

Maternal effects on offspring growth rate and weaning mass in harbour seals

W. Don Bowen, Sara L. Ellis, Sara J. Iverson, and Daryl J. Boness

Abstract: We studied maternal effects on offspring traits during lactation in harbour seals (*Phoca vitulina*) on Sable Island, Nova Scotia, from 1988 to 1996. Duration of lactation was correlated with rate of pup mass gain ($r = -0.34$, $n = 116$) and weaning mass ($r = 0.29$, $n = 154$). Pups that grew faster had shorter nursing periods, whereas those that attained higher weaning masses nursed for a greater number of days. Pup sex did not affect patterns of maternal effects. The pups of young females (4–6 years old) gained mass at a constant but lower rate (0.56 kg/d) than the pups of older females through midlactation (0.74–0.78 kg/d; $n = 75$). In older females, rates of pup mass gain decelerated between mid and late lactation. Although maternal age did not directly affect weaning mass of pups, path analysis showed that maternal age acted on weaning mass through intermediary traits. Lighter females gave birth to smaller and slower growing pups, but invested relatively more than heavier females ($n = 153$). Effects of maternal postpartum mass on weaning mass ($n = 100$) were weaker in harbour seals than in phocids that fast during lactation, but apparently stronger than in otariids that forage during lactation, suggesting that the strength of maternal effects is influenced by lactation strategy.

Résumé : Nous avons étudié les effets maternels sur les caractéristiques de la progéniture durant l'allaitement chez le Phoque commun (*Phoca vitulina*), à l'île des Sables, au large de la Nouvelle-Écosse, de 1988 à 1996. La durée de la période d'allaitement est reliée au taux de gain de masse des petits ($r = -0,34$, $n = 116$) et à la masse des petits au moment du sevrage ($r = 0,29$, $n = 154$). Les petits qui grossissent plus rapidement ont des périodes d'allaitement plus courtes, alors que ceux qui atteignent une masse importante au sevrage sont allaités pendant une longue période. Le sexe des petits n'affecte pas l'influence maternelle. Chez les petits nés de mères jeunes (4–6 ans), les gains de masse sont constants, mais moins rapides (0,56 kg/jour) que chez les petits nés de mères plus âgées jusqu'au milieu de la période d'allaitement (0,74–0,78 kg/jour; $n = 75$). Chez ces derniers, les taux de croissance en masse diminuent entre le milieu et la fin de la période d'allaitement. Bien que l'âge de la mère n'affecte pas directement la masse des petits au moment du sevrage, une analyse des pistes causales démontre que l'âge de la mère influence la masse au sevrage via des caractères intermédiaires. Les femelles moins lourdes donnent naissance à des petits moins gros, à croissance plus lente, mais elles investissent relativement plus que les femelles plus lourdes ($n = 153$). Les effets de la masse de la mère après la mise bas sur la masse des petits au moment du sevrage ($n = 100$) sont plus faibles chez ce phoque que chez les phocidés qui jeûnent pendant l'allaitement, mais, semble-t-il, plus importants que ceux des otariidés qui continuent de chercher leur nourriture durant l'allaitement, ce qui indique que l'impact des effets maternels est influencé par la stratégie de l'allaitement.

[Traduit par la Rédaction]

Introduction

A female can affect the phenotype of her offspring over and above her genetic contribution (Arnold 1994). Maternal effects represent those parts of an offspring's phenotype not accounted for by the action of its own genes or its interaction with the environment (Bernardo 1996). These effects can be behavioural or physiological, can involve the transfer

of immunological competence, and may persist beyond the period of parental care. For example, maternal size can affect offspring growth and development, which in turn can affect offspring size (Arnbom et al. 1997; Mellish et al. 1999; Pomeroy et al. 1999). This is important because variation in size can be propagated throughout the life of an individual (Chambers and Leggett 1996). In mammals, offspring growth rates during lactation and size at weaning are also correlated with the probability of juvenile survival (Guinness et al. 1978; Wauters et al. 1993; Festa-Bianchet et al. 1997; Boltnev et al. 1998). Maternal behaviour can affect where offspring are born and their risk of predation.

Lactation is the most expensive period of maternal energy expenditure in mammals, owing to the production of energy-rich milk (Millar 1977; Oftedal 1985). Although food usually provides most of the energy used to support lactation (Millar 1975; Oftedal 1984), catabolism of maternal tissues is also an important source of energy exported in milk in some species. In the latter species, females fast during all or most of lactation, so nutrients supplied to offspring and those required to meet maternal needs are derived predominantly

Received November 16, 2000. Accepted May 10, 2001.
Published on the NRC Research Press Web site at
<http://cjz.nrc.ca> on June 22, 2001.

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from body stores (Oftedal et al. 1987; Oftedal 1993). Thus, the energy a female can expend on offspring will be limited by her energy reserves at parturition, which are positively correlated with her body mass (Iverson et al. 1993; Deutsch et al. 1994; Arnbohm et al. 1997; Mellish et al. 1999). In females that forage during lactation, the amount of energy they invest in their offspring should not be limited by initial energy stores. However, variation among females in foraging success during the lactation period could be reflected in offspring phenotype (Boyd et al. 1991; Georges and Guinet 2000).

There is abundant evidence of the influence of maternal body size on offspring size and development in vertebrates (Bernardo 1996). Among pinnipeds, the larger species of the family Phocidae generally fast during lactation (Bonner 1984; Oftedal et al. 1987). The total energy stores of females in these species are positively correlated with body mass. Thus, the finding that maternal mass is a dominant factor influencing offspring size in species such as the elephant seals (*Mirounga* spp.; Fedak et al. 1996; Arnbohm et al. 1997) and grey seal (*Halichoerus grypus*; Mellish et al. 1999) is not unexpected.

Although the effects of maternal mass are well documented, the effects of maternal age are a relatively poorly explored aspect of maternal effects (Bernardo 1996). Part of the reason for this is that there are few long-term demographic studies where the ages of females are known. Forslund and Part (1995) reviewed evidence for age effects in birds. Bowen et al. (1994) and Ellis et al. (2000) found that maternal age explained much of the variability in birth mass in harbour seals (*Phoca vitulina*) even after the effects of maternal mass were accounted for. Nevertheless, few studies have examined the simultaneous effects of maternal age and body size.

Harbour seals are long-lived mammals belonging to the family Phocidae. Females first give birth between 4 and 6 years of age, but continue to grow until around age 10 (Boulva and McLaren 1979; Markussen et al. 1989). When growth continues after sexual maturity, life-history theory predicts trade-offs between the allocation of a female's resources to growth and reproduction (Gadgil and Bossert 1970). Since the adult growth rate declines with age (McLaren 1993), trade-offs between growth and reproduction are likely to be highest among young females. Unlike females of the larger phocid species, female harbour seals regularly forage during lactation (Boness et al. 1994; Thompson et al. 1994). Further, the degree to which females forage is inversely correlated with body mass, with food intake accounting for up to 70% of daily energy expenditure in small females (Bowen et al. 2001). As foraging ability may relate to experience more than to the size of the female, we expected that age of female harbour seals might have a significant effect on offspring phenotype.

We examined the influence of maternal age, postpartum mass, lactation duration, and birth date on rate of pup mass gain and weaning mass in harbour seals. In addition to univariate analyses, we used path analysis to model the causal relationships among maternal traits and pup traits from birth through weaning, and to look for the relative strength of maternal effects. We predicted that young, small females would allocate less stored energy to reproduction

than older, larger females. As a result we expected that offspring of young females would gain mass less rapidly and would be weaned at a lighter mass than pups of larger females.

Materials and methods

Data collection

Lactating harbour seals and their pups were studied in May and June from 1988 to 1996 on Sable Island, a vegetated sandbar east of Nova Scotia, Canada (43°55'N, 60°00'W). The study area was a 24-km stretch of beach on the north side of the island where most females gave birth. Newborns were sexed and weighed, then tagged in the webbing of a hind flipper with individually numbered tags. Whenever possible we also weighed mothers of newborns and tagged them in a hind flipper. Maternal age was known for a subset of females that had been tagged as pups since 1978 and had retained the tags until they were recaptured as adults.

To study mass gain by pups and mass loss by females during lactation, a subset of mother-pup pairs were weighed again near 15 d post partum (dpp), i.e., two-thirds of the way through the 24-d lactation period (Muelbert and Bowen 1993). A further subset of mother-pup pairs were weighed at or near weaning. Weaning was considered to have occurred if any of the following four conditions applied: the pup's serum was clear (i.e., showed no evidence of chylomicrons from recent milk intake), gastric intubation revealed no milk in the pup's stomach, the female was not sighted with the pup in 2 consecutive twice-daily beach surveys, or the pup lost body mass (see Muelbert and Bowen 1993). Continued absence of the female was the most commonly used weaning criterion. Although some pups were captured shortly after weaning, it was seldom possible to capture females after they had weaned their pups.

Initial body masses of pups and females were generally determined within 24 h of parturition. Pups were weighed to the nearest 0.1 kg and females to the nearest 0.5 kg. Body masses determined on the day after birth were corrected to birth mass and maternal postpartum mass (MPPM) by subtracting an average daily mass gain of 0.5 kg for pups in early lactation and adding the average daily mass loss, 1.7 kg, for females for the same period (Bowen et al. 1994). Midlactation body masses were measured between 14 and 17 dpp. To compare midlactation rates of pup mass gain and maternal mass loss, body masses were individually corrected to 15 dpp using each pup's daily rate of mass gain and each female's daily rate of mass loss.

Only pups and females weighed within 4 d of weaning, and with a lactation duration greater than 17 d, were included in analyses of mass at weaning. This threshold for lactation duration came from a 2-year study of harbour seals on Sable Island in which mean lactation duration was 24.1 ± 3.2 d (mean \pm SD) ($n = 52$; Muelbert and Bowen 1993). We defined premature weaning operationally as 2 standard deviations below the mean.

The body mass of pups just prior to weaning was corrected to weaning mass by adding 0.5 kg/d. This late-lactation rate of mass gain was estimated from a subsample of 40 pups weighed in late lactation (i.e., >15 dpp) and again on the day of weaning. The body mass of pups weighed shortly after weaning was corrected to weaning mass by adding 0.4 kg/d. Maternal mass just prior to weaning was corrected to maternal mass at weaning by subtracting a late-lactation rate of mass loss of 1.1 kg/d ($n = 27$).

To examine the effects of maternal age on offspring traits, females were grouped into three age-classes (4–6, 7–10, and 11–14+ years) representing increasing levels of reproductive experience and decreasing rates of adult growth (McLaren 1993). To examine the effects of MPPM on offspring traits, females were divided into two groups based on the median parturition mass of 85.0 kg. Over the 10-year study period there was little interannual variation in

Table 1. Life-history traits of male and female harbour seal (*Phoca vitulina*) pups on Sable Island, 1988–1996.

Trait	Males ^a	Females ^a	<i>P</i> (<i>t</i> test)	<i>P</i> (ANCOVA)
Birth mass (kg)	11.1 ± 0.09 (175)	10.7 ± 0.09 (200)	0.009 [373]	0.001 ^b [1,241]
Rate of mass gain (kg/d)	0.6 ± 0.02 (50)	0.6 ± 0.01 (66)	0.052 [114]	0.191 ^c [1,113]
Mass gain (kg)	14.8 ± 0.42 (50)	13.8 ± 0.32 (66)	0.059 [114]	0.056 ^d [1,97]
Weaning mass (kg)	25.8 ± 0.38 (70)	24.1 ± 0.34 (84)	0.001 [152]	0.106 ^c [1,113]
Lactation duration (d)	23.8 ± 0.37 (78)	24.0 ± 0.37 (97)	0.658 [173]	0.530 ^c [1,113]
Weaning date	June 18 ± 0.6 d (78)	June 19 ± 0.5 d (97)	0.103 [173]	0.504 ^e [1,172]
Weaning mass relative to MPPM	30.8 ± 0.46 (42)	29.0 ± 0.41 (58)	0.004 [98]	

Note: Numbers in parentheses are sample sizes and numbers in square brackets are degrees of freedom.

^aData are given as the mean ± SE.

^bANCOVA of log birth mass on pup sex, controlling for log postpartum mass (data from Ellis et al. 2000).

^cANCOVA controlling for birth mass.

^dANCOVA controlling for postpartum mass.

^eANCOVA controlling for birth date.

measured traits (Ellis et al. 2000). However, the sample size was not sufficiently large to investigate simultaneously the effects of maternal age, body size, and year. Therefore, in this paper we combine all years to investigate maternal effects on offspring traits.

Statistical techniques

Path analyses were conducted to explore possible causal pathways between maternal effects and pup traits and to determine the relative strengths of relationships (Petraitis et al. 1996). A path between two variables represents the expected change in a dependent variable, with other independent variables held statistically invariant (Dobson and Michener 1995). Path models were constructed a priori, based on hypothesized causal order, and multiple regressions were run on each endogenous variable to test the models and estimate parameters. Paths were considered unidirectional to allow unique estimation of parameters (Klem 1995). Standardized partial-regression coefficients were used as path coefficients to allow direct comparison of path coefficients and effect strength (Wilkinson et al. 1996). For each model a subset of data was used, so that each case was complete for all variables examined. This assured equal sample size along each path, making comparisons between paths meaningful. Significant positive relationships are represented in path diagrams by solid arrows and negative relationships by dashed arrows. The amount of unexplained variation in each endogenous variable was estimated as $1 - R^2$ for each regression within the model (Sokal and Rohlf 1995) and is shown as a percentage at the end of an open-headed arrow (Klem 1995).

All statistical analyses were performed using SPSS (version 9.0). Data were transformed as necessary to meet the assumptions of linearity required for regression analysis, ANOVA, and analysis of covariance (ANCOVA). Means are reported with standard errors (SE). Correlation coefficients are Pearson's *r*. Because conditions in the field did not permit all variables to be measured for each female–pup pair, each analysis was conducted using the largest available sample. The significance level for all tests was 0.05.

Results

Twenty-three pups were weaned prematurely (i.e., between 12 and 17 d of age). Weaning mass determined for 20 of these prematurely weaned pups was significantly less than that of successfully weaned pups (19.9 ± 0.7 ($n = 20$) versus 24.8 ± 0.3 kg ($n = 154$); *t* test, $P < 0.001$). Females that weaned pups prematurely weighed significantly less at parturition than successful females (78.2 ± 2.6 ($n = 10$) versus 83.8 ± 0.1 kg ($n = 100$); *t* test, $P = 0.03$) but did not differ in mean age (*t* test, $P = 0.42$, $n = 80$) or parturition date (*t* test, $P = 0.45$, $n = 198$). Birth masses of prematurely weaned

pups did not differ from those that were weaned successfully (*t* test, $P = 0.52$, $n = 131$).

Effects of pup sex

At weaning, male pups weighed more absolutely and relative to MPPM than females; however, the weaning masses of male and female pups did not differ significantly after the effect of birth mass were controlled for (Table 1). The rate of mass gain, total mass gain, duration of lactation, and weaning date did not differ by pup sex after covariates were controlled for (Table 1).

Duration of lactation

The duration of lactation ranged from 18 to 31 d, with a mean of 23.9 d (Table 2). Lactation duration was negatively correlated with both maternal age ($r = -0.27$, $n = 74$, $P = 0.02$) and rate of pup mass gain ($r = -0.34$, $n = 116$, $P = 0.03$) and positively correlated with weaning date ($r = 0.48$, $n = 175$, $P < 0.001$) and weaning mass ($r = 0.29$, $n = 154$, $P < 0.001$). These univariate relationships did not differ by pup sex (ANCOVA, sex by age interaction, $P = 0.37$; sex by rate of mass gain interaction, $P = 0.87$; sex by weaning date interaction, $P = 0.68$; sex by weaning mass interaction, $P = 0.12$). Maternal age, rate of pup mass gain, and weaning date explained 41.4 % (adjusted R^2) of the observed variation in lactation duration (stepwise regression, $F_{[3,48]} = 13.0$, $P < 0.001$). Lactation duration was not correlated with parturition date ($r = -0.14$, $n = 175$, $P = 0.06$), MPPM ($r = -0.07$, $n = 100$, $P = 0.50$), or log birth mass after the effects of log maternal age on lactation duration were controlled for (partial $r = -0.05$, $n = 49$, $P = 0.74$).

Pup mass gain through midlactation

By 15 dpp, pups had doubled their birth mass (Table 2). Pup body mass at midlactation was significantly greater for females aged 7–10 and 11+ years than for those aged 4–6 years (ANOVA, simple contrasts, $P < 0.001$; Fig. 1) and for heavy females (i.e., above the median MPPM of 85.0 kg) than for light females (Table 2). Total mass gain at 15 dpp and mass at weaning did not differ among females in the three age-classes, but pups of heavy females were heavier both at 15 dpp and at weaning (Table 2).

Through midlactation, pups gained mass at a rate of 0.7 ± 0.01 kg/d ($n = 191$; range = 0.3–1.1 kg/d) and rate of mass gain was positively correlated with MPPM ($r = 0.32$, $n =$

Table 2. Life-history traits for female harbour seal and pups on Sable Island, 1988–1996; all females are combined and by maternal age and body-mass class.

Trait	All females	Maternal age-class ^a			<i>P</i> (ANOVA or ANCOVA)	Maternal body mass class ^a		
		Young (4–6 years)	Intermediate (7–10 years)	Older (11–14+ years)		Light (≤85.0 kg)	Heavy (>85.0 kg)	<i>P</i> (<i>t</i> test)
Pups								
Birth mass ^b (kg)	10.9 ± 0.06 (375)	9.3 ± 0.25 (30)	11.0 ± 0.16 (27)	11.7 ± 0.15 (24)	<0.001 ^c [2,71]	10.6 ± 0.12 (127)	11.3 ± 0.08 (117)	<0.001 [242]
Mass at 15 dpp (kg)	21.9 ± 0.23 (191)	18.5 ± 0.82 (14)	22.8 ± 0.49 (39)	24.0 ± 0.46 (25)	0.002 ^d [2,70]	21.2 ± 0.33 (85)	22.9 ± 0.34 (68)	<0.001 [151]
Weaning mass (kg)	24.8 ± 0.26 (154)	23.3 ± 0.74 (17)	24.6 ± 0.54 (30)	24.8 ± 0.77 (18)	0.665 ^d [2,47]	24.0 ± 0.36 (64)	26.3 ± 0.45 (36)	<0.001 [98]
Mass gain (kg)	14.2 ± 0.26 (116)	14.0 ± 0.64 (13)	13.7 ± 0.50 (22)	13.5 ± 0.73 (17)	0.185 ^d [2,47]	13.4 ± 0.33 (64)	15.2 ± 0.38 (36)	0.001 [98]
Growth rate (kg/d)	0.6 ± 0.01 (116)	0.5 ± 0.02 (13)	0.6 ± 0.03 (22)	0.6 ± 0.03 (17)	0.957 ^d [2,47]	0.6 ± 0.02 (64)	0.7 ± 0.02 (36)	<0.001 [98]
Ratio of weaning mass to birth mass	2.3 ± 0.03 (116)	2.5 ± 0.06 (13)	2.3 ± 0.07 (22)	2.2 ± 0.06 (17)	0.099 ^d [2,47]	2.3 ± 0.04 (64)	2.4 ± 0.034 (36)	0.057 [98]
Females								
Lactation duration (d)	23.9 ± 0.24 (175)	25.3 ± 0.46 (18)	24.5 ± 0.57 (36)	23.1 ± 0.77 (20)	0.083 [2,71]	23.9 ± 0.35 (64)	23.5 ± 0.59 (36)	0.560 [98]
Mass at weaning (kg)	54.9 ± 1.04 (33)	46.7 ± 1.79 (4)	52.9 ± 1.93 (4)	60.4 ± 3.25 (2)	0.001 ^d [2,4]	51.7 ± 1.10 (14)	58.6 ± 1.40 (14)	0.001 [26]
Total mass loss (kg)	30.8 ± 0.94 (28)	31.9 ± 0.26 (3)	23.9 ± 0.82 (3)	29.4 ± 0.00 (2)	0.001 ^d [2,4]	27.7 ± 1.15 (14)	33.8 ± 0.96 (14)	<0.001 [26]
Rate of mass loss (kg/d)	1.4 ± 0.04 (28)	1.2 ± 0.03 (3)	1.3 ± 0.07 (3)	1.6 ± 0.00 (2)	0.152 ^d [2,4]	1.3 ± 0.04 (14)	1.6 ± 0.04 (14)	<0.001 [26]
Mass at weaning relative to postpartum mass (%)	64.3 ± 0.77 (28)	60.1 ± 0.56 (3)	69.2 ± 0.99 (3)	67.2 ± 1.19 (2)	0.001 [2,5]	65.2 ± 1.11 (14)	63.4 ± 1.04 (14)	0.256 [26]
Pups/females								
Weaning mass relative to postpartum mass	29.8 ± 0.32 (100)	30.3 ± 0.88 (13)	30.1 ± 0.65 (22)	29.2 ± 0.79 (16)	0.592 [2,48]	30.3 ± 0.40 (64)	28.8 ± 0.51 (36)	0.021 [98]

Note: Numbers in parentheses are sample sizes and numbers in square brackets are degrees of freedom.

^aValues are given as the mean ± SE.

^bFrom Ellis et al. 2000.

^cANCOVA of log birth mass on age-class, controlling for log postpartum mass.

^dANCOVA controlling for postpartum mass.

Fig. 1. Body masses of harbor seal (*Phoca vitulina*) pups at birth, 15 d post partum, and weaning in relation to maternal age-class. Error bars show 95% confidence limits; sample sizes at each age-class are given in Table 1.

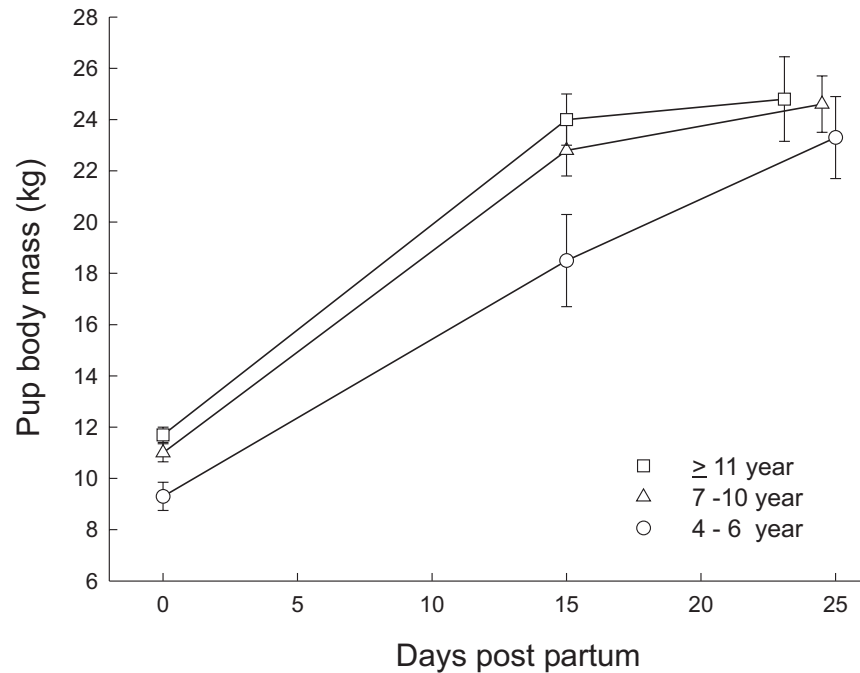


Table 3. Rate of mass gain of harbour seal pups at midlactation and over the entire lactation period in relation to maternal age and body mass class.

Maternal class	Midlactation mass gain (kg/d) ^a	Overall mass gain (kg/d) ^a	<i>P</i> (paired <i>t</i> test)
Age			
Young (4–6 years)	0.56 ± 0.030 (14)	0.54 ± 0.023 (13)	0.735 [5]
Intermediate (7–10 years)	0.74 ± 0.023 (39)	0.57 ± 0.026 (22)	<0.001 [15]
Older (11–14+ years)	0.78 ± 0.019 (25)	0.59 ± 0.029 (17)	<0.001 [14]
ANCOVA, <i>P</i> by age-class	0.001 ^b [2,70]	0.957 ^b [2,47]	—
Mass			
Small (≤85.0 kg)	0.66 ± 0.015 (85)	0.57 ± 0.015 (64)	<0.001 [44]
Large (>85.0 kg)	0.74 ± 0.016 (68)	0.66 ± 0.017 (36)	<0.001 [25]
<i>t</i> test, <i>P</i> by body-mass class	0.001 [151]	<0.001 [98]	—
All females	0.69 ± 0.011 (191)	0.60 ± 0.011 (116)	<0.001 [82]

Note: Numbers in parentheses are sample sizes and numbers in square brackets are degrees of freedom.

^aValues are given as the mean ± SE.

^bControlling for maternal postpartum mass.

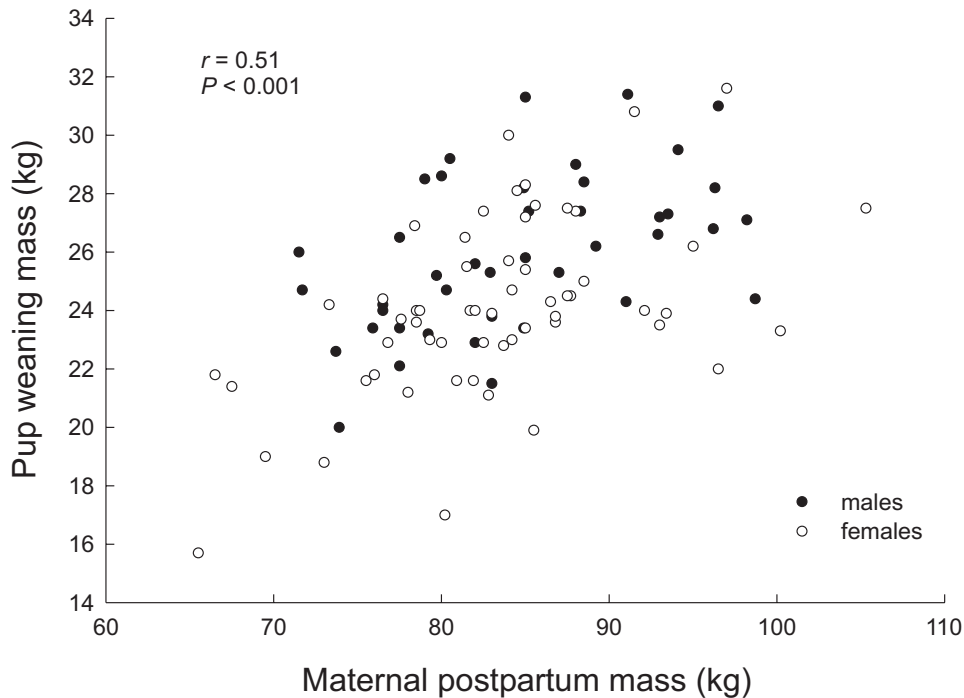
153, $P < 0.001$). Rate of pup mass gain through midlactation increased with maternal age, even after MPPM was controlled for, in male pups (partial $r = 0.35$, $n = 34$, $P = 0.04$) and female pups (partial $r = 0.48$, $n = 34$, $P = 0.003$) and for the sexes combined (partial $r = 0.37$, $n = 68$, $P = 0.001$). Pups of the youngest females gained mass more slowly through midlactation than pups of intermediate-aged and older females (Table 3, Fig. 1). By 15 dpp, pups of young females ($n = 6$) reached a significantly lower proportion of weaning mass ($75.5 \pm 3.7\%$) than did pups of intermediate-aged ($n = 16$) and older females ($n = 15$) (86.3 ± 1.6 and $89.8 \pm 1.6\%$, respectively) (ANOVA on arcsine-transformed

data, $F_{[2, 33]} = 7.2$, $P = 0.003$). Pups of light females gained mass more slowly than pups of heavy females (Table 3).

Pup mass gain throughout lactation

The rate of mass gain over the entire lactation period was strongly correlated with the rate of mass gain through midlactation ($r = 0.72$, $n = 83$, $P < 0.001$). However, the overall rate of mass gain (0.6 kg/d, range 0.3–0.9 kg/d) was lower than the rate of mass gain to midlactation (Table 3), suggesting that growth decelerated in late lactation. This deceleration of pup rate of mass gain occurred only in the pups of females ≥ 7 years of age (Table 3, Fig. 1).

Fig. 2. Positive correlation of weaning masses of harbor seal pups with maternal postpartum masses ($n = 100$).



The overall rate of mass gain by pups was positively correlated with MPPM ($r = 0.44$, $n = 100$, $P < 0.001$), but again this relationship did not differ for male and female pups (ANCOVA, sex by maternal mass interaction, $P = 0.932$). In contrast to mass gain through midlactation, there was no significant correlation between rate of mass gain over all of lactation and maternal age for male pups ($r = 0.18$, $n = 19$, $P = 0.46$), female pups ($r = 0.20$, $n = 33$, $P = 0.27$), or the sexes combined ($r = 0.14$, $P = 0.31$). The overall rate of mass gain by pups also did not differ significantly among maternal age-classes (Table 3).

Weaning mass

Pups averaged 24.8 kg at weaning (range 15.7–34.5 kg; Table 2), or 2.3 times birth mass. Pups of heavy females gained significantly more mass over the course of lactation than pups of light females (Table 2). Weaning mass of pups was positively correlated with MPPM (Fig. 2) but not with maternal age ($r = 0.14$, $n = 74$, $P = 0.25$). Nevertheless, MPPM explained only a small amount of the variation in weaning mass ($R^2 = 26.3\%$), and this correlation did not differ significantly by pup sex (test of homogeneity (Sokal and Rohlf 1995), $P > 0.50$). Weaning mass was positively correlated with log birth mass, even after the effects of log MPPM on log birth mass were controlled for (partial $r = 0.36$, $n = 97$, $P < 0.001$). Weaning mass also was correlated with both lactation duration (Fig. 3A) and the rate of mass gain by pups (Fig. 3B). These correlations did not differ by pup sex (ANCOVA, sex by lactation duration interaction, $P = 0.508$; sex by rate of mass gain interaction, $P = 0.790$). Relative weaning mass (weaning mass as a percentage of MPPM) did not differ by maternal age-class, but was significantly greater in light females than in heavy females (Ta-

ble 2) and was negatively correlated with MPPM (Pearson's $r = -0.24$, $n = 100$, $P = 0.014$).

Maternal mass loss

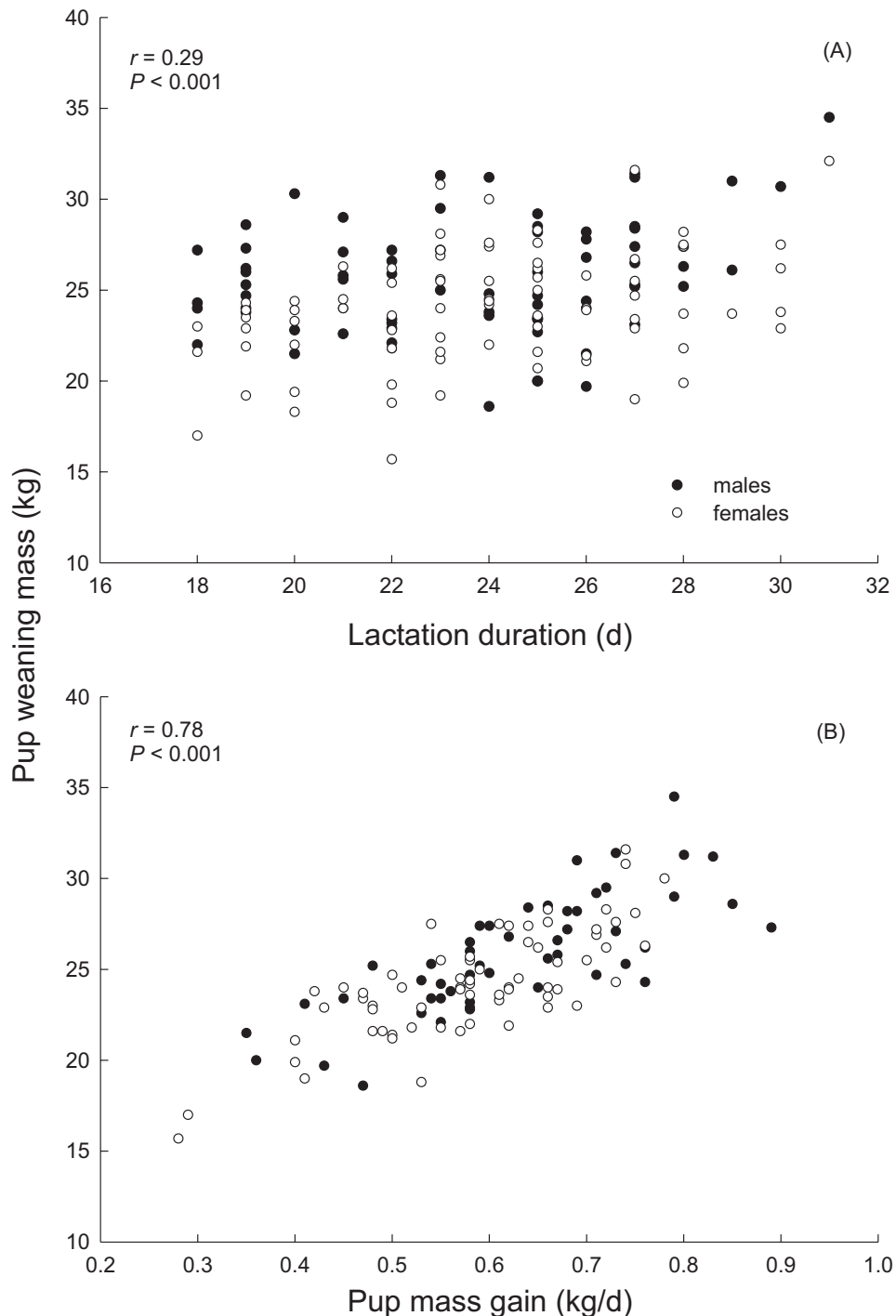
Females lost mass at a rate of 1.6 ± 0.02 kg/d ($n = 120$; range 0.7–2.0 kg/d) through midlactation and 1.4 kg/d ($n = 28$; range 0.9–1.8 kg/d) throughout lactation (Table 2), indicating that the rate of mass loss decelerated in late lactation (paired t test, $P = 0.001$, $n = 22$). On average, females lost 30.8 kg during lactation. At weaning, female mass averaged 54.9 kg (range 42.4–68.0 kg), or 64% of MPPM.

Maternal mass loss differed with maternal age after MPPM was controlled for (Table 2). At weaning, young females had lost significantly more mass than females of intermediate or older age-classes (Table 2). Large females lost more mass than small females (Table 2). Mass loss was positively correlated with MPPM ($r = 0.72$, $n = 28$, $P < 0.001$).

We also examined the 15-d mass loss of females, as we had a larger sample size ($n = 120$) at this time. Large females lost significantly more mass by 15 dpp than small females (25.2 ± 0.29 versus 21.5 ± 0.42 kg). Again, mass loss was positively correlated with MPPM ($r = 0.52$, $n = 120$, $P < 0.001$). At midlactation, maternal mass loss was correlated with pup mass gain for larger females ($r = 0.32$, $n = 56$, $P = 0.017$) but not for small females ($r = 0.20$, $n = 64$, $P = 0.097$). At weaning, the correlations between maternal mass loss and pup mass gain were stronger, and were significant for both small and large females ($r = 0.64$, $n = 14$, $P = 0.01$, and $r = 0.61$, $n = 14$, $P = 0.02$, respectively).

Pup mass gain at weaning was highly correlated with mass lost by the female ($r = 0.75$, $n = 28$, $P < 0.001$). The overall rate of maternal mass loss accounted for 44.6% of the variation in the rate of pup mass gain ($n = 28$, $P =$

Fig. 3. (A) Weak correlation of weaning masses of harbor seal pups with the duration of lactation ($n = 154$). (B) Strong correlation of weaning masses of harbor seal pups with rates of pup mass gain during lactation ($n = 116$).



<0.001). Pup sex did not affect this relationship (ANCOVA, sex by mass loss interaction, $P = 0.504$). Pup weaning mass relative to maternal postpartum mass averaged 29.8% (Table 2).

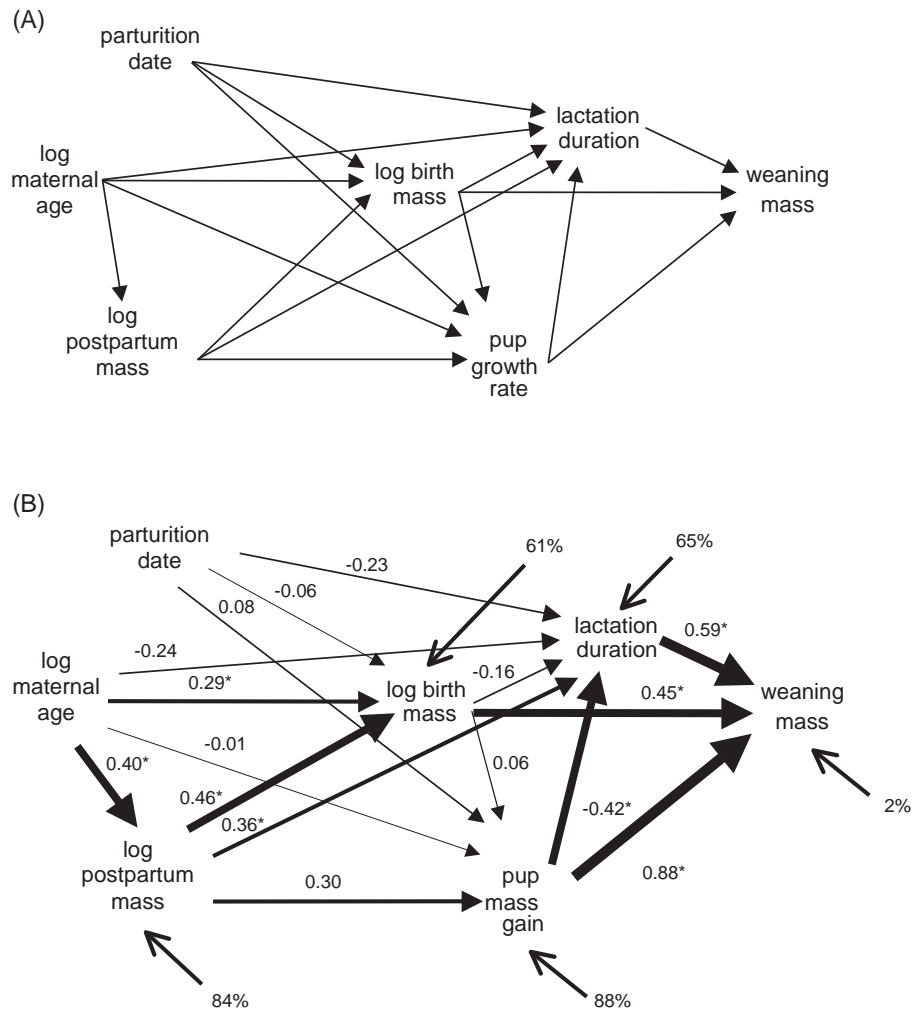
Path analysis of maternal effects on pup traits

We formulated two path models to explore the interrelationships between life-history traits of pups and females from birth through weaning. The weaning model is of greatest interest, since it encompasses the entire period of maternal

expenditure; however, we developed the midlactation model to explore the changes during lactation that were suggested in univariate analyses, and to take advantage of the larger sample size.

Birth mass, daily rate of mass gain, and lactation duration determine the weaning mass of a pup. We constructed the path model in such a way that each of these variables could have a direct effect on weaning mass (Fig. 4A). Rate of mass gain was hypothesized to affect lactation duration, since a rapidly growing pup would be likely to be weaned in a

Fig. 4. Path diagrams linking traits of female harbor seal and pups from birth to weaning. (A) Hypothesized model. (B) Model with data ($n = 51$). Values above paths are standardized partial-regression coefficients. Arrow widths are proportional to path coefficients and an asterisk denotes a coefficient that differs significantly from zero. Unexplained variance ($1 - R^2$) of each endogenous (dependent) variable is represented by a percentage at the end of an open-headed arrow. Broken lines represent negative paths.



shorter time. The maternal effects of age, postpartum mass, and parturition date were hypothesized not to act directly on weaning mass, but indirectly through their effects on birth mass, rate of mass gain, and lactation duration.

Using data from 51 females and their pups, we concluded that the strongest relationship was between rate of mass gain and weaning mass (path strength = 0.88; Fig. 4B). We calculated effect strength (the sum of direct and indirect effects of one variable on another) for all combinations of variables (Table 4B). The effect strengths of rate of mass gain, lactation duration, and maternal postpartum mass on pup weaning mass were similar and were the strongest effects in the model (Table 4B). The effect strength of pup birth mass on pup weaning mass was two-thirds that of the latter variables, whereas the effect strength of maternal age on pup weaning mass was approximately one-quarter as strong. As expected, the rate of mass gain of pups was negatively related to lactation duration. Maternal age was also negatively related to lactation duration, whereas MPPM had a small but positive effect on lactation duration. Both age and MPPM had positive effects on rate of pup mass gain, but the effect strength

of MPPM on rate of mass gain was more than twice that of age. Each had similar effects on birth mass (Table 4B).

In the midlactation model ($n = 69$ female-pup pairs) we also considered the effect of rate of maternal mass loss (Fig. 5A). As in the weaning model, the strongest path coefficient (Fig. 5B) and the greatest effect strength were between rate of mass gain and 15-d pup mass (Table 5B). The second strongest effect was that of MPPM on maternal mass loss. Maternal age had strong effects on rate of mass gain and 15-d pup mass. In the midlactation model, MPPM had weaker effects than maternal age on 15-d pup mass and growth rate. MPPM had about twice the effect of maternal age on the rate of maternal mass loss.

Discussion

Pinnipeds exhibit two major lactation strategies (Bonner 1984). The larger phocid species exhibit the “fasting strategy” in which females meet the cost of milk production and their own metabolic requirements from energy stored largely in the form of blubber. The smaller phocid species, such as

Table 4. Correlation matrix (A) and effect strength^a of variables (B) in the path model of 51 female-pup pairs from birth through weaning (see Fig. 4B).

(A) Variables.						
	Log maternal age	Log MPPM	Parturition date	Log birth mass	Rate of pup mass gain	Lactation duration
Log maternal age	—					
Log MPPM	0.40**	—				
Parturition date	0.36*	0.16	—			
Log birth mass	0.46**	0.57**	0.12	—		
Rate of pup mass gain	0.16	0.34*	0.13	-0.23	—	
Lactation duration	-0.32*	-0.01	-0.33*	-0.19	-0.41**	—
Weaning mass	0.17	0.54**	-0.03	0.54**	0.74**	0.15

(B) Dependent variables.						
	Independent variable					
	Log maternal age	Log MPPM	Parturition date	Log birth mass	Rate of pup mass gain	Lactation duration
Log maternal age	—					
Log MPPM	0.40	—				
Log birth mass	0.47	0.46	-0.06			
Rate of pup mass gain	0.12	0.33	0.08	0.06		
Lactation duration	-0.36	0.16	-0.25	-0.16	-0.42	
Weaning mass	0.15	0.57	-0.11	0.39	0.63	0.59

^aThe effect strength of one variable on another is the sum of the direct path coefficient (if any) and the product of path coefficients of each compound path (Klem 1995).

* $P < 0.05$.

** $P < 0.01$.

Table 5. Correlation matrix (A) and effect strength^a of variables (B) in the path model of 69 female-pup pairs from birth to midlactation (see Fig. 5B).

(A) Variables.						
	Log maternal age	Log MPPM	Parturition date	Log birth mass	Rate of maternal mass loss to 15 dpp	Rate of pup mass gain to 15 dpp
Log maternal age	—					
Log MPPM	0.44**	—				
Parturition date	0.29*	0.17	—			
Log birth mass	0.51**	0.43**	0.06	—		
Rate of maternal mass loss to 15 dpp	0.30*	0.61**	-0.04	0.34**	—	
Rate of pup mass gain to 15 dpp	0.53**	0.41**	0.19	0.45**	0.41**	—
15-d pup mass	0.58**	0.48**	0.06	0.72**	0.43**	0.87**

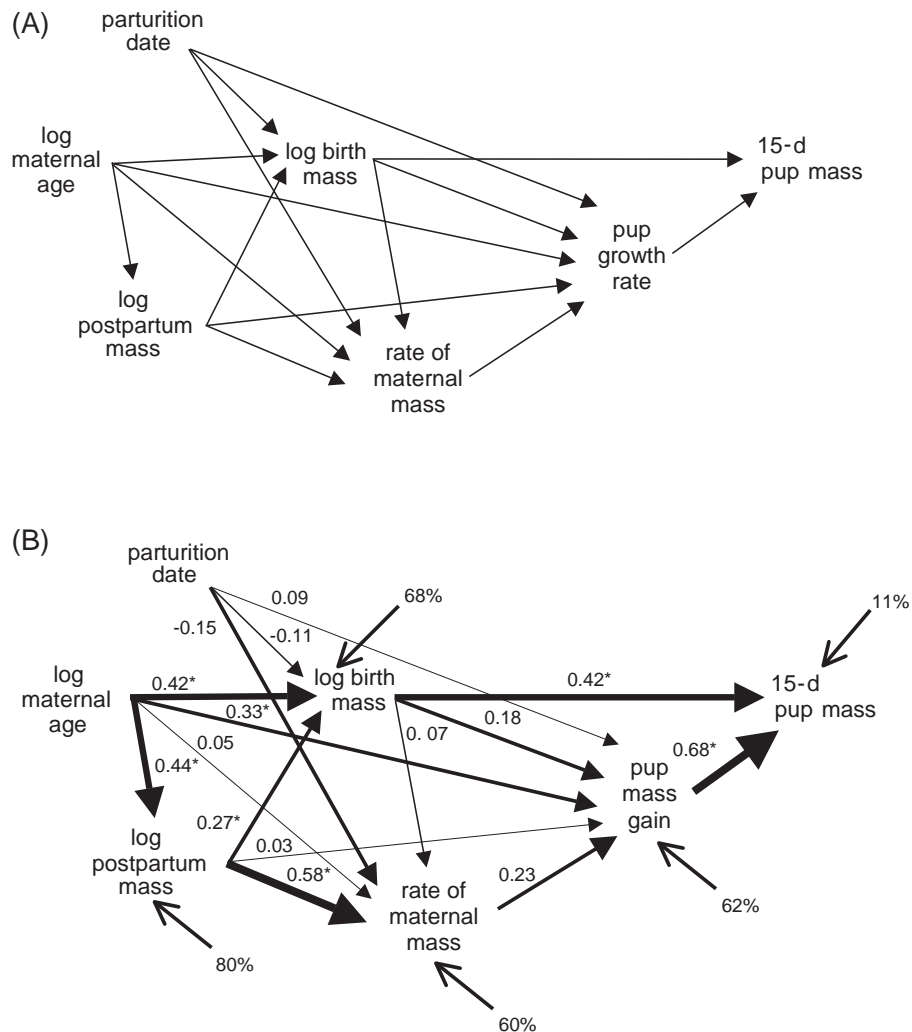
(B) Dependent variables.						
	Independent variable					
	Log maternal age	Log MPPM	Parturition date	Log birth mass	Rate of maternal mass loss to 15 dpp	Rate of pup mass gain to 15 dpp
Log maternal age	—					
Log MPPM	0.44	—				
Log birth mass	0.54	0.27	-0.11			
Rate of maternal mass loss to 15 dpp	0.34	0.60	-0.16	0.07		
Rate of pup mass gain to 15 dpp	0.52	0.27	0.03	0.20	0.23	
15-d pup mass	0.53	0.30	0.02	0.55	0.16	0.68

^aThe effect strength of one variable on another is the sum of the direct path coefficient (if any) and the product of path coefficients of each compound path (Klem 1995).

* $P < 0.05$.

** $P < 0.01$.

Fig. 5. Path diagram linking traits of female harbor seal and pups from birth to midlactation. (A) Hypothesized model. (B) Model with data ($n = 69$). For details see Fig. 4.



the harbour seal (Boness et al. 1994; Thompson et al. 1994; Bowen et al. 2001) and otariids, exhibit a “foraging-cycle strategy” whereby females alternate feeding trips to sea with periods of nursing on land, and body energy stores are used primarily to support early lactation. Much of our understanding of maternal effects in phocid seals comes from studies on the larger species, such as the southern elephant seal (*Mirounga leonina*; Arnborn et al. 1997; Fedak et al. 1996), northern elephant seal (*Mirounga angustirostris*; Deutsch et al. 1994), grey seal (Mellish et al. 1999; Pomeroy et al. 1999), and Weddell seal (*Leptonychotes weddelli*; Hastings and Testa 1998). However, body mass is correlated with many life-history traits in vertebrates (Roff 1992) and with pinniped lactation strategies (Boness and Bowen 1996; Boyd 1998). Therefore, a complete understanding of maternal effects in pinnipeds will require information on species across the full range of body sizes. The harbour seal is a small-bodied species of the Phocidae, thus our results extend the basis for a comparative understanding of maternal effects in pinnipeds.

Pup sex and maternal effects

On average, male pups weighed significantly more at

weaning (1.7 kg, or 7.1% heavier) than female pups. This dimorphism presumably represents the early expression of the sexual size dimorphism observed in adults, where males are about 27% heavier than females. Despite this sex difference in weaning mass, there was no evidence for differential maternal expenditure on males during lactation. After controlling statistically for birth mass, we found that the difference in weaning mass between males and females was not significant. This suggests that greater male mass at weaning results from greater initial mass (Bowen et al. 1994; Ellis et al. 2000) rather than from differential maternal energy expenditure during lactation according to pup sex. The lack of sex-related differences in other traits during lactation, such as lactation duration, total mass gain, and rate of mass gain (Table 1), supports this suggestion.

In other phocids such as grey seals, although males weighed more at birth than females, growth rates during lactation and suckling times and frequencies did not differ by sex (Smiseth and Lorentsen 1995). On Sable Island, male and female grey seal pups grew at the same rate during lactation (Bowen et al. 1992). In southern elephant seals, pup growth rates, mass gain, and weaning mass also did not vary by pup sex after maternal postpartum mass was controlled

for (Arnbom et al. 1997). Larger pups of larger mothers received more resources than smaller pups regardless of pup sex (Arnbom et al. 1997). Therefore, although polygynous and sexually size dimorphic pinnipeds may invest differentially prenatally, they do not appear to do so during lactation (cf. Trivers and Willard 1973; Maynard Smith 1980). Similar conclusions have been reached for otariids. In Antarctic fur seals, *Arctocephalus gazella*, Lunn and Arnould (1997) did not find sex-biased differences in pup growth rates, suckling behaviour, milk consumption, or maternal diving and attendance patterns. California sea lion, *Zalophus californianus*, mothers produced more milk for male pups than for females, but the difference was not significant after heavier male mass at birth was controlled for (Ono and Boness 1996). Thus, it appears that in pinnipeds, if mothers expend more energy on male pups during lactation, it is in response to the greater energy demands of initially larger offspring (Ono and Boness 1996) rather than representing differential expenditure based on pup sex.

We do not have the data to evaluate whether the greater overall energy expenditure on male harbour seal pups, as demonstrated by larger weaning mass, translates into a greater reproductive cost (sensu Trivers 1972) of raising a male pup. In other large mammals, greater mass of males at birth or weaning does not necessarily lead to increased maternal reproductive costs as measured by subsequent survival or fecundity. For example, although male bison (*Bison bison*) were heavier at birth, subsequent maternal fecundity, mass loss, and interbirth intervals did not vary with offspring sex (Green and Rothstein 1991). Similarly, although male northern elephant seal pups weighed approximately 8% more at birth and weaning, pup sex did not significantly affect a female's reproductive performance the following year, or her subsequent survival (Le Boeuf et al. 1989).

Maternal effects of age and MPPM

Our results show that both maternal mass and age affect the weaning mass of harbour seal pups, but that their effects are expressed at different times during lactation and in different ways. Through midlactation, pup mass and rate of mass gain were significantly lower for pups of young females than for pups of intermediate-aged or older females even after the effects of MPPM had been removed. Between mid and late lactation, growth rates remained constant for pups of young mothers, but decelerated for pups of older mothers. Although the difference was not statistically significant, lactation also tended to last several days longer for young females than for old females. These differences among maternal age-classes enabled the pups of young females effectively to "catch up," so that weaning mass of the pups did not differ among female age-classes. Some of the strongest effects in the midlactation path model were those of maternal age on pup mass and rate of mass gain, whereas in the weaning path model, age had only weak, indirect effects on weaning mass and rate of mass gain. That these age effects were weak in the weaning model but strong in the midlactation model supports the notion that late lactation represents a "catch-up" period for the pups of young females. This is also supported by evidence of increased foraging effort and food energy intake, especially by light

females, in late lactation (Bowen et al. 2001). Hence, light females may be forced to lactate longer in order to transfer sufficient resources to offspring prior to weaning.

As young females are also among the lightest (Ellis et al. 2000), the lower rate of mass gain by their pups might have resulted from lighter females producing less milk (e.g., Iverson et al. 1993), delivering their milk less effectively, or being less able to supplement body energy stores by foraging during lactation. A consequence of the lower rate of mass gain by the pups of young females was that these pups achieved only about 75% of weaning mass by midlactation compared with 85–90% for pups of older females. This could result in the pups of younger females being more severely affected by premature separation from their mothers during storms (Boness et al. 1992), or by short-term changes in food availability resulting in reduced milk production by females. If so, we would expect young females to have lower reproductive success than older females, particularly when resources are scarce.

Significant maternal age effects on rate of pup mass gain have not been found among the larger species of phocids (Stewart 1986; Arnbom et al. 1997; Pomeroy et al. 1999). It is not clear why there should be age effects in harbour seals but not in larger phocids. One possibility is that in species which forage during lactation, such as the harbour seal, age (i.e., foraging experience) may have a more important influence than body size on the ability to provision offspring.

Lactation duration was inversely related to female age. As indicated in the path diagram, part of this was due to the positive effect of age on MPPM and thus on pup mass gain, as well as the positive effect of age on birth mass. However, there was also a direct negative relationship between maternal age and lactation duration that explained variation in lactation duration which was unaccounted for by MPPM or birth mass. This may reflect behavioural or physiological traits in younger females that prolong lactation, such as inefficient suckling behaviour, low milk output, or that fact they must spend more time foraging than heavier females (Bowen et al. 2001).

Whereas maternal age exerted its effects at birth (Bowen et al. 1994; Ellis et al. 2000) and during early lactation, MPPM was the dominant maternal effect on weaning mass of harbour seal pups. Although MPPM was the best predictor of weaning mass, only 26% of the variance in weaning mass was explained by this maternal trait. This level of explained variation is low compared with that in phocid species that fast during lactation (see below) and may reflect the ability of female harbour seals to supplement energy stores by foraging during lactation (Boness et al. 1994; Thompson et al. 1994; Bowen et al. 2001). The effect of MPPM was also expressed early in lactation, although its effect was less pronounced, as prematurely weaned pups weighed less and were born to lighter females of similar age than successfully weaned pups. MPPM is a good measure of absolute energy stores available to support lactation (Bowen et al. 1992), as the percentage of body fat is independent of maternal body mass in lactating harbour seals (Bowen et al. 2001). Because there was no difference in the age of these females, it appears that prematurely weaned pups were born to females with lower body energy stores than successful females.

The path models provided a more comprehensive picture of how maternal effects interact to produce pup traits. However, the parameter estimates in our path diagrams should be considered tentative, since the sample size is relatively small for this kind of analysis (Petraitis et al. 1996). Furthermore, as a large amount of the variation in rate of pup mass gain was unexplained (88% in the overall model and 65% in the midlactation model), there must be variables not included in the model that affect mass gain. Such variables may include milk intake, pup energy expenditure, and maternal food intake. Nevertheless, variance in weaning mass was well explained by the variables in the path models.

Maternal mass loss during lactation

Excessive loss of body mass by females during lactation represents a potential cost in terms of future reproduction and survival (Rogowitz 1996). In harbour seals, young females lost more body mass than older females, both absolutely and relative to MPPM, suggesting that younger females are more at risk of excessive loss of body stores than are older females. However, these conclusions must be considered tentative given our small sample size. We found no evidence that lighter (and probably younger) females depleted relatively more of their energy stores than heavier (and probably older females) to achieve the same weaning mass of their offspring. Nevertheless, light females are forced to rely to a greater extent than heavy females on food intake to support lactation (Bowen et al. 2001). Although the consequences of high levels of expenditure (i.e., mass loss) for future reproduction are not known in harbour seals, in grey seals, females that invested heavily through high mass loss in one year were lighter in the following year and invested less in their offspring (Pomeroy et al. 1999).

The negative relationship between maternal expenditure relative to offspring weaning mass in harbour seals suggests a mass-dependent negative maternal effect as found in bighorn sheep (*Ovis canadensis*; Reale and Festa-Bianchet 2000). Light female harbour seals produced small, slow-growing offspring, but provided more care in terms of relatively greater offspring weaning mass than heavier females, resulting in a weak relationship between MPPM and pup weaning mass.

Maternal effects in relation to lactation strategies

Our results combined with those from previous studies suggest that the strength of maternal effects in pinnipeds may vary according to lactation strategy. We might expect MPPM to have a weaker effect on pup weaning mass in species exhibiting the foraging-cycle strategy because females fuel most of the energetic cost of lactation by feeding during lactation. Short-term variation in local food supply, differences among females in foraging efficiency, and perhaps more variable energy expenditure of aquatically active pups would also serve to weaken the correlation between MPPM and pup weaning mass.

In species that fast throughout lactation, MPPM generally accounts for about 40–60% of the variance in pup weaning mass (Kovacs and Lavigne 1992; Iverson et al. 1993; Deutsch et al. 1994; Arnbohm et al. 1997; Mellish et al. 1999). In species that exhibit a foraging-cycle strategy, such as the har-

bour seal, MPPM explained only about 26% of the variance in pup weaning mass. In another foraging-cycle species, the Antarctic fur seal, maternal body condition (measured as the ratio of mass to length) did not significantly influence pup mass near weaning (Arnbohm et al. 1993).

In other large mammals, the correlation between maternal body mass and offspring mass is also variable. In the polar bear (*Ursus maritimus*), maternal mass accounts for a similarly high fraction of the variance in the body mass of autumn cubs (Derocher and Stirling 1998) as found among the large phocid seals. Like phocid seals, much of milk production in the polar bear is fuelled from stored energy. By contrast, in bighorn sheep there is only a weak correlation between offspring weaning mass and maternal mass (Reale and Festa-Bianchet 2000). Although bighorn sheep are regarded as capital breeders (Festa-Bianchet et al. 1998), the weak correlation of offspring mass with maternal mass likely results from the negative maternal effects on offspring size in this species (Reale and Festa-Bianchet 2000). As we found evidence of negative maternal effects on offspring weaning mass in harbour seals, this may explain the low correlation found in this small phocid species.

It is less clear whether the effects of maternal age on offspring growth rate and weaning mass also differ between lactation strategies. Although maternal age affects offspring survival probability (e.g., Hastings and Testa 1998), age effects on offspring size at weaning have not yet been found in species exhibiting the fasting lactation strategy (Arnbohm et al. 1997). Nor were maternal age effects significant for pup growth or mass at weaning in Antarctic fur seals (Lunn and Boyd 1993). Maternal age accounted for about 11 and 21% of the variance in body mass of female and male polar bear cubs, respectively, from single litters (Derocher and Stirling 1998). However, it is not clear whether age would have been significant if the effect had been corrected for maternal body mass. In harbour seals, direct effects of maternal age were evident only at birth and in rates of mass gain through midlactation. By the time pups were weaned, MPPM accounted for more of the variance in pup mass. Thus, the effects of age on offspring traits may often be masked by prolonged lactation. This may partly explain why age effects have not been found in other pinniped species.

Acknowledgements

We are grateful to B. Beck, D. Benoit, D.W. Coltman, K. Jensen, P. Kirsch, J. Lawson, J. McMillan, M.M.C. Muelbert, O.T. Oftedal, E.A. Perry, P.S. Ross, M. Temple, L. Vedder, and B.G. Walker for help with the fieldwork. We thank G. Forbes, Officer-in-Charge of the Atmospheric Environmental Service, for logistical support on Sable Island. C.A. Beck and E.H. Miller provided constructive comments on a previous version of the manuscript. We also thank A.W. Trites for helpful suggestions. Research was supported by the Department of Fisheries and Oceans, the Natural Sciences and Engineering Research Council of Canada (NSERC), The Friends of the National Zoo, and the National Zoological Park, Smithsonian Institution. S.L.E. received support from an NSERC postgraduate fellowship and the Patrick Lett Fund. Procedures used on the animals in this

study were approved and follow Canadian Council on Animal Care guidelines.

References

- Arnbom, T., Fedak, M.A., Boyd, I.L., and McConnell, B.J. 1993. Variation in weaning mass of pups in relation to maternal mass, postweaning fast duration, and weaned pup behaviour in southern elephant seals (*Mirounga leonina*) at South Georgia. *Can. J. Zool.* **71**: 1772–1781.
- Arnbom, T., Fedak, M.A., and Boyd, I.L. 1997. Factors affecting maternal expenditure in southern elephant seals during lactation. *Ecology*, **78**: 471–483.
- Arnold, S.J. 1994. Multivariate inheritance and evolution: a review of concepts. In *Quantitative genetic studies of behavioral evolution*. Edited by C.R.B. Boake. University of Chicago Press, Chicago. pp. 17–48.
- Bernardo, J. 1996. Maternal effects in animal ecology. *Am. Zool.* **36**: 83–105.
- Boltnev, A.I., York, A.E., and Antonelis, G.A. 1998. Northern fur seal young: interrelationships among birth size, growth, and survival. *Can. J. Zool.* **76**: 843–854.
- Boness, D.J., and Bowen, W.D. 1996. The evolution of maternal care in pinnipeds. *BioScience*, **46**: 645–654.
- Boness, D.J., Bowen, W.D., Iverson, S.J., and Oftedal, O.T. 1992. Influence of storms and maternal size on mother–pup separations and fostering in the harbour seal, *Phoca vitulina*. *Can. J. Zool.* **70**: 1640–1644.
- Boness, D.J., Bowen, W.D., and Oftedal, O.T. 1994. Evidence of a maternal foraging cycle resembling that of otariid seals in a small phocid, the harbor seal. *Behav. Ecol. Sociobiol.* **34**: 95–104.
- Bonner, W.N. 1984. Lactation strategies in pinnipeds: problems for a marine mammalian group. *Symp. Zool. Soc. Lond.* No. 51. pp. 253–272.
- Boulva, J., and McLaren, I.A. 1979. Biology of the harbour seal, *Phoca vitulina*, in eastern Canada. *Bull. Fish. Res. Board Can.* No. 200.
- Bowen, W.D., Oftedal, O.T., Boness, D.J., and Iverson, S.J. 1994. The effect of maternal age and other factors on birth mass in the harbour seal. *Can. J. Zool.* **72**: 8–14.
- Bowen, W.D., Oftedal, O.T., and Boness, D.J. 1992. Mass and energy transfer during lactation in a small phocid, the harbor seal (*Phoca vitulina*). *Physiol. Zool.* **65**: 844–866.
- Bowen, W.D., Iverson, S.J., Boness, D.J., and Oftedal, O.T. 2001. Foraging effort, energy intake, and lactation performance depend on maternal mass in a small phocid seal. *Funct. Ecol.* **15**: 325–334.
- Boyd, I.L. 1998. Time and energy constraints in pinniped lactation. *Am. Nat.* **152**: 717–728.
- Boyd, I.L., Lunn, N.J., and Barton, T. 1991. Time budget and foraging characteristics of lactating Antarctic fur seals. *J. Anim. Ecol.* **60**: 577–592.
- Chambers, R.C., and Leggett, W.C. 1996. Maternal influences on variation in egg sizes in temperate marine fishes. *Am. Zool.* **36**: 180–196.
- Derocher, A.E., and Stirling, I. 1998. Maternal investment and factors affecting offspring size in polar bears (*Ursus maritimus*). *J. Zool. (Lond.)*, **245**: 253–260.
- Deutsch, C.J., Crocker, D.E., Costa, D.P., and Le Boeuf, B.J. 1994. Sex- and age-related variation in reproductive effort of northern elephant seals. In *Elephant seals: population ecology, behavior, and physiology*. Edited by B.J. Le Boeuf and R.M. Laws. University of California Press, Berkeley. pp. 169–210.
- Dobson, F.S., and Michener, G.R. 1995. Maternal traits and reproduction in Richardson's ground squirrels. *Ecology*, **76**: 851–862.
- Ellis, S.L., Bowen, W.D., Boness, D.J., and Iverson, S.J. 2000. Maternal effects on offspring mass and stage of development at birth in the harbour seal, *Phoca vitulina*. *J. Mammal.* **81**: 1143–1156.
- Fedak, M.A., Arnbom, T., and Boyd, I.L. 1996. The relation between the size of southern elephant seal mothers, the growth of their pups, and the use of maternal energy, fat, and protein during lactation. *Physiol. Zool.* **69**: 887–911.
- Festa-Bianchet, M., Jorgenson, J.T., Berube, C.H., Portier, C., and Wishart, W.D. 1997. Body mass and survival of bighorn sheep. *Can. J. Zool.* **75**: 1372–1379.
- Festa-Bianchet, M., Gaillard, J.M., and Jorgenson, J.T. 1998. Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. *Am. Nat.* **152**: 367–379.
- Forslund, P., and Part, T. 1995. Age and reproduction in birds—hypotheses and tests. *Trends Ecol. Evol.* **10**: 374–378.
- Gadgil, M., and Bossert, W.H. 1970. Life historical consequences of natural selection. *Am. Nat.* **104**: 1–24.
- Georges, J.-Y., and Guinet, C. 2000. Maternal care in the subantarctic fur seals on Amsterdam Island. *Ecology*, **81**: 295–308.
- Green, W.C.H., and Rothstein, A. 1991. Sex bias or equal opportunity? Patterns of maternal investment in bison. *Behav. Ecol. Sociobiol.* **29**: 373–384.
- Guinness, F.E., Clutton-Brock, T.H., and Albon, S.D. 1978. Factors affecting calf mortality in red deer (*Cervus elaphus*). *J. Anim. Ecol.* **47**: 817–832.
- Hastings, K.K., and Testa, J.W. 1998. Maternal and birth colony effects on survival of Weddell seal offspring from McMurdo Sound, Antarctica. *J. Anim. Ecol.* **67**: 722–740.
- Iverson, S.J., Bowen, W.D., Boness, D.J., and Oftedal, O.T. 1993. The effect of maternal size and milk output on pup growth in grey seals (*Halichoerus grypus*). *Physiol. Zool.* **66**: 61–88.
- Klem, L. 1995. Path analysis. In *Reading and understanding multivariate statistics*. Edited by L.G. Grimm and P.R. Yarnold. American Psychological Association, Washington, D.C. pp. 65–98.
- Kovacs, K.M., and Lavigne, D.M. 1992. Mass-transfer efficiency between hooded seal (*Cystophora cristata*) mothers and their pups in the Gulf of St. Lawrence. *Can. J. Zool.* **70**: 1315–1320.
- Le Boeuf, B.J., Condit, R., and Reiter, J. 1989. Parental investment and the secondary sex ratio in northern elephant seals. *Behav. Ecol. Sociobiol.* **25**: 109–117.
- Lunn, N.J., and Arnould, J.P.Y. 1997. Maternal investment in Antarctic fur seals: evidence for equality in the sexes? *Behav. Ecol. Sociobiol.* **40**: 351–362.
- Lunn, N.J., and Boyd, I.L. 1993. Effects of maternal age and condition on parturition and the perinatal period of female Antarctic fur seals. *J. Zool. (Lond.)*, **229**: 55–67.
- Markussen, N.H., Bjorge, A., and Oritsland, N.A. 1989. Growth in harbour seals (*Phoca vitulina*) on the Norwegian coast. *J. Zool. (Lond.)*, **219**: 433–440.
- Maynard Smith, J. 1980. A new theory of sexual investment. *Behav. Ecol. Sociobiol.* **7**: 247–251.
- McLaren, I.A. 1993. Growth in pinnipeds. *Biol. Rev. Camb. Philos. Soc.* **68**: 1–79.
- Mellish, J.-A.E., Iverson, S.J., and Bowen, W.D. 1999. Individual variation in maternal energy allocation and milk production in grey seals and consequences for pup growth and weaning characteristics. *Physiol. Biochem. Zool.* **72**: 677–690.
- Millar, J.S. 1975. Tactics of energy partitioning in breeding *Peromyscus*. *Can. J. Zool.* **53**: 967–976.

- Millar, J.S. 1977. Adaptive features of mammalian reproduction. *Evolution*, **31**: 370–386.
- Muelbert, M.M.C., and Bowen, W.D. 1993. Duration of lactation and postweaning changes in mass and body composition of harbour seal, *Phoca vitulina*, pups. *Can. J. Zool.* **71**: 1405–1414.
- Oftedal, O.T. 1984. Milk composition, milk yield and energy output at peak lactation: a comparative review. *Symp. Zool. Soc. Lond. No. 51*. pp. 33–85.
- Oftedal, O.T. 1985. Pregnancy and lactation. *In* *Bioenergetics of wild herbivores*. Edited by R.J. Hudson and R.G. White. CRC Press, Inc., Boca Raton, Fla. pp. 215–238.
- Oftedal, O.T. 1993. The adaptation of milk secretion to the constraints of fasting in bears, seals, and baleen whales. *J. Dairy Sci.* **76**: 3234–3246.
- Oftedal, O.T., Boness, D.J., and Tedman, R.A. 1987. The behavior, physiology, and anatomy of lactation in the pinnipedia. *Curr. Mammal.* **1**: 175–245.
- Ono, K.A., and Boness, D.J. 1996. Sexual dimorphism in sea lion pups: differential maternal investment, or sex-specific differences in energy allocation? *Behav. Ecol. Sociobiol.* **38**: 31–41.
- Petraitis, P.S., Dunham, A.E., and Niewiarowski, P.H. 1996. Inferring multiple causality: the limitations of path analysis. *Funct. Ecol.* **10**: 421–431.
- Pomeroy, P.P., Fedak, M.A., Rothery, P., and Anderson, S. 1999. Consequences of maternal size for reproductive expenditure and pupping success of grey seals at North Rona, Scotland. *J. Anim. Ecol.* **68**: 235–253.
- Reale, D., and Festa-Bianchet, M. 2000. Mass-dependent reproductive strategies in wild bighorn ewes: a quantitative genetic approach. *J. Evol. Biol.* **13**: 679–688.
- Roff, D.A. 1992. *The evolution of life histories: theory and analysis*. Chapman and Hall, New York.
- Rogowitz, G.L. 1996. Trade-offs in energy allocation during lactation. *Am. Zool.* **36**: 197–204.
- Smiseth, P.T., and Lorentsen, S.-H. 1995. Evidence of equal maternal investment in the sexes in the polygynous and sexually dimorphic grey seal (*Halichoerus grypus*). *Behav. Ecol. Sociobiol.* **36**: 145–150.
- Sokal, R.R., and Rohlf, F.J. 1995. *Biometry: the principles and practice of statistics in biological research*. 3rd ed. W.H. Freeman and Co., San Francisco.
- Stewart, R.E.A. 1986. Energetics of age-specific reproductive effort in female harp seals, *Phoca groenlandica*. *J. Zool. (Lond.)*, **208**: 503–517.
- Thompson, P.M., Miller, D., Cooper, R., and Hammond, P.S. 1994. Changes in the distribution and activity of female harbour seals during the breeding season: implications for their lactation strategy and mating patterns. *J. Anim. Ecol.* **63**: 24–30.
- Trivers, R.L. 1972. Parental investment and sexual selection. *In* *Sexual selection and the descent of Man 1871–1971*. Edited by B. Campbell. Aldine Publishing Co., Chicago. pp. 136–179.
- Trivers, R.L., and Willard, D.E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science (Washington, D.C.)*, **179**: 90–91.
- Wauters, L., Bijmens, L., and Dhondt, A.A. 1993. Body mass at weaning and juvenile recruitment in the red squirrel. *J. Anim. Ecol.* **62**: 280–286.
- Wilkinson, L., Black, G., and Gruber, C. 1996. *Desktop analysis with SYSTAT*. Prentice Hall Inc., Englewood Cliffs, N.J.