

## MATERNAL EFFECTS ON OFFSPRING MASS AND STAGE OF DEVELOPMENT AT BIRTH IN THE HARBOR SEAL, *PHOCA VITULINA*

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We studied effects of maternal age, body mass, and parturition date on birth mass and stage of development at birth in harbor seals (*Phoca vitulina*) on Sable Island, Nova Scotia, over a 10-year period. As predicted, effects of maternal mass and age on pup traits varied with maternal age. Premature pups, characterized by extensive fetal pelage termed lanugo, weighed 20% less than newborns without lanugo and were born early in the season to low-body-mass females 4–6 years of age. Among intermediate-age females (7–10 years old), percentage of lanugo on pups was correlated negatively with female postpartum body mass but not with female age. Thus, maternal condition rather than age had stronger effects on stage of development of offspring at birth. Overall, maternal age explained 54% of the variance in birth mass, whereas postpartum mass of females explained only 20% of the variance. These relationships did not differ with sex of the pup, although male pups were 3.7% heavier than female pups. Effects of maternal age were strongest among young females; however, reproductive parity was more important than age itself in determining offspring birth mass.

Key words: birth date, birth mass, harbor seal, maternal age, maternal mass, *Phoca vitulina*

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A female can affect the phenotype of her offspring through her experience with and response to the environment (Mousseau and Fox 1998). Maternal effects can influence offspring size and development through physiological or behavioral mechanisms (Bernardo 1996). For example, maternal food intake can affect maternal growth and condition, which in turn can affect birth mass of an offspring (Lunn et al. 1994; Robinson 1977; Willis and Wilson 1974). Offspring size is important because variation in size can be propagated throughout the life of an individual (Chambers and Legget 1996), affecting subsequent growth

and survival (Boltnev et al. 1997; Garnett 1979; Guinness et al. 1978b).

A number of factors are known to affect birth mass in mammals, including maternal age, body mass, nutritional condition, parity, parturition date, social rank, and offspring sex (Clutton-Brock et al. 1984; Guinness et al. 1978a; Reiter et al. 1981; Trites 1991). Several researchers have shown that birth mass is correlated positively with maternal postpartum mass in pinnipeds (Bowen et al. 1994; Boyd and McCann 1989; Costa et al. 1988). Maternal body mass is thought to be the dominant maternal trait influencing offspring size in pinnipeds (Arnbom et al. 1997; Fedak et al. 1996; Mellish et al. 1999). However, this

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conclusion is based primarily on studies of the larger pinnipeds, such as elephant seals (*Mirounga*) and grey seals (*Halichoerus grypus*), that have evolved a reproductive strategy whereby females fast during lactation (Boness and Bowen 1996; Bonner 1984; Oftedal et al. 1987). Recent studies have demonstrated that, unlike the larger phocid species, female harbor seals (*Phoca vitulina*) forage during lactation, exhibiting a reproductive strategy that more closely resembles the foraging-cycle strategy seen in fur seals and sea lions (Boness and Bowen 1996). Thus, a full understanding of the relative importance of maternal traits on traits of offspring will benefit from studies on smaller pinniped species, such as the harbor seal.

Harbor seals are long-lived, iteroparous mammals in the family Phocidae. They give birth on land and, like most pinnipeds, bear single precocial offspring (Bonner 1984). Offspring enter the water within hours of birth (Lawson and Renouf 1985). Such early entry into the water contrasts with the situation for other land-breeding phocids, which usually do not swim until after weaning (Bowen 1991). Adult females may live 30 years (Boulva and McLaren 1979). They give birth for the 1st time between 4 and 6 years of age but continue to grow until around 10 years of age (Boulva and McLaren 1979). Adult growth rate declines with age (McLaren 1993); therefore, trade-offs between growth and reproduction are likely to be highest among young females.

Although maternal age, body size, and condition can affect life-history traits of offspring (Roff 1992), relative effects of maternal age and condition may change throughout the lifetime of a female (Hastings and Testa 1998; Forslund and Pärt 1995). In many vertebrates that exhibit little or no growth after sexual maturity, clutch or litter size remain constant throughout adult life (Rockwell et al. 1993). However, in animals that continue to grow after sexual maturity, such as pinnipeds, there may be trade-offs between growth and reproduc-

tion (Gadgil and Bossert 1970; Roff 1992). Thus, a growing female might allocate less energy to reproduction than would a non-growing female.

To examine effects of maternal phenotype on offspring traits, we studied relationships of maternal age, postpartum body mass, parity, and parturition date with birth mass and stage of development at birth in neonatal harbor seals. Because male harbor seal pups weigh more at birth than do female pups (Bowen et al. 1994), we also examined whether maternal effects differed by sex of the pup. Greater reproductive experience is often accompanied by behavioral and physiological changes in the female that increase her chance of carrying a fetus to term (McKeown et al. 1976). We predicted that among young females, birth mass and stage of development of pups at birth (measured by presence of the lanugo, the whitish fetal pelage usually shed before birth—Ling and Button 1975) would be correlated positively with maternal age and that relative birth mass would be lower than that for pups of older females. Among older females, we expected that condition rather than age would affect birth mass and stage of development of pups.

#### MATERIALS AND METHODS

Data were collected in May and June 1987–1996 on Sable Island, a vegetated sand bar about 300 km southeast of Halifax, 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. Each day throughout the pupping season, the beach was searched for newborn pups (Bowen et al. 1994), which were captured by hand or with hoop nets. Pups were marked with a unique Rototag in the webbing of the hind flipper. Pup sex was recorded, and percentage of lanugo covering newborns was categorized as low (0–5%), moderate (6–49%), or extensive (50–100%). Those categories likely represented differing stages of development at birth, with low lanugo representing normal gestation and moderate to extensive lanugo indicating premature birth (Bowen et al. 1994).

When possible, mothers of newborns were

captured at the same time using a hand-held net fastened between 2 aluminum poles. These females also were tagged in the hind flipper (Bowen et al. 1992). Pups were weighed to the nearest 0.1 kg, and females were weighted to the nearest 0.5 kg. Maternal age at parturition was known for females that had been tagged as a pup and had retained the tag until being recaptured. Pup tagging began in 1978 and continued throughout this study. Known-age females were grouped into 3 classes (4–6, 7–10, and 11–16 years of age). The 1st class represented females with little or no maternal experience (having produced 0–2 pups), the 2nd class represented females that may have had 3–5 pups, and the 3rd class represented females that had likely given birth to >5 pups. Females in the 1st and 2nd groups were still growing (Boulva and McLaren 1979; McLaren 1993).

Pup mass and maternal postpartum mass were recorded generally  $\leq 24$  hours after parturition. Body mass measured on the day after parturition was extrapolated to birth mass by subtracting a daily gain of 0.5 kg for pups and to postpartum mass by adding a daily loss of 1.7 kg for females (Bowen et al. 1994). Maternal postpartum mass was a good measure of body condition in harbor seals because it reflected absolute energy stores available to the female to support lactation (Bowen et al. 1992).

*Statistical analyses.*—Some females were studied in >1 year. To avoid problems caused by serial correlation, data for only 1 year were chosen randomly for each identifiable female. Females that were not individually marked at initial capture were considered unique and were included in analyses. Although most analyses were conducted on those cross-sectional data, longitudinal data were used to examine within-female variability in parturition date and lanugo coverage of pups.

We conducted path analyses (Kingsolver and Schemske 1991; Wilkinson et al. 1996) to simultaneously determine the magnitude and direction of maternal effects on traits of newborns. In the path analyses, we used data on females for which all 5 variables (maternal age, postpartum mass, parturition date, pup birth mass, and percent lanugo) were measured. Path models were constructed a priori, based on hypothesized causal order. Paths were considered unidirectional to allow unique estimation of parameters (Klem 1995). We used log-transformed data on

maternal age, postpartum mass, and birth mass in path models to meet assumptions of linearity (Sokal and Rohlf 1995). Standardized partial regression coefficients were used as path coefficients and were obtained from multiple regression on each dependent (endogenous) variable (Sokal and Rohlf 1995; Wilkinson et al. 1996). The amount of unexplained variance for each endogenous variable was estimated as  $1 - R^2$  for each regression within the model (Sokal and Rohlf 1995) and was shown in path diagrams as a percentage at the end of an open-headed arrow (Klem 1995).

During the 2nd half of our study, few known-age females were recruited into the population (Ellis 1998); therefore, our sample size of known-age females was biased toward older females in later years. Thus, we controlled for year effects in statistical analyses involving maternal age. The distribution of parturition dates also shifted over the study period, with mean parturition date occurring 6 days later in the 2nd half of the study (Ellis 1998). Thus, we also controlled for year effects in statistical analyses involving parturition date. All statistical analyses were performed using SPSS version 7 (SPSS 1997) and SYSTAT version 7 (SYSTAT 1997). Data were transformed as necessary to meet assumptions of linearity required for regression analyses, analysis of variance (ANOVA), and analysis of covariance (ANCOVA). Means are reported with  $\pm SE$ . Correlation coefficients are Pearson's  $r$ , unless stated otherwise. Because sampling did not allow all variables to be collected for each mother-pup pair, each set of analyses was conducted using the largest available sample. The significance level for all tests was 0.05.

## RESULTS

*Interannual variability.*—Over the 10-year study period, there was little interannual variation in birth mass or maternal postpartum mass (Fig. 1). Neither variable differed by year after controlling for interannual variation in maternal age (ANCOVA on log-transformed age and mass data: birth mass,  $F = 1.4$ ;  $d.f. = 9, 70$ ;  $P = 0.225$ ; postpartum mass,  $F = 1.7$ ;  $d.f. = 9, 64$ ;  $P = 0.115$ ). At birth, pups weighed between 6.5 and 14.2 kg, averaging 10.9 kg ( $n = 375$ , Table 1). Overall, male pups were

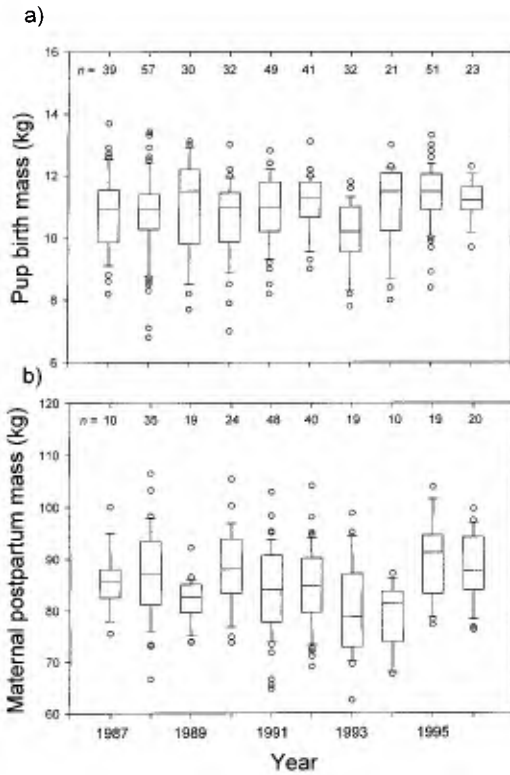


FIG. 1.—Interannual variation in a) pup birth mass ( $n = 375$ ) and b) maternal postpartum mass (maternal postpartum mass;  $n = 244$ ) of harbor seals on Sable Island, 1987–1996. The 25th, 50th, and 75th percentiles are shown by lines at the bottom, middle, and top of each box, respectively. The largest and smallest values that are not outliers are shown as the thin horizontal lines; open circles show outliers.

3.7% heavier at birth than female pups ( $11.1 \pm 0.09$  kg,  $n = 175$  versus  $10.7 \pm 0.09$  kg,  $n = 200$ ;  $t$ -test,  $P = 0.009$ ). Adult females weighed between 62.5 and 106.4 kg at parturition, averaging 85.1 kg (Table 1). Neither relative birth mass nor percentage of lanugo on pups differed by year after controlling for effects of maternal age (ANCOVA on arcsine-transformed data: relative birth mass,  $F = 1.3$ ;  $d.f. = 9, 64$ ;  $P = 0.25$ ; percentage of lanugo,  $F = 1.1$ ;  $d.f. = 9, 66$ ;  $P = 0.35$ ). Thus, data from all years were pooled for further analyses.

*Relationships among maternal traits.*—Maternal postpartum mass increased nonli-

TABLE 1.—Life-history traits ( $\bar{X} \pm SE$ ) of female harbor seals and offspring at parturition, Sable Island, 1987–1996. Analysis of variance was performed on maternal age class, year, and interactions (sample size in parentheses).

Variable	Maternal age class			P		
	All females	Young (4–6 years)	Intermediate (7–10 years)	Older (11–16 years)	Age class	Year by year
Pup birth mass (kg)	$10.9 \pm 0.06$ (375)	$9.3 \pm 0.25$ (30)	$11.0 \pm 0.16$ (27)	$11.7 \pm 0.15$ (24)	<0.001	0.309
Maternal postpartum mass (kg)	$85.1 \pm 0.54$ (244)	$75.6 \pm 1.19$ (24)	$83.8 \pm 1.10$ (27)	$90.1 \pm 1.37$ (24)	<0.001	0.220
Birth mass relative to maternal postpartum mass (%) <sup>a</sup>	$12.9 \pm 0.09$ (244)	$12.1 \pm 0.30$ (24)	$13.2 \pm 0.27$ (27)	$13.1 \pm 0.26$ (24)	0.003	0.472
Parturition date	$26 \text{ May} \pm 0.3$ (375)	$26 \text{ May} \pm 0.3$ (30)	$26 \text{ May} \pm 0.3$ (27)	$29 \text{ May} \pm 0.3$ (24)	0.151	0.034
Percentage lanugo <sup>a</sup>	$12.5 \pm 1.6$ (332)	$46.5 \pm 8.41$ (27)	$6.0 \pm 3.31$ (26)	$0.0 \pm 0.00$ (24)	<0.001	0.376

<sup>a</sup> Analysis of variance on arcsine-transformed dependent variable.

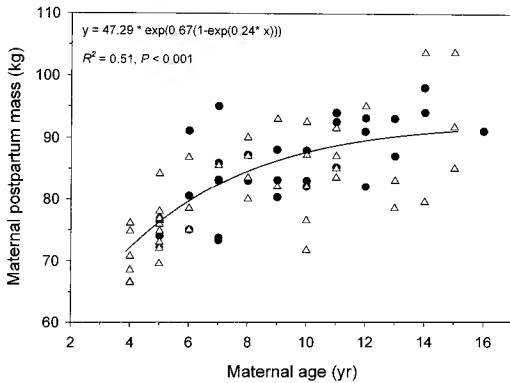


FIG. 2.—Relationship between maternal postpartum mass and age at parturition of adult female harbor seals on Sable Island ( $n = 75$ ). Females with male pups are represented by solid circles, and female pups are represented by triangles.

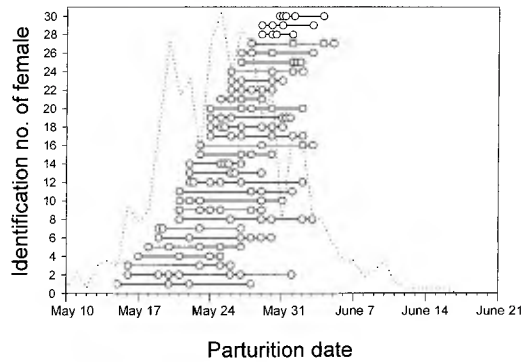


FIG. 3.—Parturition dates of 30 female harbor seals with  $\geq 4$  pups between 1987 and 1996 on Sable Island. Overlapping symbols indicate pups born on the same day in different years; dotted line shows the population frequency distribution of parturition dates.

nearly with maternal age, although females of a given age varied considerably in body mass (Fig. 2). Mean maternal postpartum mass among the 3 maternal age classes also increased significantly (Table 1). Parturition date was not correlated with maternal postpartum mass ( $r = 0.04$ ,  $P = 0.57$ ,  $n = 244$ ) or maternal age after controlling for effects of year on maternal age (partial  $r = 0.19$ ,  $P = 0.08$ ). Parturition date was not related to maternal postpartum mass for mothers of male pups ( $r = 0.13$ ,  $P = 0.16$ ,  $n = 118$ ) or female pups ( $r = -0.04$ ,  $P = 0.69$ ,  $n = 126$ ). Overall, mean parturition date of male pups was 1 day earlier than that of female pups (25 May  $\pm$  0.4 days,  $n = 251$  versus 26 May  $\pm$  0.4 days,  $n = 294$ ). However, that difference was not significant after controlling for year effects on parturition date (2-way ANOVA: year,  $P < 0.001$ ; sex of pup,  $P = 0.08$ ; interactions,  $P = 0.65$ ).

Maternal postpartum mass for mothers of male ( $85.2 \pm 0.74$  kg,  $n = 118$ ) and female ( $85.0 \pm 0.78$  kg,  $n = 126$ ) pups did not differ overall ( $t$ -test,  $P = 0.86$ ) or within maternal age class ( $P = 0.67$ , 0.26, and 0.41 for young, intermediate, and older females, respectively). Age of mothers of male ( $8.0 \pm 0.49$  years,  $n = 41$ ) and female

( $8.5 \pm 0.51$  years,  $n = 50$ ) pups did not differ ( $P = 0.49$ ). There were no differences in the distributions of maternal postpartum mass or age by pup sex (Kolmogorov-Smirnov test,  $P = 0.96$ ,  $P = 0.62$ , respectively).

There was considerable variation in parturition dates of individual females. Some females tended to give birth around the same date each year, but others did not (Fig. 3). Mean parturition dates differed among 30 females of known age that produced 4–7 pups during the study (ANOVA,  $F = 3.5$ ;  $df = 29, 114$ ;  $P < 0.001$ ). The maximum range of parturition dates among females during the study was 36 days. Each of the 30 females that had  $>4$  pups had a narrower range of parturition dates than that, but some were more variable than others. The greatest range in parturition dates within females was 16 days (over 7 years); the smallest range was 3 days (over 6 years). Differences in range of maternal age did not explain that variability because variance in parturition date of each female was not correlated with variance in maternal age ( $r = -0.06$ ,  $P = 0.79$ ,  $n = 30$ ). Similarly, individual variability in parturition date was not related to maternal mass because variance in parturition date of each female was not



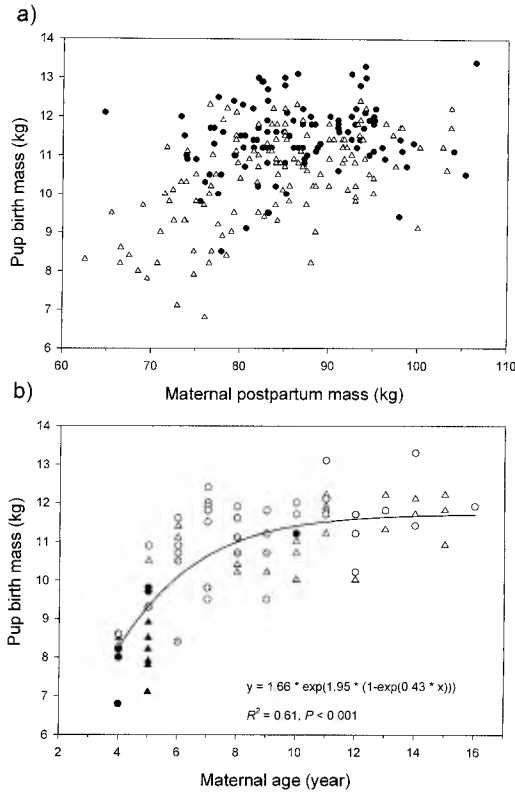


FIG. 4.—Relationships between pup birth mass and a) maternal postpartum mass ( $n = 244$ ) or b) maternal age ( $n = 75$ ) at parturition for harbor seals on Sable Island, 1987–1996. a) Male pups are represented by solid circles and female pups are represented by open triangles. b) Male pups are represented by circles and female pups are represented by triangles. Pups with no (open symbols,  $n = 56$ ), moderate (shaded symbols,  $n = 8$ ), and extensive (solid symbols,  $n = 14$ ) lanugo coverage also are shown.

correlated with variance in postpartum mass ( $r = -0.39, P = 0.17, n = 14$ ).

*Effect of maternal traits on birth mass.*—Birth mass was not correlated with parturition date of male ( $r = 0.11, P = 0.14, n = 175$ ) or female ( $r = 0.10, P = 0.15, n = 200$ ) pups. Birth mass increased nonlinearly with maternal postpartum mass and age (Figs. 4a and 4b). Correlations between log-transformed maternal postpartum mass and birth mass did not differ between male pups

( $r = 0.41, n = 118$ ) and female pups ( $r = 0.50, n = 126$ ; test of homogeneity between 2 correlation coefficients,  $P > 0.50$ ). Overall, maternal postpartum mass accounted for 20% of the variation in birth mass (log-transformed data,  $r = 0.45, P < 0.001, n = 244$ ). Similarly, the correlation between log-transformed maternal age and birth mass did not differ between male ( $r = 0.72, n = 43$ ) and female ( $r = 0.79, P > 0.20, n = 38$ ) pups. Overall, maternal age accounted for 54% of the variation in birth mass (log-transformed data,  $r = 0.74, P < 0.001, n = 81$ ). Age log-transformed data explained more variation in birth mass than did maternal postpartum mass (test of homogeneity between 2 correlation coefficients;  $P < 0.001$ ).

Older mothers bore heavier pups, even after controlling for maternal postpartum mass (partial correlation for log-transformed data;  $r = 0.56, P < 0.001, n = 72$ ). Conversely, heavier females did not bear heavier pups after controlling for maternal age (partial correlation for log-transformed data;  $r = 0.17, P = 0.16, n = 72$ ). Pups of females in the youngest maternal age class weighed less, on average, than did pups of females in intermediate and older age classes (Table 1), even after controlling for maternal postpartum mass (ANCOVA of birth mass on maternal age class, controlling for parturition mass,  $P < 0.001$ ). Differences in birth mass between young and old females were not due to young females bearing a preponderance of lighter female pups or older females bearing heavier male pups.

*Effects of reproductive parity on birth mass.*—To test whether age affected birth mass of pups of young females, we compared females of different ages but equal reproductive parity (i.e., primiparous 4-year-old females versus 5-year-olds). Primiparous 4-year-old females ( $70.5 \pm 1.68$  kg,  $n = 6$ ) weighed less than primiparous 5-year-old females ( $75.7 \pm 0.96$  kg;  $t$ -test,  $P = 0.01, n = 14$ ). However, birth mass of pups of those primiparous 4-year-old females did not differ from those of primiparous 5-year-old fe-

TABLE 2.—Relationship between stage of development at birth (measured as lanugo coverage) and other life-history traits in harbor seals ( $\bar{X} \pm SE$ , sample sizes in parentheses). In each row, all means differed, except for those followed by the same lowercase letter (Fisher's least-significant-difference test).

Variable	Lanugo coverage at birth			<i>P</i> <sup>a</sup>
	Extensive (50–100%)	Medium (6–49%)	Low (0–5%)	
Pup birth mass (kg)	9.0 ± 0.17 (43)	10.0 ± 0.23 (22)	11.2 ± 0.06 (267)	<0.001
Parturition date	22 May ± 0.7 (66)	25 May ± 1.0a (28)	27 May ± 0.6a (480)	<0.001
Maternal age (years)	5.6 ± 0.58b (18)	6.4 ± 0.93b (5)	9.4 ± 0.44 (58)	<0.001
Maternal postpartum mass (kg)	75.0 ± 1.35 (24)	82.3 ± 2.06 (15)	86.5 ± 0.56 (194)	<0.001

<sup>a</sup> One-way analysis of variance.

males, either absolutely ( $8.1 \pm 0.27$  kg versus  $9.0 \pm 0.35$  kg; *t*-test,  $P = 0.13$ ) or relative to maternal postpartum mass ( $11.5 \pm 0.56$  % versus  $11.8 \pm 0.46$  %; *t*-test,  $P = 0.66$ ).

To examine the influence of reproductive parity on birth mass, we compared primiparous and multiparous females while controlling statistically for maternal age. Females  $\geq 6$  years of age were assumed to be multiparous and were pooled for comparison with primiparous 4- and 5-year-olds. Maternal postpartum mass did not differ between primiparous ( $74.2 \pm 0.98$  kg,  $n = 20$ ) and multiparous ( $85.2 \pm 1.06$  kg,  $n = 55$ ) females after controlling for maternal age (ANCOVA for log-transformed data,  $P = 0.51$ ). However, pups of primiparous females ( $8.7 \pm 0.27$  kg) weighed less at birth than did pups of multiparous females ( $11.0 \pm 0.16$  kg) even after controlling for maternal age (ANCOVA for log-transformed data,  $P = 0.004$ ). Relative birth mass was also less in primiparous females than in multiparous females (*t*-test,  $P = 0.006$ ).

*Effects of maternal traits on stage of development of offspring.*—Most pups (84%) were born without lanugo. Pups with extensive lanugo weighed significantly less than did those with medium to low lanugo or those without lanugo (Table 2). Maternal age class affected lanugo coverage (Table 1). Pups with extensive lanugo were born earlier mainly to younger, lighter females (Table 2; Fig. 4b). Among known-age fe-

males, 13 premature pups were born to young females, 1 to an intermediate-age female, and none to the oldest females. Each sex was represented equally within the 3 categories of lanugo (Pearson  $\chi^2 = 0.33$ ,  $P = 0.85$ ).

Most females that were studied for  $>1$  year produced only pups without lanugo (88% of 209). However, the remaining 25 females bore  $\geq 1$  pup with lanugo. Eleven females that bore pups with extensive lanugo in the 1st year they were studied ranged in age from 4 to 7 years. In the following year, each of those females bore pups with moderate to no lanugo. Nine of those 11 females were primiparous 4- or 5-year-olds. However, 3 older females (8, 9, and 13 years of age) also gave birth to premature pups (i.e., pups with extensive lanugo) after each had previously delivered a nonlanugo pup. Maternal postpartum mass was known for 2 of those females. In both cases, when the premature pup was born, each female weighed less than her mean maternal postpartum mass over the study period.

*Effect of maternal traits on prenatal reproductive expenditure.*—At birth, pups weighed between 8.9% and 18.7% of maternal postpartum mass, with a mean of 12.9% (Table 1). Relative birth mass was not correlated with parturition date ( $r = -0.04$ ,  $P = 0.53$ ,  $n = 244$ ) but increased with maternal age (log-transformed data,  $r = 0.32$ ,  $P = 0.006$ ,  $n = 75$ ). The slope of

this relationship did not differ by pup sex (ANCOVA, sex by age interaction,  $P = 0.312$ ). Relative birth mass was lowest for the youngest maternal age class but was similar between the 2 older age classes (Table 1). Relative birth mass was higher for male pups ( $13.2\% \pm 0.14\%$ ,  $n = 118$ ) than for female pups ( $12.6\% \pm 0.12\%$ ,  $n = 126$ ). Pup sex and maternal age class influenced relative birth mass (2-way ANOVA; sex,  $P = 0.017$ ; age class,  $P = 0.020$ ), but there was no interaction between sex and age class ( $P = 0.156$ ), indicating that sex effects on relative birth mass were similar across maternal age classes.

Scaling of offspring mass with maternal mass can be expressed as a power function in the form  $y = bx^a$  (Leutenegger 1977). In harbor seals, the slope of the regression was  $<1.0$  (log-transformed data, slope = 0.52,  $P < 0.001$ ), indicating that prenatal reproductive expenditure increased less rapidly than did maternal postpartum mass. The slope of the line did not differ by pup sex (ANCOVA, sex by maternal postpartum mass interaction,  $P = 0.73$ ).

*Path analysis of maternal effects on offspring traits.*—We used path analysis to simultaneously examine the relative influence of maternal age, maternal postpartum mass, and parturition date on birth mass and percentage of lanugo. We hypothesized a model with 8 paths (Fig. 5) wherein maternal age (an indicator of reproductive experience) could have direct effects on maternal postpartum mass, birth mass, and percentage of lanugo. Age could also have indirect effects on birth mass through maternal postpartum mass and on percentage of lanugo through birth mass and maternal postpartum mass. We hypothesized that maternal postpartum mass (an indicator of maternal condition) and parturition date could have direct effects on birth mass and percentage of lanugo and indirect effects on percentage of lanugo through birth mass. We did not hypothesize a relationship between maternal age and parturition date because there was no relationship between those traits after

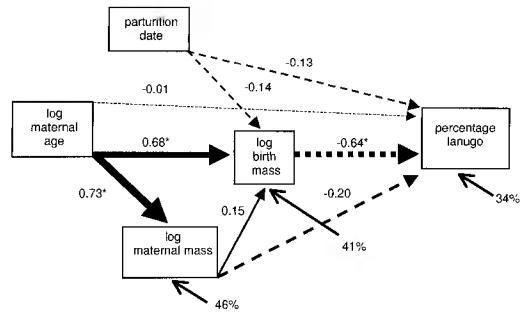


FIG. 5.—Path diagram linking life-history traits of female harbor seals and their pups at parturition ( $n = 74$ ). Values above paths are standardized partial regression coefficients or path coefficients. Arrow widths are proportional to path coefficients and asterisks denote coefficients significantly different from 0. Dashed lines indicate negative paths. Unexplained variance ( $1 - R^2$ ) of each endogenous (dependent) variable is represented by a percentage at the end of an open-headed arrow. Model includes pups of both sex and all maternal ages.

controlling for concurrent shifts in distribution of parturition dates and maternal ages over the study period (Ellis 1998).

In the overall model (Fig. 5), maternal age and sex of pup were examined together. The only significant paths in the model were between maternal age and birth mass, maternal age and maternal postpartum mass, and birth mass and lanugo (Fig. 5). Effect strengths of age on pup birth mass and maternal postpartum mass were similar in magnitude and direction (Table 3). The next 2 strongest and similar effects were negative effects of age and birth mass on percentage of lanugo (Table 3). Effect of age on percentage of lanugo was  $>2$  times greater than the effect of maternal postpartum mass on percentage of lanugo (Table 3). Effect strengths of maternal postpartum mass and parturition date on birth mass were  $<20\%$  the magnitude of age on birth mass (Table 3). The unexplained variance of each endogenous variable was 34% for percentage of lanugo, 41% for birth mass, and 46% for maternal postpartum mass (Fig. 5).



TABLE 3.—Effect strengths of independent variables on dependent variables in the path models linking life-history traits of female harbor seals and their pups at parturition (Figs. 5 and 6). Effect strength of 1 variable on another is the sum of the direct path coefficient and the product of path coefficients of each compound path (Klem 1995).

Dependent variable	Independent variable			
	Log maternal age	Log maternal postpartum mass	Parturition date	Log birth mass
Overall model (Fig. 5)				
Log maternal postpartum mass	0.73			
Log birth mass	0.79	0.15	-0.14	
Percentage lanugo	-0.67	-0.30	-0.04	-0.64
Mothers 4–6 years old (Fig. 6a)				
Log maternal postpartum mass	0.66			
Log birth mass	0.61	0.20	-0.14	
Percentage lanugo	-0.65	-0.10	-0.18	-0.67
Mothers 7–10 years old (Fig. 6b)				
Log maternal postpartum mass	0.02			
Log birth mass	0.06	-0.06	-0.18	
Percentage lanugo	0.21	-0.37	-0.43	-0.16
Mothers 11–16 years old (Fig. 6c)				
Log maternal postpartum mass	0.20			
Log birth mass	-0.03	0.04	0.17	
Percentage lanugo				

To test whether the model was valid for all ages, we evaluated each of the 3 maternal age classes representing differing levels of reproductive experience. Only the model for young mothers ( $n = 24$ ; Fig. 6a) had the same significant paths as the overall model, but the path coefficients were smaller and the unexplained variances were greater. For the intermediate age class ( $n = 26$ ), the only 2 significant paths (i.e., the negative paths from parturition date and maternal postpartum mass to percentage of lanugo) were not significant in the overall model (Fig. 6b). Effects of age on birth mass and maternal postpartum mass were small, leaving the unexplained variance for those dependent variables extremely high (Fig. 6b). Within the oldest female age class, no pups were born with lanugo; therefore, it was not possible to run a regression on percentage of lanugo. In the reduced model for the oldest females ( $n = 24$ ), no paths were significant and unexplained variance was high (Fig. 6c).

## DISCUSSION

Intraspecific effects of maternal phenotype on birth mass have been studied in few pinniped species, and these species do not adequately represent the diversity of maternal reproductive strategies within this taxon (Boness and Bowen 1996; Bonner 1984; Oftedal et al. 1987). Studies based on a reasonable sample are available for only 1 fur seal, and 3 of the large-body phocid species. This study extends our knowledge of relationships among maternal traits and offspring traits at birth to a small-body phocid species and thus provides a basis for a fuller understanding of phenotypic maternal effects in pinnipeds.

*Effect of parturition date on birth mass.*—Conditions may change over the course of a breeding season such that it may be beneficial to females of different genotypes or phenotypes to give birth at a particular time. The size and age distributions of females giving birth often differ over the

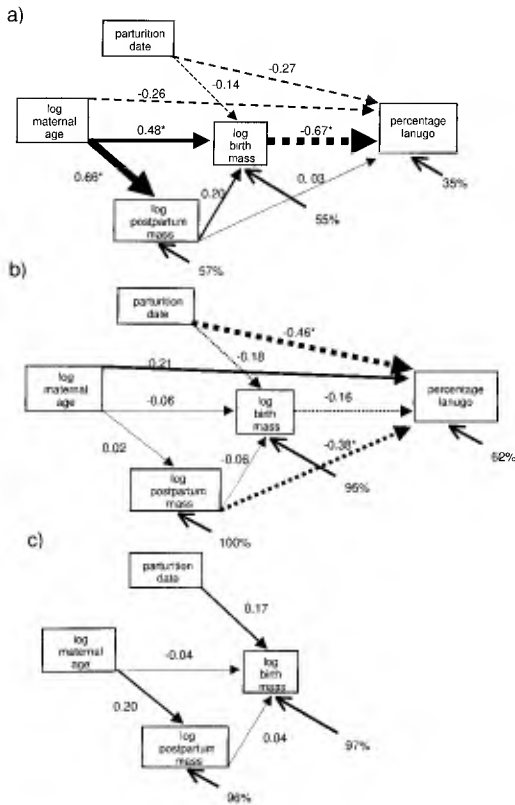


FIG. 6.—Path diagrams of maternal effects at birth in harbor seals by maternal age class. Values above paths and at ends of arrows are as indicated in Fig. 5. a) Females 4–6 years old ( $n = 24$ ). b) Females 7–10 years old ( $n = 26$ ). c) Females 11–16 years old ( $n = 24$ ).

course of the breeding season. In northern elephant seals (*Mirounga angustirostris*), grey seals at North Rona, and Antarctic fur seals (*Arctocephalus gazella*), older and larger females tend to give birth early in the season (Anderson and Fedak 1987; Lunn and Boyd 1993; Reiter et al. 1981). However, our data on harbor seals and those on grey seals at Sable Island and Weddell seals (*Leptonychotes weddellii*) showed that parturition date was not related to maternal age or maternal postpartum mass (Boness et al. 1995; Hastings 1996).

Selection for parturition date seems to act similarly on all harbor seal females that carry their offspring to term. Why should par-

turition date be important in some species or populations and not in others? One reason may be related to differences in the effect of density on reproductive performance. Female Weddell seals and harbor seals raise their young in low-density colonies where density does not change substantially during the breeding season. In contrast, densities of colonies of grey seals are considerably higher than those of harbor and Weddell seals. Nevertheless, the colony of grey seals, in which age affected birth date (North Rona) had a higher density than that in which no maternal age effects on birth date were seen (Sable Island).

The range of parturition dates of individual female harbor seals was narrower than that of the population in general, and mean parturition date differed among individuals. Similar results have been reported in Antarctic fur seals (Boyd 1996). Nevertheless, there was considerable variability in successive parturition dates within some females, suggesting that there are year effects on the ability of females to dampen environmental variability affecting fetal growth. Boyd (1996) concluded that duration of pregnancy and hence parturition date is affected by environmental variation, but the tendency of females to give birth at the same time of year suggested a range of responses to photoperiod. Boyd (1996) further suggested that this response might be genetically determined, as indicated in studies of wild rodents (Desjardins et al. 1986).

*Effects of maternal postpartum mass and age on birth mass.*—Maternal postpartum mass explained little of the variation in birth mass of harbor seals. This level of explained variation is low compared with that for larger phocids (Deutsch et al. 1994; Iverson et al. 1993; McCann et al. 1989). In contrast to maternal postpartum mass, maternal age explained about half of the variation in birth mass of harbor seals. Again, harbor seals differ from northern elephant seals in that maternal age in the latter had no effect on pup birth mass after controlling for maternal mass (Deutsch et

al. 1994). This difference could be an artifact of the lack of data for young female northern elephant seals. For example, most northern elephant seals give birth for the 1st time at 3–4 years of age (Reiter and Le Boeuf 1991); however, in the study by Deutsch et al. (1994), there were only two 3-year-olds and three 4-year-olds among 41 known-age females. Because age effects are usually most pronounced among young females, this underrepresentation of young females may have contributed to the nonsignificant effect of age on birth mass (after controlling for maternal postpartum mass).

It is common among vertebrates for females to increase reproductive expenditure with age; this trend has been well-studied in birds (Curio 1983; Newton 1989). In red deer (*Cervus elaphus*), calves of 3–4-year-old females weigh less than calves of 5–10-year-old females (Guinness et al. 1978a). Such changes are often explained by the constraint hypothesis, which asserts that developmental processes involving morphology, physiology, and behavior are not advanced sufficiently in young adults to allow full reproductive expenditure over the 1st few reproductive events (Curio 1983; Newton 1989; Rockwell et al. 1993). We found that relative birth mass increased with maternal age in harbor seals, consistent with the constraint hypothesis and the prediction of trade-offs between growth and reproduction. It was mainly young females with little or no prior reproductive experience that accounted for this weak positive correlation. Primiparous females of different ages bore pups of similar birth mass, suggesting that reproductive experience was more important than age in determining birth mass among young females. However, because our analysis had low power to reject the null hypothesis, this conclusion should be viewed as tentative. Nevertheless, pups of experienced females weighed more than pups of 1st-time mothers, even after controlling for age and mass, lending further support to the role of reproductive experience in determining birth mass.

Studies of effects of maternal phenotype on offspring birth mass in mammals usually have considered maternal mass and age separately (e.g., red deer—Guinness et al. 1978a; northern elephant seals—Reiter et al. 1981; southern elephant seals, *Mirounga leonina*—Arnbom et al. 1993). Where both maternal variables have been measured (Deutsch et al. 1994), the effect of each variable was determined over the full range of measured ages rather than within different age classes. Thus, differential effects with increasing age, if present, were not detected. By simultaneously examining effects of maternal age and mass, we gained a greater insight into how these effects may change over a female's reproductive life.

In our study, the relative importance of maternal postpartum mass and age on pup traits changed with maternal age. In Richardson's ground squirrels (*Spermophilus richardsonii*), the effect of maternal body condition of older females on offspring birth mass was only half that of yearling mothers (Dobson and Michener 1995). Our finding is consistent with the expectation that young females may have different reproductive tactics than older females because they are growing, are inexperienced, and have greater life expectancy (Charnov and Schaffer 1973). Among young females, age rather than maternal postpartum mass had a significant influence on birth mass and stage of development, whereas in 7–10-year-old females, body mass, but not age, influenced stage of development. Premature births were observed only among intermediate-age females with relatively low postpartum mass, perhaps reflecting poor condition. Thus, after the 1st few reproductive events, maternal condition appeared to influence birth traits more than reproductive experience. For females >10 years of age, neither maternal age nor body mass affected traits of pups at birth.

Several mechanisms may underlie changes in relative effects of maternal age and mass on offspring traits. In mammals, the maternal environment can be critical for fe-

tal growth (McKeown et al. 1976), and there may be limitations on the amount of nutrients a primiparous female can give to her growing fetus. Trites (1991) found that after controlling for age and maternal postpartum mass, pups of primiparous northern fur seals (*Callorhinus ursinus*) weighed less than pups of multiparous females. Trites (1991) suggested that females were physiologically altered by their 1st pregnancy and hypothesized that after the 1st parturition, higher numbers of intrauterine blood vessels supplying the placenta improved provisioning of the fetus. In humans, size of the placenta increases with parity, leading to higher offspring birth mass among females with more reproductive experience (McKeown and Record 1953; Roberts 1976). In addition to physiological changes, maternal experience can lead to behavioral changes (Forslund and Pärt 1995), and these changes could affect offspring birth mass. For example, foraging success may improve with age and experience, as seen in individual European blackbirds (*Turdus merula*—Desrochers 1992). We do not know if foraging ability increases with maternal age in female harbor seals, but improved foraging success during pregnancy might increase nutrient supply to the fetus during gestation, resulting in increased birth mass of offspring.

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