (Table 2).

After accounting for shared ancestry, lactation length was still significantly negatively correlated with daily milk energy output, average percent milk fat, and pup growth rate (Table 2). Although the positive correlation

TABLE 2. Correlation coefficients and probability values for correlations between life-history variables. Significant correlations ($P < 0.05$) are in bold.

Hypothesis and independent variable	Dependent variable	Data	<i>n</i>
Body-size hypothesis			
Maternal mass	lactation length	1	33
	percentage of time spent at sea	1	24
	total milk energy output	1	14
	total milk energy output	3	9
	daily milk energy output	1	14
	neonatal mass	1	33
	weaning mass	1	19
Maternal-overhead hypothesis			
Lactation length	percentage of maternal energy devoted to maternal overhead	1	10
Milk-energy-costs hypothesis			
Lactation length	total milk energy output per metabolic mass	1	14
Energy-transfer hypothesis			
Lactation length	daily milk energy output per metabolic mass	1	14
	average percentage milk fat	1	23
	pup growth rate	1	24
Average percentage milk fat	pup growth rate	1	23
Daily milk energy output	pup growth rate	1	14
Seasonal-productivity hypothesis			
Latitude	lactation length	1	33
	lactation length	2	14
	percentage of time spent at sea	1	24
	percentage of time spent at sea	2	14
Thermoregulation hypothesis			
Latitude	maternal mass	1	33
	neonatal mass	1	33
	average percentage milk fat	1	23
Neonatal mass	daily milk energy output	1	14
Additional correlations			
Neonatal mass	weaning mass	1	19

Notes: Individual correlations that test broad adaptive hypotheses are grouped under subheadings for each hypothesis. Categories of data used in correlations are: (1) all available species estimates; (2) otariid estimates only; (3) phocid estimates only. The species estimates used in this analysis can be found in the Appendix. The sample size (*n*) refers to the number of species estimates used in testing each particular hypothesis. The effect of body size was corrected for by using the residuals of the ordinary least-squares regression of each variable against maternal mass in subsequent analyses. The estimates of total and daily milk energy output per metabolic mass were calculated by dividing the estimates of total and daily milk energy output by metabolic mass (maternal mass to the exponent 0.75).

between daily milk energy output and pup growth rate remained significant after accounting for phylogeny, the positive relationship between average percent milk fat and pup growth rate did not (Table 2).

Seasonal-productivity hypothesis

As predicted under the seasonal-productivity hypothesis, there was a significant negative correlation between latitude (a proxy for oceanic productivity) and lactation length for the pinnipeds as a whole (Table 2). However, this cross-species correlation was not significant after the effect of MPPM was removed, casting doubt on the validity of this hypothesis. Although latitude was not significantly correlated with time spent at sea within the otariids, latitude was strongly correlated with lactation length when the influence of MPPM was removed (Table 2). There was a significant positive

cross-species correlation between latitude and percentage of time spent at sea for pinnipeds as a whole, but again only when accounting for MPPM. However, in both cases, these significant correlations are artifacts of the heteroscedasticity of the residuals between these traits and maternal mass, thereby negating their validity.

When corrected for phylogeny, latitude was not significantly correlated with lactation length when all pinnipeds were used in the analysis (Table 2), contrary to predictions of the seasonal-productivity hypothesis. However, there was a significant correlation between latitude and lactation length within Otariidae that was not evident in the cross-species analysis (Table 2).

Thermoregulation hypothesis

Based on cross-species data, the thermoregulation hypothesis was supported in that latitude was signifi-

TABLE 2. Extended.

Conventional approach				Phylogenetic approach			
No correction for body mass		Correcting for body mass		No correction for body mass		Correcting for body mass	
<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
-0.370	0.034			0.059	0.743		
-0.546	0.006			-0.068	0.752		
0.426	0.128			0.689	0.006		
0.775	0.014			0.590	0.062		
0.773	0.001			0.739	0.003		
0.926	<0.001			0.751	<0.001		
0.959	<0.001			0.914	<0.001		
0.864	0.001	0.818	0.004	0.448	0.194	0.464	>0.10
0.921	<0.001			0.802	0.001		
-0.912	<0.001			-0.728	0.003		
-0.737	<0.001	-0.833	<0.001	-0.433	0.039	-0.488	<0.05
-0.831	<0.001	-0.930	<0.001	-0.463	0.023	-0.609	<0.05
0.399	0.059	0.760	<0.001	0.013	0.954	0.365	>0.05
0.971	<0.001	0.932	<0.001	0.937	<0.001	0.856	<0.001
-0.358	0.041	-0.224	0.211	-0.041	0.82	-0.070	>0.50
-0.523	0.055	-0.770	0.001	-0.641	0.014	-0.708	<0.05
0.075	0.726	0.441	0.031	0.355	0.088	0.412	<0.05
0.114	0.698	0.135	0.645	0.113	0.700	-0.092	>0.50
0.471	0.006			0.396	0.022		
0.501	0.003	0.195	0.278	0.311	0.078	0.022	>0.50
0.092	0.677	0.149	0.498	-0.379	0.075	-0.265	>0.20
0.781	0.001	0.201	0.492	0.789	0.001	0.409	>0.10
0.951	<0.001	0.441	0.059	0.91	<0.001	0.538	<0.05

FIG. 3. Plot of the residuals of maternal overhead (percentage of maternal expenditure devoted to maintenance metabolism during lactation) on maternal postpartum mass against the residuals of lactation length on maternal postpartum mass for 10 of 33 species of pinnipeds. The least-squares linear regression line is from conventional analysis ($b = 29.536$, $r = 0.818$). The family of each species is indicated by the symbols: Phocidae (solid circles), Otariidae (open circles). Species abbreviations are: Ag, *Arctocephalus gazella*; Cu, *Callorhinus ursinus*; Cc, *Cystophora cristata*; Hg, *Halichoerus grypus*; Lw, *Leptonychotes weddelli*; Ma, *Mirounga angustirostris*; MI, *Mirounga leonina*; Pg, *Phoca groenlandica*; Ph, *Phoca hispida*; Pv, *Phoca vitulina*.

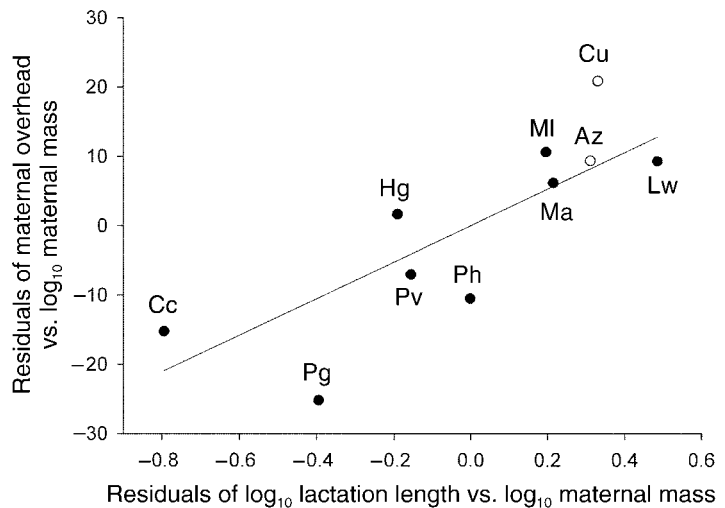


TABLE 3. Least-squares and major-axis regression statistics for allometric relationships of life-history variables with parturition mass and neonate mass.

Independent variable	Dependent variable	Data	Study	<i>n</i>	Conventional method				Phylogenetic method			
					Least squares		Major axis		Least squares		Major axis	
					Slope (<i>b</i>)	<i>P</i>	Slope (<i>b</i>)	<i>P</i>	Slope (<i>b</i>)	<i>P</i>	Slope (<i>b</i>)	<i>P</i>
Maternal mass	neonatal mass	1	A	33	0.861	0.035	0.930	0.281	0.678	0.005	0.901	0.582
		1	C		0.87							
		2	A	18	0.895	0.464	1.056	0.706	0.455	0.019	0.955	0.853
		2	B	24	0.815	0.100	0.959	0.716				
		3	A	15	0.845	0.006	0.862	0.012	0.804	0.055	0.871	0.420
	3	C	16	0.832	0.003	0.851	0.007					
	4	A	14	0.751	0.002	0.781	0.004	0.741	0.057	0.847	0.499	
								0.001				
		lactation length	4	C	14	0.674	<0.001	0.712				
		total milk energy output	1	A	33	-0.576	0.113	-1.557	0.086			
	weaning mass	2	A	9	0.651	0.126	0.841	0.480				
Neonatal mass	weaning mass	1	A	19	0.901	0.140	0.939	0.357	0.900	0.315	0.984	0.903
	daily milk energy output	1	A	19	1.021	0.796	1.073	0.381	0.994	0.957	1.092	0.569
		1	A	14	1.092	0.721	1.489	0.162	0.812	0.325	1.030	0.941

Note: Regression slopes were tested for their difference from 1.0. Those that were significantly different from 1.0 ($P < 0.05$) are in boldface type. Phylogenetic slopes and P values are not presented when the slope was not significantly different from 0.0 or phylogenetic analyses were not conducted. Data used: (1) all available species estimates; (2) phocid estimates; (3) otariid and odobenid estimates; (4) otariid estimates. Analyzed slopes were from three studies: (1) this study; (2) Kovacs and Lavigne (1986); (3) Kovacs and Lavigne (1992). The species estimates used in this analysis can be found in the Appendix. The sample size (n) refers to the number of species estimates used in testing each particular hypothesis.

cantly correlated with both maternal and neonatal mass (Table 2), indicating that species at high latitudes (and thus cold climates) are larger in body size. Neonatal mass was also significantly correlated with latitude, but only because of the confounding influence of maternal mass. Latitude was not significantly correlated with average percent milk fat (Table 2). Neonatal mass was highly correlated with daily milk energy output, but only before the confounding effect of maternal mass was removed (Table 2).

Pinniped species at high latitudes were heavier than those at lower latitudes after statistically accounting for phylogeny, providing support for the thermoregulation hypothesis (Table 2). However, latitude was not significantly correlated with either neonatal mass or average percent milk fat, after removing the effects of phylogeny (Table 2). Neonatal mass and daily milk energy output were not significantly correlated after removing the influence of maternal mass and phylogenetic history (Table 2).

Offspring and maternal body mass allometry

Several hypotheses predicted allometric scaling of traits with either MPPM or neonatal mass. As expected, the use of RMA regressions resulted in steeper slopes than OLS regressions (Table 3) and the difference between the two estimates increased as the strength of the correlation between variables decreased. The slope

of neonatal mass against MPPM for all pinnipeds was significantly <1.0 using OLS regression, but was not significantly different from 1.0 using the RMA regression. Neonatal mass also scaled isometrically with maternal mass within the phocid seals. In contrast, under both regression models, the slopes of neonatal mass against maternal mass within otariids and the walrus were significantly <1.0 , indicating that larger otariid species give birth to relatively smaller young. The absolute slope of the relationship between lactation length and MPPM was significantly <1.0 using both regression models. However, the sign of the slope changed from negative to positive using major-axis regression, making conclusions problematic. The slopes of both total milk energy output and weaning mass against maternal mass did not differ significantly from 1.0. Although this suggested that both traits increased isometrically with maternal size, milk energy output has been measured in only 9 of the 33 species. The highly significant correlation between weaning mass and neonatal mass became nonsignificant when the influence of MPPM was removed (Table 2). Under both regression models, neither the slopes of weaning mass or daily milk energy output against neonatal mass differed significantly from 1.0 (Table 3).

After accounting for both phylogeny and maternal mass, weaning mass was still positively correlated with neonatal mass (Table 2). After accounting for phylog-

eny, only the OLS regression slopes between neonatal mass and MPPM for the pinnipeds as a whole and within Phocidae differed significantly from 1.0 (Table 3). None of the RMA slopes were significantly different from 1.0 once the effect of phylogeny had been removed, indicating that neonatal and weaning masses scale isometrically with maternal mass in pinnipeds. Removing the walrus did not change the relationship between lactation length and maternal mass ($b = -0.84$, $P < 0.001$) under the OLS model, but did change the relationship ($b = -2.3$, $P = 0.21$) under the RMA model.

DISCUSSION

Our study is the first to use independent contrasts in an attempt to unravel the relative influence of ecological factors and phylogeny on the evolution of lactation strategies in pinnipeds. By summarizing and testing previously proposed hypotheses, this paper serves to underscore the nature of the debate over the past several decades and to clarify the factors that have presumably influenced the evolution of pinniped lactation strategies. Although the phylogenetic methods used here have proven valuable in testing adaptive relationships between life-history characters, ambiguity in the underlying phylogeny can undermine the confidence of adaptive conclusions when small trees with several soft polytomies are used (Garland and Diaz-Uriarte 1999). Because the phylogenies in the present study are relatively small (ranging in size from 9 to 33 species depending on the variables considered) and contain several soft polytomies, the significance of some of our correlations may change as more species are studied and phylogenetic relationships are better resolved.

Lactation strategies are embedded within the life histories, which evolve largely in response to the impact of environmental variation on survival and natality (Partridge and Harvey 1988). Thus, lactation strategies should be considered in relation to this broader context. We have attempted to do this in the verbal models present below. Our results suggest that the selective pressures influencing lactation length are breeding substrate, the relative energetic costs of milk production, and in the otariids, latitude (presumably a proxy for oceanic productivity). Although lack of species estimates makes them difficult to test, proximity and richness of prey and predation may also affect lactation length and strategy. In contrast, maternal mass has relatively little current influence on lactation length and maternal attendance strategy. Rather the variation in lactation length and attendance strategy as influenced by body size is likely constrained by an ancestral divergence between phocids and otariids, with the caveat, however, that data from some species thought critical to examine this hypothesis are still lacking.

Body-size hypothesis

There is little evidence for correlated evolution between either lactation strategy or lactation length and

maternal mass, indicating that the relationships we see today are likely a result of an early divergence in the lactation strategies of these lineages and phylogenetic inertia (also see Trillmich 1996). However, the lack of an adaptive relationship between maternal mass and lactation strategy might also reflect limitations in the quality of data and the species available for analyses. Although several of the larger ice-breeding phocid species forage to some degree during lactation, several authors (Costa 1991b, Boness and Bowen 1996, Trillmich 1996) have noted that it is unclear what fraction of total maternal energy expenditure is provided from food intake during lactation (see Tedman and Green 1987, Baker et al. 1995, Lydersen and Kovacs 1996, Lydersen et al. 1996). Furthermore, due to lack of data, we used the percentage of time spent at sea as a proxy for the percentage of expenditures accounted for by feeding during lactation. Unfortunately, this index may not accurately reflect feeding, particularly in phocids, which appear to spend much of their time near the surface when at sea during lactation (Bowen et al. 2001). Females may return to sea during lactation not to feed, but to avoid thermal stress (Pierotti and Pierotti 1980, Stewart 1983), engage in mating activities (Stirling 1983), and avoid terrestrial predators (Oftedal et al. 1987). Furthermore, in ice-breeding species, where food may often be close enough to make foraging during lactation economical, some supplementary feeding presumably may occur regardless of body size (Boyd 1998).

Moreover, the underlying adaptive relationship might not be evident because most of the smaller phocid species remain poorly studied (Schulz and Bowen 2004). Small body size and consequently small fat and protein stores appear to constrain most otariids and some well-studied small phocids (e.g., *Phoca vitulina*) to a foraging strategy despite the lactation strategy of their close relatives (Boness and Bowen 1996). We predict that future research on the poorly studied small phocids (e.g., *Phoca sibirica*, *Phoca caspica*, *Phoca largha*) will find that they also exhibit a form of the foraging-cycle strategy. Furthermore, we expect that accurate measurements of food intake by large phocids during lactation will show that such feeding is facultative and trivial relative to the energy stored in blubber prior to parturition. If so, there may well be an adaptive relationship between lactation strategy and maternal mass, with larger seals adopting a fasting strategy with some supplementary feeding. Clearly, a stronger test of this hypothesis will only be possible when these additional species data are available.

Although the small body size of some phocid species might constrain females to a lactation strategy similar to that of otariids, differences in mammary gland structure between the families may constrain the ability of phocid females to evolve a full-fledged foraging-cycle lactation strategy. Recent research on harbor seal milk composition indicates that, as in other phocids, females

cannot abstain from suckling for more than a day without initiating mammary gland involution (S. Lang and S. J. Iverson, *personal communication*). This physiological constraint indicates that maternal foraging trip duration must be short during lactation. This behavior contrasts with the exceptional ability of otariid females to undertake prolonged feeding trips of >14 days without mammary gland involution. Thus an early evolutionary divergence in mammary gland structure may provide strong constraints on lactation strategies in pinnipeds. Although future research on small, unstudied phocids may lend support to the adaptive hypothesis that MPPM and concomitant energy stores influence the lactation strategy of a pinniped species, our results indicate that MPPM currently has little effect on the lactation length of extant pinnipeds (also see Trillmich 1996).

Breeding-substrate hypothesis

Early phocids breeding at high latitudes may have evolved an ice-breeding habit either to avoid predation by land predators or because land habitats were inaccessible due to the presence of ice (Stirling 1975). When corrected for phylogenetic effects and maternal body mass, as suggested by Trillmich (1996), our results support the breeding-substrate-stability hypothesis wherein pinnipeds (excluding the walrus) that breed on unstable pack-ice have significantly shorter lactations than those that breed on land or fast-ice. This relationship holds within the Phocidae as well. By abbreviating lactation, pagophilic seals reduce the likelihood that the complete transfer of milk energy will be interrupted by the breakup of the pack-ice. Although this hypothesis might appear invalidated by the extremely long lactation of the pack-ice breeding walrus, walrus calves accompany their mothers during feeding trips, thereby eliminating the threat of shifting pack-ice. Moreover, the unusually long lactation of odobenids might also be a result of their unique habit of feeding on mollusks, as it can take several years for walrus calves to develop the facial musculature and diving ability to feed on mollusks (Fay 1982).

Even though our analysis confirms previous findings that breeding-substrate stability is an important influence on lactation length, several phocid species have short lactation periods and yet breed on land (e.g., monk seals, *Monachus* sp. and elephant seals, *Mirounga* sp.). To explain this, Stirling (1975, 1983) hypothesized that the short lactation of phocids is a characteristic retained from a pagophilic ancestor. However, paleontological evidence shows that although ancestral phocids first appeared in the North Atlantic $\sim 16 \times 10^6$ years ago (Bininda-Emonds et al. 1999), northern ice did not develop until the late Pliocene ($\sim 3 \times 10^6$ years ago) (Shackleton and Opdyke 1977). The temperate and tropical monk seals, which are some of the oldest living phocids (Ray 1976, Repenning and Ray 1977), thus likely never had a pagophilic ancestor. Therefore, we

conclude that, although breeding substrate is an important factor in further abbreviating the lactation period within Phocidae, other selective pressures must have been responsible for the initial differences in lactation length between phocids and otariids.

Maternal-overhead hypothesis

An abbreviated lactation period appears to be associated with a reduction in maternal overhead relative to milk energy output, thereby allowing a female to allocate a larger fraction of her energy reserves to pup growth rather than maintenance metabolism. Although our phylogenetic analysis suggests that this relationship is not adaptive, the nonsignificant correlation is likely a result of small sample size ($n = 10$) biased towards large phocid species. We predict that further research on small phocids with relatively short lactations, and additional otariids, will reveal that an abbreviated lactation period is an adaptation to minimize the expenditure of maternal reserves on maintenance metabolism. The selection pressure to reduce maternal overhead by abbreviating lactation would be especially strong in large species that are capable of relying solely on blubber stores throughout lactation, such as the ancestral phocid and large extant phocids. However, we suggest that the energy savings incurred by abbreviating lactation could have produced a positive feedback loop in phocids, such that an abbreviated lactation is maintained, even in small species that do not fast throughout lactation.

Milk-energy-costs hypothesis

Abbreviation of lactation length reduces not only maternal energetic overhead but also the relative amount of milk energy a female transfers throughout lactation (Oftedal et al. 1987). Although the small number of species estimates (i.e., only 14 species) limits our conclusions, we found some support for the milk-energy-costs hypothesis in that shortening the period of maternal care could be considered an adaptation to reduce milk energy output. Thus our results do not support the hypothesis that the ability to store and transfer energy in the form of milk allows pinnipeds to compensate for differences in the length of lactation without significantly altering total energy investment (Costa 1991a). Although Costa (1991a) examined the relationship between lactation length and total milk energy output per metabolic mass separately within the two families, our analysis for pinnipeds as a whole indicates that by abbreviating the lactation period, pinniped species reduce the total relative milk energy costs experienced by the female (Oftedal et al. 1987). Given that milk energy output is often the most costly component of lactation (see Costa et al. 1986, Mellish et al. 1999, 2000), we might expect that a reduction in this component would be under strong selection. Thus, once initial selection pressures favored an abbreviation in the lactation period, the energetic advantages gained

by doing so most likely imposed a correlated response on lactation length. Therefore, not only might the reduction of total milk energy costs have been an important initial influence in the abbreviation of lactation, but also this reduction appears to be currently adaptive.

Energy-transfer hypothesis

Our phylogenetic analyses lend support to the energy-transfer hypothesis, which suggests that high pup growth rates and energy-rich milk are adaptations to an abbreviated lactation. Contrary to previous conclusions (Bonner 1984, Bowen et al. 1985), however, is the finding that milk fat is not significantly correlated with pup growth rates. This is likely because the milk energy that a pup receives is not only dependent on the percentage of fat in the milk, but also on the quantity of milk consumed each day. Given the significant correlation between daily milk energy output and pup growth rate even after accounting for phylogeny, we conclude that a high rate of daily milk energy output, not just high-fat milk, is an adaptation to increase the rate of pup development and ensure optimum weaning mass in an abbreviated lactation period (Bonner 1984, Bowen et al. 1985, Oftedal and Iverson 1995). Species with short lactations invest more energy in milk on a daily basis to satisfy the high metabolic needs of rapidly growing pups and maximize energy transfer in a brief period of time (Oftedal et al. 1996).

The hypothesis that pinniped species with larger neonates transfer more milk energy on a daily basis does not hold up when the effect of maternal mass is removed. Large pups receive more daily milk energy only because they have large mothers that are capable of transferring large amounts of energy to their young. Under the body-size hypothesis, Costa (1991a) predicted that larger species are adapted to invest more energy in their pups during lactation than smaller species. Although our current findings refute this suggestion, it is premature to draw firm conclusions because so few species have been studied.

Seasonal-productivity hypothesis

Lactation length is negatively correlated with breeding latitude in otariids after accounting for maternal mass and phylogeny, suggesting that the duration of lactation is dependent on features that vary inversely with latitude. Although the mechanism remains unclear, the distribution and quality of food seems a likely candidate as high prey availability and productivity would permit females to rapidly acquire and transfer milk energy to their offspring (Gentry et al. 1986, Oftedal et al. 1987). Nevertheless, there is no correlation between percentage of time spent at sea during lactation and breeding latitude, suggesting that the amount of time otariid females spend at sea may be more influenced by the prey patch quality and distance of prey from the rookery than by large-scale environmental seasonality (Boness and Bowen 1996).

Thermoregulation hypothesis

Our phylogenetic analysis supports the thermoregulation hypothesis that large body size is adaptive in pinnipeds in the conservation of heat in cold climates. The evolution of a large body size in early phocids to increase energy stores and reduce heat loss would have allowed them to invade higher latitudes and take advantage of more productive oceanic waters. However, despite the adaptive relationship between latitude and female body size, neither pup size nor milk fat are influenced by latitude and thus climate.

Hypotheses not tested

We could not test the prey-proximity hypothesis (Costa 1991a, 1993) as the spatial and temporal distribution of prey with respect to the location of current breeding colonies is poorly known for most species. Furthermore, to test this hypothesis it would be necessary to identify the location of prey prior to parturition, as some species may travel thousands of kilometers between foraging grounds and breeding sites before giving birth (Boyd 1998). We do know, however, that the foraging trip durations of some otariid species can last as much as 23 days (Georges and Guinet 2000), indicating that, in at least some species, the targeted prey resources are of low density, poor nutritional quality, or distant rather than nearby. Although empirical data are lacking, modeling supports Costa's hypothesis that large pinnipeds are adapted to exploit highly dispersed and distant prey, whereas small species are adapted to forage on locally abundant and predictable prey (Boyd 1998). However, Boyd's model suggests that, contrary to Costa's hypothesis, large species probably need to feed on richer sources of prey than small species because of their overall greater metabolic requirements.

Predation has also likely played a role in shaping the life histories of phocids and otariids (Stirling 1975, 1977, 1983, Cassini 1999). However, as with prey proximity, the general importance of predation on the evolution of lactation strategies is difficult to evaluate, leaving researchers to speculate on the influence of this factor on pinniped evolution. Because phocids are especially handicapped on land, pups and all but the largest phocid species are at risk from predators such as foxes and wolves while on shore (Bonner 1984). Furthermore, ice-breeding seals in the Northern Hemisphere face the potentially significant impact of polar bear (*Ursus maritimus*) predation (Stirling and Archibald 1977, Bowen 1991, Lydersen and Kovacs 1999). Although terrestrial predation by polar bears, which are thought to have evolved only as recently as 500 000 years ago (Kurtén 1964, 1968, Talbot and Shields 1996), may represent a recent evolutionary pressure for pinnipeds, predation by extinct terrestrial carnivores may have been an important initial selective influence on pinniped lactation length. By adopting a

brief but intense lactation, females minimize the probability that they will be preyed upon before the transfer of milk energy is complete (Bonner 1984).

In contrast to phocids, otariids have better terrestrial mobility and breed almost exclusively on predator-free islands (Trillmich 1996), thus reducing the selective pressure of terrestrial predation on this group. By extending the interval of maternal care, otariids delay the need for young to enter deep waters to forage until they have reached a critical weaning mass and developed sufficient foraging and locomotion abilities, thereby reducing the risk of shark and killer whale predation (Trillmich 1984, Gentry et al. 1986, Trillmich 1990, Bowen 1991). Although this argument is weakened by the fact that pups swimming in shallow waters could be preyed upon by killer whales (*Orcinus orca*) and sharks, it is currently unclear how this level of predation compares to that on individuals foraging at sea.

Offspring and maternal body mass allometry

We found a strong isometric relationship between weaning mass and neonatal mass, suggesting that despite differences in maternal mass and phylogenetic history, pinniped females are selected to wean offspring at a consistent multiple of neonatal mass (see Lee et al. 1991). Since weaning mass is inversely correlated with juvenile mortality (Promislow and Harvey 1990, Baker and Fowler 1992, Le Boeuf et al. 1994, Hall et al. 2001), females may be under selection to wean their pups at a critical mass relative to neonatal mass, thereby maximizing pup survival and the fitness of the mother (Lee et al. 1991).

In most eutherian mammal groups, total litter mass scales with maternal mass with an exponent less than 1.0 (Leitch et al. 1959, Spencer 1971, Blueweiss et al. 1978, Millar 1981). Kovacs and Lavigne (1986, 1992) reported that pinniped species follow this mammalian pattern. However, in our analyses, the RMA slopes estimated from phylogenetic contrasts indicate an isometric relationship between neonatal mass and maternal mass for all sets of species studied. Therefore, the correlation between offspring mass and maternal mass within the families, or among all pinnipeds, is not a recent adaptation, but rather an early adaptation of all pinnipeds. This grade shift with respect to other eutherian mammals is presumably associated with the thermal costs of invading the aquatic environment, as cetaceans also fall above the eutherian mammal line (Webb 1997). Some of our results differ from previous findings because Kovacs and Lavigne (1986, 1992) incorrectly tested allometric relationships under the null hypothesis that the slope is equal to 0.0 rather than 1.0.

We also found that weaning mass scaled isometrically with maternal mass across all pinnipeds, although otariids were underrepresented in this test. This contradicts the conclusions of both Bowen (1991) and Costa (1991b) that otariid offspring are weaned at a larger fraction of maternal mass than phocids. However, both

analyses included some rather uncertain estimates or estimates based on extrapolation of pup growth rate. Given the variable nature of growth over the course of lactation and the uncertainty associated with the length of lactation in otariids, this approach cannot be recommended. Thus, there is little support of the conclusion that otariids wean relatively larger offspring than phocids, although additional data may indeed show that this is the case.

Evolution of pinniped lactation strategies

Several hypotheses have been advanced to account for the evolution of pinniped lactation strategies (e.g., Stirling 1975, 1983, Bonner 1984). However, with the exception of that proposed by Costa (1993), all have assumed separate origins for the otariids, odobenids, and phocids. Pinnipeds are now widely regarded as a monophyletic group most closely related to ursid arctoid carnivores, with mustelids forming the next closest outgroup (Mitchell and Tedford 1973, Wyss 1988, Lento et al. 1995, Berta and Sumich 1999). The early divergent lineage of pinnipeds originated in the North Pacific during the late Oligocene ($33.7\text{--}23.8 \times 10^6$ years ago) when there was a sharp drop in global temperature and lowering of sea level. Although the South Pole was ice covered, the Arctic was not. Lipps and Mitchell (1976) hypothesized that the mammalian invasion of the marine environment was made possible by increased coastal upwelling and concomitant primary and secondary productivity, particularly during the Miocene ($23.8\text{--}5.3 \times 10^6$ years ago). However, interspecific competition among a diverse assemblage of mammalian carnivores, including the amphicyonids or bear-dogs, during the Oligocene and early Miocene periods (Van Valkenburgh 1999) may have also favored the exploitation of new habitats. Although these events may account for the successful invasion of the marine environment, they do not account for the evolution of different pinniped lactation strategies. For this, we need to understand the potentially interacting roles of food distribution, breeding substrate, and body size on maternal physiology and provisioning of offspring.

In a seminal paper, Costa (1993) incorporated a monophyletic origin of pinnipeds with the energetics of maternal foraging and milk production to provide a framework for how phocid and otariid lactation strategies may have evolved. Our findings, coupled with information on pinniped paleobiology and paleoclimatology, allow us to elaborate on Costa's verbal model. Ancestral phocids and otariids apparently responded to selective pressures in different ways (Figs. 4 and 5). Early phocids evolved large size (Wyss 1994), presumably to reduce heat loss and the risk of predation, and increase energy stores and foraging range (Fig. 4). This enabled them to inhabit cold, seasonally productive oceans and to take advantage of sea-ice for parturition and nursing, which in turn, selected for an abbreviated duration of lactation, as well as high rates of milk en-

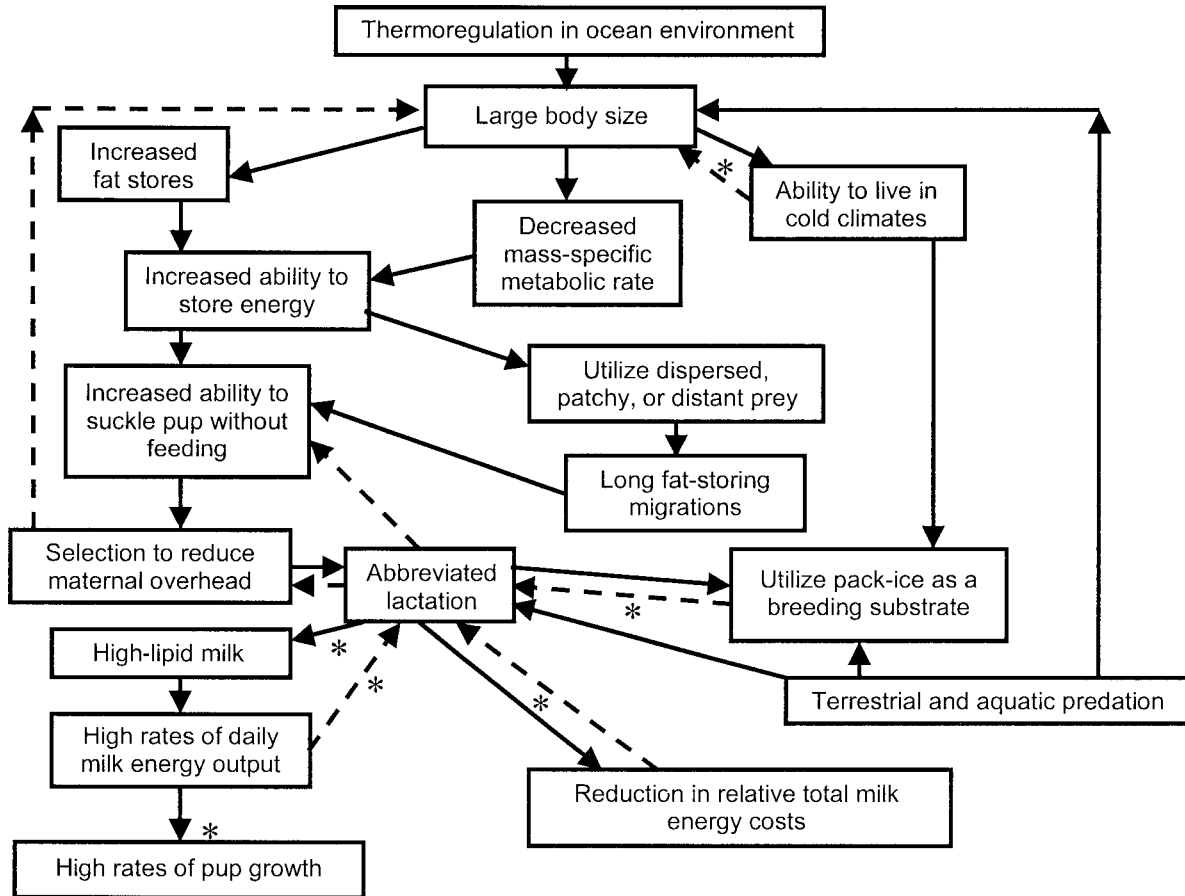


FIG. 4. A verbal model of the evolution of maternal life-history traits and lactation strategy in phocids. Asterisks denote relationships suggested to be adaptive by our analyses. Dashed arrows indicate feedback loops.

ergy output and pup mass gain. In contrast, ancestral otariid females retained a smaller body size and likely bred at isolated rookeries to reduce exposure to terrestrial predators and gain proximity to highly productive local prey resources (Fig. 5). As differences in body mass between phocids and otariids appear to have been established early in their evolutionary history, then to the extent that broad differences in lactation strategy between phocids and otariids are constrained by body mass, presumably the differences in lactation strategies also began to develop early in their evolutionary past.

Enaliarctos mealsi is regarded as a basal otariid and may in fact be the ancestral pinniped (Berta et al. 1989, Fordyce 2002). Enaliarctids retained the heterodont dentition of their terrestrial ancestor, which suggests that they engaged in coastal feeding and frequently returned to land to consume prey. These small animals showed no evidence of sexual size dimorphism and likely had dense underfur, which has been retained by living fur seals (Repenning 1976). They probably exhibited a primitive form of the otariid foraging-cycle lactation strategy (Costa 1993) and retained a lactation

length in the order of several months, both of which are typical of many terrestrial carnivores (Gittleman and Oftedal 1987). The earliest otariids appeared about 11×10^6 years ago and, although smaller than *Enaliarctos*, had evolved homodont dentition presumably to more effectively capture marine prey, which could be swallowed whole at sea. Climate cooling during much of the Miocene selected for increased body size and thus more efficient thermoregulation while foraging. As the early otariids became larger and could forage more efficiently on marine prey, they began to exploit resources farther offshore, increasing the duration but reducing the frequency of foraging trips during lactation (Costa 1993). Longer trips favored rapid travel at the surface to and from offshore feeding grounds and thus greater energy return per trip to compensate for the increased rate of energy expenditure during foraging. This increase in the duration of foraging trips during lactation would also have selected for the remarkable ability of otariid mammary glands to remain functional despite sustained interruptions in suckling activity.

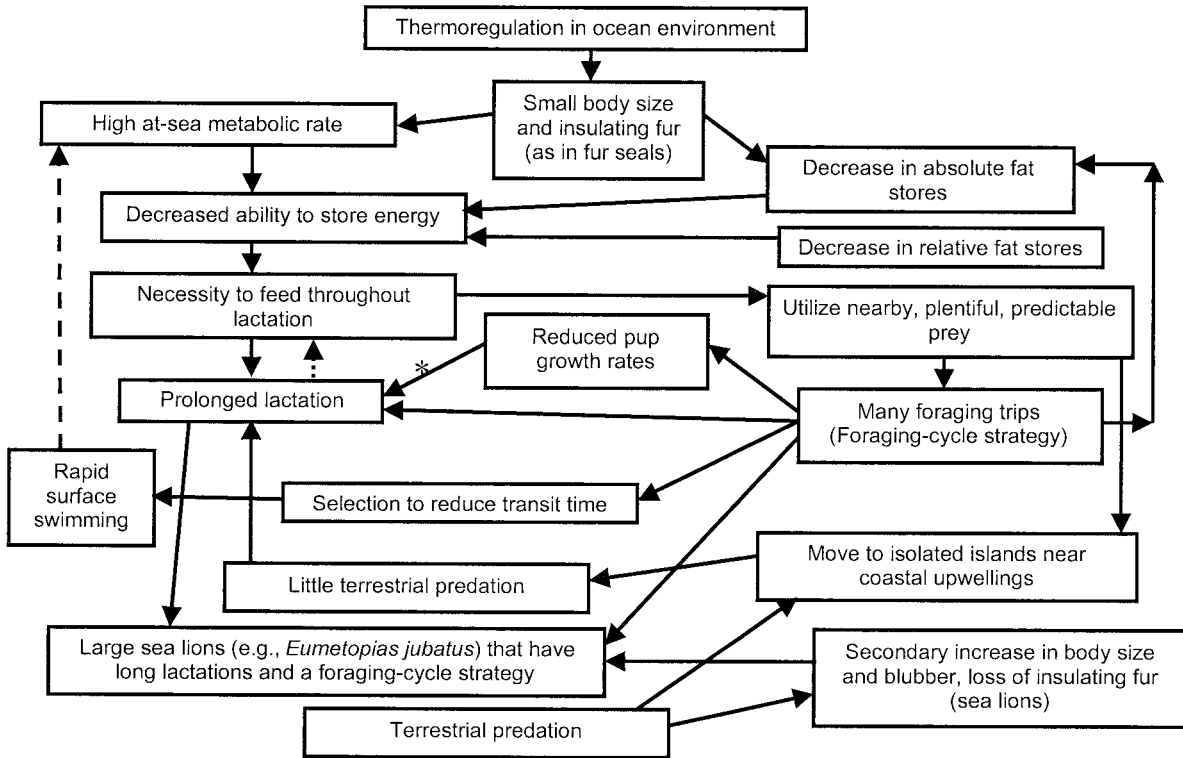


FIG. 5. A verbal model of the evolution of maternal life-history traits and lactation strategy in otariids. Asterisks denote relationships suggested to be adaptive by our analyses. Dashed arrows indicate feedback loops.

Reduced frequency of milk provisioning to offspring selected for lower offspring growth rate and extended duration of lactation to ensure the sufficient transfer of energy (Fig. 5). We speculate that reduced prey availability led to further lengthening of the lactation period in most species, particularly those in tropical waters of lower and less predictable productivity (e.g., Galapagos fur seal and Galapagos sea lion, *Zalophus californianus wollebaeki*). In contrast, otariids at higher latitudes retained a lactation period similar to their terrestrial ancestors, presumably because of increased oceanic productivity in colder waters permitting greater efficiency in provisioning offspring. Sea lions diverged from fur seals $\sim 3\text{--}5 \times 10^6$ years ago, and both clades dispersed into the Southern Hemisphere (Berta 2002). Although some sea lion species evolved a larger body size, they still retain the foraging strategy, high metabolic rates, and hence the prolonged lactation that likely characterized early otariids.

Other lineages of ancestral pinnipeds of the early to mid-Miocene period, *Desmatophoca* and *Allodesmus*, were allied to phocid seals (Berta 2002). These two groups differed from enaliarctids in having evolved homodont dentition, which suggests that they developed an early adaptation to marine foraging on small prey. Both of these extinct lineages evolved into large species exhibiting sexual size dimorphism (Repenning 1976). Their large size and homodont dentition meant

that they could efficiently exploit distant and less predictable prey and store energy in the form of blubber. Increasing reliance on stored maternal energy to support milk production meant that nutrient transfer to young would be optimized by concentrating milk energy and reducing maternal overhead by minimizing the duration of lactation (Costa 1993 and Fig. 4). Thus, the fundamental characteristics of the phocid lactation strategy also appeared early in pinniped evolution.

Ancestral monk seals (i.e., Monachinae) are thought to be the earliest members of the Phocidae family. They were large (Wyss 1994) and presumably had separated maternal foraging and lactation to some extent. Once the initial separation of maternal foraging and lactation had been established, early phocid species could disperse into warmer waters of lower productivity where prey was perhaps more dispersed and less predictable. Adaptive radiation of monachine and phocine lineages into the Atlantic and Caribbean Sea, through the Central American Seaway, occurred during the middle Miocene (Costa 1993, Berta 2002). Once in the Atlantic, phocids dispersed both north and south with no competition from otariids (Costa 1993). Once further cooling during the late Miocene led to the development of Arctic ice sheets (Elverhoi et al. 1998), phocids in both the Northern and Southern Hemisphere may have been prevented from accessing terrestrial habitats, forcing them to breed on unstable pack-ice, which favors

the abbreviation of lactation (Stirling 1975, 1983, Costa 1993). The short lactation lengths of some modern species of northern phocids (e.g., grey seals and harbor seals) that breed mainly on land reflect their ancestral dependence on sea ice, with some populations of these species maintaining a pagophilic habit (Perry et al. 1995). Furthermore, breeding on ice would have exposed northern phocids to terrestrial predation by polar bears, which would similarly select for an abbreviated lactation period. In contrast, the large monk seals, which invaded temperate and tropical waters, would not have been as pressured to abbreviate the lactation period as those phocid species that encountered ice and terrestrial predators. Likewise, although Antarctic phocids raise young on unstable sea ice, they may be under less selective pressure than northern phocids due to a lack of terrestrial predators. In fact, Antarctic phocids may actually be under selection to prolong lactation due to the greater threat of aquatic predators relative to terrestrial ones (Stirling 1975, 1977, Oftedal et al. 1987).

The energetic benefits of reducing milk energy output and likely maternal overhead continue to favor an abbreviated lactation and maintain this adaptation in the absence of initial selection factors. Although phocid radiation into the Southern Hemisphere during the Pliocene was associated with a further increase in body size, several of the phocids of the Northern Hemisphere showed a reversal toward small body size (Wyss 1994). And while the small body size of such phocids necessitates (or permits) a foraging lactation strategy (Bowen et al. 2001), ancestry and the adaptive benefit of minimizing lactation costs, that likely first evolved in the large, fasting phocid ancestor, explain the short lactations in these species.

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LITERATURE CITED

- Arnason, U., K. Bodin, A. Gullberg, C. Ledje, and S. Mouchaty. 1995. A molecular view of pinniped relationships with particular emphasis on the true seals. *Journal of Molecular Evolution* **40**:78–85.
- Baker, J. D., and C. W. Fowler. 1992. Pup weight and survival of northern fur seals *Callorhinus ursinus*. *Journal of Zoology* **227**:231–238.
- Baker, S. R., C. Barrette, and M. O. Hammill. 1995. Mass transfer during lactation of an ice-breeding pinniped, the grey seal (*Halichoerus grypus*) in Nova Scotia, Canada. *Journal of Zoology, London* **236**:531–542.
- Bartholomew, G. A. 1970. A model for the evolution of pinniped polygyny. *Evolution* **24**:546–559.
- Berta, A. 2002. Pinniped evolution. Pages 913–921 in W. F. Perrin, B. Wursig, and J. G. M. Thewissen, editors. *Encyclopedia of marine mammals*. Academic Press, San Diego, California, USA.
- Berta, A., C. G. Ray, and A. R. Wyss. 1989. Skeleton of the oldest known pinniped, *Enaliarctos mealsia*. *Science* **244**:60–62.
- Berta, A., and J. L. Sumich. 1999. *Marine mammals: evolutionary biology*. Academic Press, San Diego, California, USA.
- Berta, A., and A. R. Wyss. 1994. Pinniped phylogeny. Pages 33–56 in A. Berta and T. A. Demere, editors. *Contributions in marine mammal paleontology honoring Frank C. Whitmore, Jr.* Volume 29. *Proceedings of the San Diego Society of Natural History*, San Diego, California, USA.
- Bininda-Emonds, O. R. P., J. L. Gittleman, and A. Purvis. 1999. Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora (Mammalia). *Biological Reviews* **74**:143–175.
- Blueweiss, L., H. Fox, V. Kudzma, D. Nakashima, R. Peters, and S. Sams. 1978. Relationships between body size and some life history parameters. *Oecologia* **37**:257–272.
- Boness, D. J., and W. D. Bowen. 1996. The evolution of maternal care in pinnipeds. *BioScience* **46**:645–654.
- Bonner, W. N. 1984. Lactation strategies in pinnipeds: problems for a marine mammalian group. *Symposium of the Zoological Society of London* **51**:253–272.
- Bowen, W. D. 1991. Behavioural ecology of pinniped neonates. Pages 66–127 in D. Renouf, editor. *Behaviour of pinnipeds*. Cambridge University Press, Cambridge, UK.
- Bowen, W. D., S. J. Iverson, D. J. Boness, and O. T. Oftedal. 2001. Foraging effort, food intake and lactation performance depend on maternal mass in a small phocid seal. *Functional Ecology* **15**:325–334.
- Bowen, W. D., O. T. Oftedal, and D. J. Boness. 1985. Birth to weaning in 4 days: remarkable growth in the hooded seal, *Cystophora cristata*. *Canadian Journal of Zoology* **63**:2841–2846.
- Boyd, I. L. 1998. Time and energy constraints in pinniped lactation. *American Naturalist* **152**:717–728.
- Brashares, J. S., T. Garland, Jr., and P. Arcese. 2000. Phylogenetic analysis of coadaptation in behavior, diet, and body size in the African antelope. *Behavioral Ecology* **11**:452–463.
- Cassini, M. H. 1999. The evolution of reproductive systems. *Behavioral Ecology* **10**:612–616.
- Clutton-Brock, T. H. 1991. *The evolution of parental care*. Princeton University Press, Princeton, New Jersey, USA.
- Costa, D. P. 1991a. Reproductive and foraging energetics of high latitude penguins, albatrosses and pinnipeds: implications for life history patterns. *American Zoologist* **31**:111–130.
- Costa, D. P. 1991b. Reproductive and foraging energetics of pinnipeds: implications for life history patterns. Pages 300–344 in D. Renouf, editor. *Behaviour of pinnipeds*. Chapman and Hall, Cambridge, UK.
- Costa, D. P. 1993. The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia. *Symposia of the Zoological Society of London* **66**:293–314.
- Costa, D. P., B. J. Le Boeuf, A. C. Huntley, and C. L. Ortiz. 1986. The energetics of lactation in the Northern elephant seal, *Mirounga angustirostris*. *Journal of Zoology, London* **209**:21–33.
- Elverhoi, A., J. A. Dowdeswell, S. Funder, J. Mangerud, and R. Stein. 1998. Glacial and oceanic history of the polar North Atlantic margins: an overview. *Quaternary Science Reviews* **17**:1–10.
- Fay, F. H. 1982. Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. U. S. Fish and Wildlife Service North American Fauna **74**:1–279.

- Fedak, M. A., and S. S. Anderson. 1982. The energetics of lactation: accurate measurements from a large wild mammal, the grey seal (*Halichoerus grypus*). *Journal of Zoology (London)* **198**:473–479.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* **125**:1–15.
- Ferguson, S. H., J. A. Virgl, and S. Lariviere. 1996. Evolution of delayed implantation and associated grade shifts in life history traits of North American carnivores. *Ecoscience* **3**:7–17.
- Fordyce, R. E. 2002. Fossil record. Pages 453–471 in W. F. Perrin, B. Wursig, and J. G. M. Thewissen, editors. *Encyclopedia of marine mammals*. Academic Press, San Diego, California, USA.
- Garland, T., Jr. 1992. Rate tests for phenotypic evolution using phylogenetically independent contrasts. *American Naturalist* **140**:509–519.
- Garland, T., Jr., and R. Diaz-Uriarte. 1999. Polytomies and phylogenetically independent contrasts: an examination of the bounded degrees of freedom approach. *Systematic Biology* **48**:547–558.
- Garland, T., Jr., A. W. Dickerman, C. M. Janis, and J. A. Jones. 1993. Phylogenetic analysis of covariance by computer simulation. *Systematic Biology* **42**:265–292.
- Garland, T., Jr., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology* **41**:18–32.
- Gentry, R. L., D. P. Costa, J. P. Croxall, J. H. M. David, R. W. Davis, G. L. Kooyman, P. Majluf, T. S. McCann, and F. Trillmich. 1986. Pages 220–264 in R. L. Gentry and G. L. Kooyman, editors. *Fur seals: maternal strategies on land and at sea*. Princeton University Press, Princeton, New Jersey, USA.
- Georges, J.-Y., and C. Guinet. 2000. Maternal care in the subantarctic fur seals on Amsterdam Island. *Ecology* **81**:295–308.
- Gittleman, J. L., and O. T. Oftedal. 1987. Comparative growth and lactation energetics in carnivores. *Symposia of the Zoological Society of London* **57**:41–77.
- Gubernick, D. J., and P. H. Klopfer, editors. 1981. *Parental care in mammals*. Plenum Press, New York, New York, USA.
- Hall, A. J., B. J. McConnell, and R. J. Birker. 2001. Factors affecting first-year survival in grey seals and their implications for life history strategy. *Journal of Animal Ecology* **70**:138–149.
- Harvey, P. H., and M. D. Pagel. 1991. *The comparative method in evolutionary biology*. Oxford University Press, Oxford, UK.
- Jenness, R., and R. E. Sloan. 1970. The composition of milks of various species: a review. *Dairy Science Abstracts* **32**:599–612.
- Kovacs, K. M., and D. M. Lavigne. 1986. Maternal investment and neonatal growth of phocid seals. *Journal of Animal Ecology* **55**:1035–1051.
- Kovacs, K. M., and D. M. Lavigne. 1992. Maternal investment in otariid seals and walruses. *Canadian Journal of Zoology* **70**:1953–1964.
- Kurtén, B. J. 1964. The evolution of the polar bear, *Ursus maritimus* Phipps. *Zoologica Fennica* **108**:1–26.
- Kurtén, B. J. 1968. Pleistocene mammals of Europe. *Weidenfeld and Nicolson*, London, UK.
- Le Boeuf, B. J., P. Morris, and J. Reiter. 1994. Pages 121–136 in B. J. Le Boeuf and R. M. Laws, editors. *Elephant seals: population ecology, behavior, and physiology*. University of California Press, Berkeley, California, USA.
- Lee, P. C., P. Majluf, and I. J. Gordon. 1991. Growth, weaning and maternal investment from a comparative perspective. *Journal of Zoology (London)* **225**:99–114.
- Leitch, L., F. E. Hytten, and W. Z. Billewicz. 1959. The maternal and neonatal weights of some Mammalia. *Proceedings of the Zoological Society of London* **133**:11–28.
- Lento, G. M., R. E. Hickson, G. K. Chambers, and D. Penny. 1995. Use of spectral analysis to test hypotheses on the origin of pinnipeds. *Molecular Biology and Evolution* **12**:28–52.
- Lipps, J. H., and E. Mitchell. 1976. Trophic model for the adaptive radiations and extinctions of pelagic marine mammals. *Paleobiology* **2**:147–155.
- Lydersen, C., and M. O. Hammill. 1993. Activity, milk intake and energy consumption in free-living ringed seal (*Phoca hispida*) pups. *Journal of Comparative Physiology B* **163**:433–438.
- Lydersen, C., and K. M. Kovacs. 1996. Energetics of lactation in harp seals (*Phoca groenlandica*) from the Gulf of St. Lawrence, Canada. *Journal of Comparative Physiology B* **166**:295–304.
- Lydersen, C., and K. M. Kovacs. 1999. Behaviour and energetics of ice-breeding, North Atlantic phocid seals during the lactation period. *Marine Ecology Progress Series* **187**:265–281.
- Lydersen, C., K. M. Kovacs, M. O. Hammill, and I. Gjert. 1996. Energy intake and utilization by nursing bearded seal (*Erignathus barbatus*) pups from Svalbard, Norway. *Journal of Comparative Physiology, B* **166**:405–411.
- Martin, R. D. 1984. Scaling effects and adaptive strategies in mammalian lactation. *Symposia of the Zoological Society of London* **51**:87–117.
- Martins, E. P., and T. Garland, Jr. 1991. Phylogenetic analyses of the correlated evolution of continuous characters: a simulation study. *Evolution* **45**:534–557.
- McLaren, I. A. 1958. The biology of the ringed seal (*Phoca hispida* Schreber) in the eastern Canadian Arctic. *Fisheries Research Board of Canada Bulletin* **118**:1–97.
- Mellish, J. E., S. J. Iverson, and W. D. Bowen. 2000. Metabolic compensation during high energy output in fasting, lactating grey seals (*Halichoerus grypus*): metabolic ceilings revisited. *Proceedings of the Royal Society of London B Biological Sciences* **267**:1245–1251.
- Mellish, J. E., S. J. Iverson, W. D. Bowen, and M. O. Hammill. 1999. Fat transfer and energetics during lactation in the hooded seal: the roles of tissue lipoprotein lipase in milk fat secretion and pup blubber deposition. *Journal of Comparative Physiology, B* **169**:377–390.
- Millar, J. S. 1977. Adaptive features of mammalian reproduction. *Evolution* **31**:370–386.
- Millar, J. S. 1981. Pre-partum reproductive characteristics of eutherian mammals. *Evolution* **35**:1149–1163.
- Mitchell, E. D., and R. H. Tedford. 1973. The Enaliarctinae: a new group of extinct aquatic Carnivora and a consideration of the origin of the Otariidae. *Bulletin of the American Museum of Natural History* **151**:201–284.
- Nunn, C. L., and R. A. Barton. 2000. Allometric slopes and independent contrasts: a comparative test of Kleiber's law in primate ranging patterns. *American Naturalist* **156**:519–533.
- Oftedal, O. T., D. J. Boness, and R. A. Tedman. 1987. The behavior, physiology, and anatomy of lactation in the Pinnipedia. *Current Mammalogy* **1**:175–245.
- Oftedal, O. T., W. D. Bowen, and D. J. Boness. 1996. Lactation performance and nutrient deposition in pups of the harp seal, *Phoca groenlandica*, on ice floes off southeast Labrador. *Physiological Zoology* **69**:635–657.
- Oftedal, O. T., and S. J. Iverson. 1995. Comparative analysis of nonhuman milks. A. Phylogenetic variation in the gross composition of milks. Pages 749–789 in R. G. Jensen, editor. *Handbook of milk composition*. Academic Press, San Diego, California, USA.

- Pagel, M. D., and P. H. Harvey. 1988. Recent developments in the analysis of comparative data. *Quarterly Review of Biology* **63**:413–440.
- Partridge, L., and P. H. Harvey. 1988. The ecological context of life history evolution. *Science* **241**:1449–1455.
- Perry, E. A., S. M. Carr, S. E. Bartlett, and W. S. Davidson. 1995. A phylogenetic perspective on the evolution of reproductive behavior in pagophilic seals of the northwest Atlantic as indicated by mitochondrial DNA sequences. *Journal of Mammalogy* **76**:22–31.
- Pierotti, R., and D. Pierotti. 1980. Effects of cold on the evolution of pinniped breeding systems. *Evolution* **34**:494–507.
- Promislow, D. E. L., and P. H. Harvey. 1990. Living fast and dying young: a comparative analysis of life-history variation among mammals. *Journal of Zoology (London)* **220**:417–437.
- Ray, C. E. 1976. Geography of phocid evolution. *Systematic Zoology* **25**:391–406.
- Rayner, J. M. V. 1985. Linear relations in biomechanics: the statistics of scaling functions. *Journal of Zoology (London)* **206**:415–439.
- Repenning, C. A. 1976. Adaptive evolution of the sea lions and walruses. *Systematic Zoology* **25**:375–390.
- Repenning, C. A., and C. E. Ray. 1977. The origin of the Hawaiian Monk seal. *Proceedings of the Biological Society of Washington* **89**:667–688.
- Ricklefs, R. E., and J. M. Starck. 1996. The application of phylogenetically independent contrasts: a mixed progress report. *Oikos* **77**:167–172.
- Schulz, T. M., and W. D. Bowen. 2004. Pinniped lactation strategies: evaluation of data on maternal and offspring life-history traits. *Marine Mammal Science* **20**:86–114.
- Shackleton, N. J., and N. D. Opdyke. 1977. Oxygen isotope and palaeomagnetic evidence for early Northern Hemisphere glaciation. *Nature* **270**:216–219.
- Spencer, R. P. 1971. The study of the maternal–fetal weight relationship in several mammalian species. *Physiologist* **14**:235–236.
- S-PLUS. 1998. S-PLUS 4.5. MathSoft, Seattle, Washington, USA.
- SPSS. 1999. SPSS version 10.0. SPSS, Chicago, Illinois, USA.
- Stewart, R. E. A. 1983. Behavioral and energetic aspects of reproductive effort in female harp seals. Dissertation. Guelph University, Guelph, Ontario, Canada.
- Stirling, I. 1975. Factors affecting the evolution of social behaviour in Pinnipedia. *Rapports et Proces-verbaux des Reunions Conseil international pour l'exploration de la Mer* **169**:205–212.
- Stirling, I. 1977. Adaptations of Weddell and ringed seals to exploit the polar fast ice habitat in the absence and presence of surface predators. Pages 741–748 in G. A. Llano, editor. Adaptations within Antarctic ecosystems. Proceedings of the Third SCAR [Scientific Committee on Antarctic Research] Symposium on Antarctic Biology, Washington, DC, August 26–30, 1974. Gulf Publishing Company, Houston, Texas, USA.
- Stirling, I. 1983. The evolution of mating systems in pinnipeds. Pages 489–527 in J. F. Eisenberg and D. G. Kleinman, editors. *Advances in the study of mammalian behavior*. American Society of Mammalogists Special Publication Number 7. Allen Press, Lawrence, Kansas, USA.
- Stirling, I., and W. R. Archibald. 1977. Aspects of predation of seals by polar bears. *Journal of the Fisheries Research Board of Canada* **34**:1126–1129.
- Symonds, M. R. E. 2002. The effects of topological inaccuracy in evolutionary trees on the phylogenetic comparative method of independent contrasts. *Systematic Biology* **51**:541–553.
- Talbot, S. L., and G. F. Shields. 1996. A phylogeny of bears (Ursidae) inferred from complete sequences of three mitochondrial genes. *Molecular Phylogenetics and Evolution* **5**:567–575.
- Tedman, R., and B. Green. 1987. Water and sodium fluxes and lactational energetics in suckling pups of Weddell seals (*Leptonychotes weddellii*). *Journal of Zoology, London* **212**:29–42.
- Trillmich, F. 1984. The natural history of the Galapagos fur seal, *Arctocephalus galapagoensis* Heller. Pages 215–223 in R. Perry, editor. *Key environments—Galapagos*. Pergamon Press, Oxford, UK.
- Trillmich, F. 1990. The behavioral ecology of maternal effort in fur seals and sea lions. *Behavior* **114**:3–19.
- Trillmich, F. 1996. Parental investment in pinnipeds. Pages 533–577 in J. S. Rosenblatt and C. T. Snowdon, editors. *Parental care: evolution, mechanisms, and adaptive significance*. Advances in the study of behavior. Volume 25. Academic Press, San Diego, California, USA.
- Trivers, R. L. 1972. Parental investment and sexual selection. Pages 136–179 in B. Campbell, editor. *Sexual selection and the descent of man*. Aldine Press, Chicago, Illinois, USA.
- Van Valkenburgh, B. 1999. Major patterns in the history of carnivorous mammals. *Annual Review of Earth and Planetary Sciences* **27**:463–493.
- Webb, P. I. 1997. Relative body size of neonatal marine mammals. *Canadian Journal of Zoology* **75**:1732–1736.
- Wyss, A. R. 1988. Evidence from flipper structure for a single origin of pinnipeds. *Nature* **334**:427–428.
- Wyss, A. R. 1994. The evolution of body size in phocids: some ontogenetic and phylogenetic observations. Pages 69–75 in A. Berta and T. A. Demere, editors. *Contributions in marine mammal paleontology honoring Franck C. Whitmore, Jr.* Volume 29. Proceedings of the San Diego Society of Natural History, San Diego, California, USA.

APPENDIX

A table showing the pinniped estimates of life-history traits used in the analysis is available in ESA's Electronic Data Archive: *Ecological Archives* M075-006-A1.