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**MATERNAL EFFECTS ON OFFSPRING TRAITS
FROM BIRTH THROUGH WEANING
IN THE HARBOUR SEAL, *PHOCA VITULINA***

by

Sara L. Ellis

**Submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy**

at

**Dalhousie University
Halifax, Nova Scotia
March 1998**

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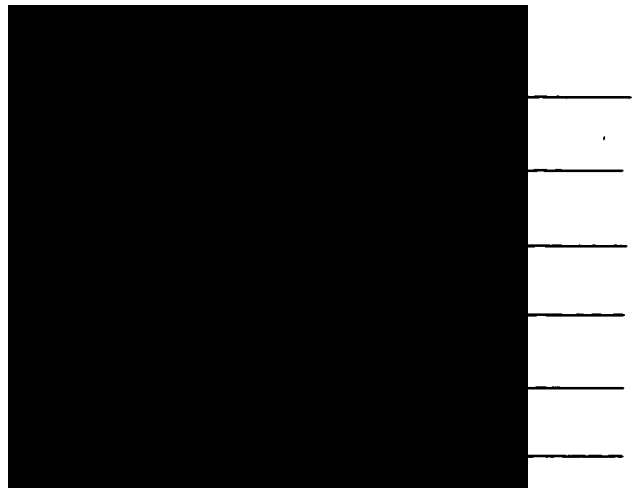
The undersigned hereby certify that they have read and recommend to the Faculty of Graduate Studies for acceptance a thesis entitled "Maternal Effects on Offspring Traits from Birth through Weaning in Harbour Seals, Phoca Vitulina"

by Sara Lynn Ellis

in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

Non-genetic influences of females on offspring phenotype are known as maternal effects. Maternal effects can influence offspring traits such as mass at birth and weaning, which can in turn affect offspring survival. Since survival ultimately affects fitness of parents and offspring, maternal effects on such traits are of particular interest.

I examined maternal effects on offspring traits from birth through weaning in harbour seals (*Phoca vitulina*) on Sable Island, 1987-1996. I explored relationships between maternal mass at parturition, age, and pupping date on birth mass, growth rate, and weaning mass of offspring.

Pupping date did not significantly affect pup traits. Maternal age and mass had significant effects, but their relative influence changed between birth and weaning. At birth, a female's age significantly affected birth mass, while maternal mass did not. Age effects on birth mass were significant only among young females. Reproductive experience of young females may have affected birth mass more than did age *per se*. During lactation, maternal mass at parturition had stronger effects on pup traits than did maternal age. Pups of large females had high growth rate and high weaning mass.

Harbour seal females make brief foraging trips during lactation, thus their pattern of maternal care is intermediate between those of otariids and fasting phocids. As predicted, effects of mass at parturition on pup growth rate and weaning mass were weaker than in fasting phocids, and stronger than in otariids. Small females appeared to begin foraging earlier in lactation than did large females, and postnatal investment of energy was lower for small females. Thus maternal body mass in species that forage during lactation may affect maternal behaviour and limit maternal investment generally.

Sexual selection theory predicts that in polygynous, sexually dimorphic species small, young females will bear fewer males than females, and that mothers will invest more energy in male offspring. In this study, sex ratio at birth did not vary with maternal age or mass. Birth mass was higher for males than females. Weaning mass was also higher for males, but this resulted from differences in birth mass, rather than differential maternal investment during lactation. At weaning, sex ratio did not differ from unity.

ABBREVIATIONS

ANCOVA	-analysis of covariance
ANOVA	-analysis of variance
d	-days
dpp	-day post-partum
d.f.	-degrees of freedom
kg	-kilogram
kg/d	-kilograms per day
<i>n</i>	-sample size
<i>p</i>	-probability
<i>r</i>	-Pearson's product-moment correlation coefficient
R^2	-coefficient of determination
SD	-standard deviation
SE	-standard error
TDRs	-time-depth recorders
yr	-year

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CHAPTER 1

GENERAL INTRODUCTION

Maternal effects

An organism's phenotype is shaped by complex interactions between its genotype and the environment. A female can, however, influence offspring phenotype, over and above her own genetic contribution (Mather and Jinks 1971; Arnold 1994). For example, in domestic animals, birth mass can be affected by nutritional intake of the female (Willis and Wilson 1974; Robinson 1977). Non-genetic influences of females on offspring are known as maternal effects, and can be defined succinctly as *direct effects of a female's phenotype on the phenotype of its offspring* (Bernardo 1996).

Maternal effects can occur only during the period of maternal care. In mammals, the period of maternal care usually consists of three phases: gestation, lactation, and post-weaning care (Clutton-Brock 1991). Maternal effects can be physiological (e.g., maternal mass affecting offspring mass) or behavioural (e.g., foraging ability or predator defense) (Bernardo 1996). Maternal age can affect offspring traits even after traits correlated with maternal age (such as body mass) are statistically adjusted (Bowen et al. 1994; Bernardo 1996). Age-related effects may result from behavioural and physiological changes in the female that influence her ability to provide for offspring (Forslund and Part 1995).

Maternal effects can be studied by examining relationships of life-history traits between females and offspring. Life-history traits are characteristics that directly

influence reproduction and survival (Stearns 1992). In mammals, life-history characters include mass at birth, mass at weaning, growth rate, and age- and mass-specific reproductive investments. These traits interact to affect the fitness of an organism, and are linked together by constraining relationships, or trade-offs.

The term “trade-off” implies that one trait cannot be increased without decreasing another. Many trade-offs have a physiological basis. This can be explained by the principle of allocation, and can occur at several stages in the life history (Gadgil and Bossert 1970; Boyce 1988). The basic premise of this principle is that animals have finite resources of energy or nutrients, that must be allocated among the competing sinks of reproduction, growth, and maintenance.

Offspring phenotype can affect offspring fitness, and thus parental fitness. For instance, an offspring's birth mass may be positively related to subsequent survival (Garnett 1979; Clutton-Brock et al. 1982), particularly in times of environmental stress (Hutchings 1991). In mammals, weaning mass (Guinness et al. 1978; Baker and Fowler 1992) and offspring growth rate can also be positively correlated with survival. For example, low rates of mass gain during lactation tend to be associated with reduced survival in red deer, *Cervus elaphus* (Clutton-Brock et al. 1982), and in grey seals, *Halichoerus grypus* (Coulson and Hickling 1964). Since survival ultimately affects fitness of parents and offspring, maternal effects on offspring mass and growth rates are of particular interest.

Some researchers have used maternal mass alone to explain maternal effects in mammals (Millar 1977; Arnbom et al. 1993), whereas others have used age alone (Reiter and Le Boeuf 1991). In some cases, the use of either age or mass exclusively has been

due to the difficulty of measuring age or mass in certain species. But this practice also reflects the fact that there have traditionally been two approaches to life history: age-based and state-based. Age-based life-history theory assumes that, within a population, all individuals of the same age are physiologically equivalent. It attempts to predict how organisms vary reproductive effort throughout their lifespan in response to changes in age-specific survival and age-specific fecundity (Roff 1992; Stearns 1992). The state-based approach recognizes that individuals generally differ in condition or quality, and these differences are important in determining reproductive success (Clutton-Brock et al. 1982; Lunn and Boyd 1993). An individual's condition may include the quality of its territory, reserves of protein or fat, and foraging skills. State-based life-history theory looks for the best level of reproductive effort as a function of the organism's state, or condition (McNamara and Houston 1996). Age may also be considered a component of state, however, if there are major differences between individuals of the same age, other state variables must be considered (McNamara and Houston 1996).

It is realistic, therefore, to expect that both maternal age and condition affect life-history traits of offspring. The relative influences of these factors are likely to change over a female's lifetime due to behavioural and physiological changes. Such a change may be particularly true of mammals like pinnipeds that continue to grow after sexual maturity. Because of expected trade-offs between growth and reproduction, small, young females may have proportionately less energy to invest in current offspring.

Maternal effects can also vary by offspring sex. In sexually dimorphic, polygynous species in which males are larger than females, reproductive success is more variable and more dependent on size in males than females (Le Boeuf and Reiter 1988).

Theory predicts that females should invest more energy in the sex that will have the greatest effect on their own fitness. To invest differently with respect to offspring sex, females could either vary sex ratio at birth in relation to maternal body condition (Trivers and Willard 1973), or invest energy differentially during the period of maternal care (Maynard-Smith 1980).

Pinniped life histories

Pinnipeds belong to the order Carnivora and consist of three families: Phocidae, true seals; Otariidae, fur seals and sea lions; and Odobenidae, the walrus. Several features of pinniped life history make these organisms convenient candidates for studies of maternal effects. Females bear single pups, thus maternal effects at each reproductive event are limited to one offspring only. Females usually return annually to breeding sites on land or sea ice (Bonner 1984), thus it is possible to follow known individuals over time, and to gather data on large numbers of females under similar environmental conditions. Maternal care ceases abruptly at weaning (Bonner 1984), thus maternal effects in pinnipeds are limited to gestation and lactation. In phocid seals, the end of this period of investment is easily defined and lactation is relatively brief, averaging only 23 days (Boness and Bowen 1996). Pinnipeds are large, long-lived, iteroparous mammals that continue to grow after sexual maturity (McLaren 1993), making it possible to study the relative influence of maternal effects over a wide range of maternal ages and sizes. Since pinnipeds exhibit polygyny and size dimorphism (Bartholomew 1970) theory predicts that maternal investment will vary with offspring sex.

The harbour seal, *Phoca vitulina concolor*, is a small phocid that breeds on isolated beaches and islands along the eastern coast of North America (Boulva and

McLaren 1989). Females usually give birth annually after reaching sexual maturity around 4 years of age (Bigg 1969), and continue to grow until around age 10 (Boulva and McLaren 1989). Female harbour seals forage during lactation (Bowen et al. 1992a). Thus, they exhibit a strategy of maternal care during lactation that is intermediate between most phocid species, which fast during lactation, and otariid species, which forage during lactation (Boness et al. 1994; Boness and Bowen 1996). Adult males are slightly larger than adult females, and show low levels of polygyny (Coltman et al. in press (a)).

Here I analyze a long-term data set on harbour seal females and pups from Sable Island, Nova Scotia. I examine the relative influence of maternal effects on offspring traits throughout the period of maternal investment, i.e., from birth through weaning. Over the 10 years for which I have data on Sable Island harbour seals, an unanticipated change in demography occurred. Pup production declined and maternal age distribution shifted to older females. To study the consequences of these demographic changes, I investigated interannual variation in life-history traits of females and offspring (Chapter 2).

After determining that data could be pooled across years (Chapter 2), I analyzed maternal effects at different stages of maternal care. Chapters 3 and 4 focus on the end of gestation (i.e., birth), and Chapter 5 encompasses the periods of lactation and weaning. In Chapter 3, I examine the relationships of maternal age, parturition mass, pupping date, and reproductive experience to birth mass and state of development of newborns. I continue these analyses in Chapter 5, by examining maternal effects on pup growth rate during lactation and weaning mass. I also make interspecific comparisons of maternal effects during lactation among pinnipeds and relate them to the harbour seal's intermediate

strategy of maternal care (Chapter 5). I use path analysis to model possible causal relationships among maternal traits and pup traits at birth (Chapter 3), and through lactation and weaning (Chapter 5). I also describe patterns of reproductive investment (pre-natal investment: Chapter 3; post-natal investment: Chapter 5) in harbour seals as examples of large, iteroparous, mammals that continue to grow after maturity.

I examine sex differences in birth mass (Chapter 3), as well as in pup growth rate and weaning mass (Chapter 5), with respect to differential investment theory. I test for deviations in sex ratio at birth (Chapter 4) and weaning (Chapter 5) in relation to maternal age class and maternal mass class. In Chapter 6, I summarize and synthesize the main results of my work.

CHAPTER 2

INTERANNUAL VARIATION IN TRAITS OF HARBOUR SEAL FEMALES AND PUPS ON SABLE ISLAND

Introduction

Interannual variation in the environment can influence life history traits. Environmental effects can be biological or physical. For example, an extreme El Niño event in 1982-83 led to changes in ocean temperature that, in turn, led to shortages of prey for several species of pinnipeds (Trillmich and Ono 1991). In California sea lions, *Zalophus californianus*, this caused reduced maternal investment and slower pup growth (Ono et al. 1987). In a less extreme example, a long-term decline in quality of foraging habitat of snow geese, *Anser caerulescens*, led to a decline in offspring growth rates, parental body size (Cooch et al. 1991), and female reproductive success (Rockwell et al. 1993). Such interannual variation could alter maternal effects on offspring traits, such as the effect of female mass at parturition on offspring birth or weaning mass.

The main objective of my research was to assess the relative influence of maternal age, parturition mass, and pupping date on offspring traits of harbour seals, such as birth mass, growth rate, and weaning mass. Data were collected on Sable Island from 1987 to 1996 (Chapters 3-5). Halfway through the study period, an unexpected demographic change began; the number of pups born dropped progressively from around 600 in 1991, to 86 by 1996 (Figure 2.1). The age structure of parturient females also changed, with fewer young females represented in later years (Figure 2.2).

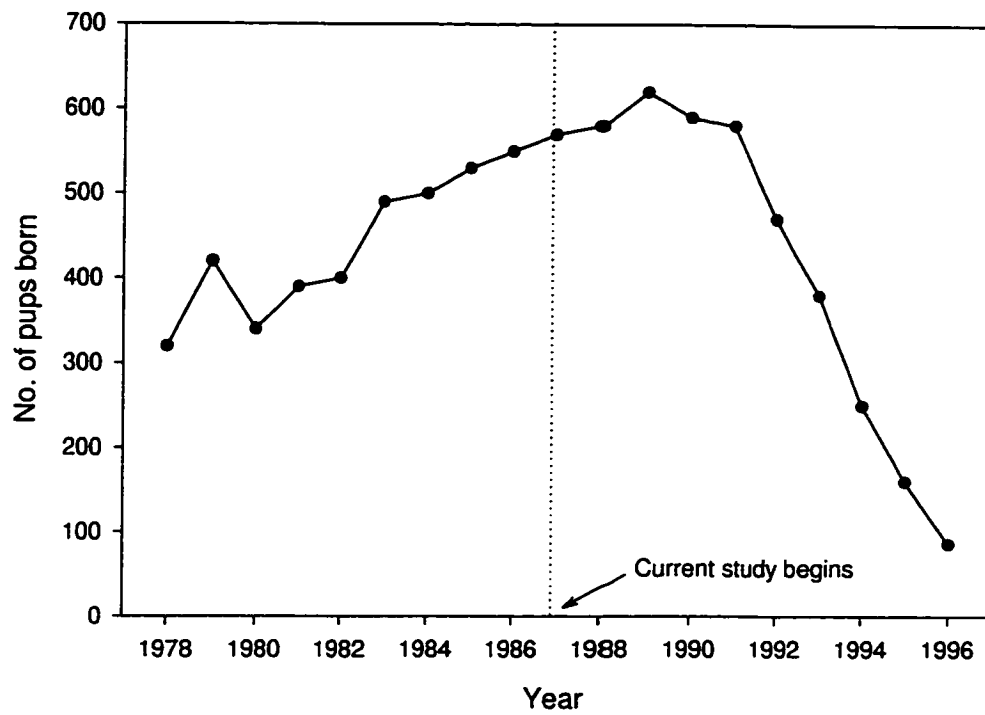


Figure 2.1. Annual production of harbour seal pups on Sable Island from 1978 to 1996. Numbers come from tagging of all pups in each cohort (Marine Fish Division, Dept. of Fisheries and Oceans, Canada).

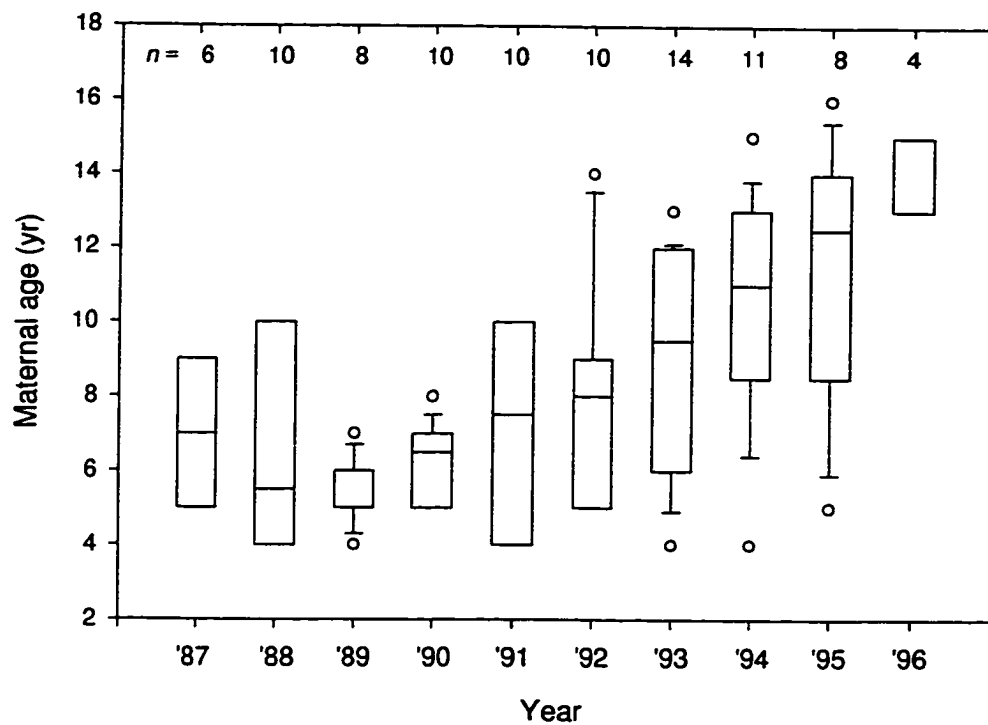


Figure 2.2. Changing age distribution of female harbour seals giving birth on Sable Island between 1987 and 1996 ($n = 91$). Data are cross-sectional, with each female being represented only once. (In this “box-and-whiskers plot” the 25th, 50th, and 75th percentiles are shown by the bottom of the box, the horizontal bar, and the top of the box, respectively. The largest and smallest values that are not outliers are shown as thin horizontal lines or “whiskers.” Open circles show outliers.)

These changes provided an unanticipated opportunity to study effects on life-history traits of females and pups. Here I examined interannual variation in traits of females (e.g., pupping date and parturition mass) and of pups (birth mass, rate of mass gain during lactation, and weaning mass). To address concerns that the demographic changes may have altered the effects of maternal age and parturition mass on these offspring traits, I compared traits between two 5-year periods, i.e., before and after pup production began to decline. I also compared relative birth and weaning mass as energetic measures of reproductive effort between these periods. Possible causes for the shifts in maternal age and pupping date were explored.

Methods

Data on females and newborns were collected in May and June each year from 1987 to 1996, and on weaned pups from 1988 to 1996. The study area was a 24-km stretch of beach on the north side of Sable Island, a vegetated sand bar off Nova Scotia, Canada (43°55'N, 60°00'W).

Each day throughout the pupping season, newborn pups were captured, sexed, and weighed as described in Chapter 3. When mothers of newborns were present, they were captured and weighed (Chapter 3). Body mass of pups and females taken within 24 hours of birth were defined as “birth mass” and “parturition mass,” respectively.

Maternal age was known in cases where the female was first tagged as a pup and the tag was retained to the time of recapture. Annual pup tagging first began in 1978 by the Department of Fisheries and Oceans (W. T. Stobo and W. D. Bowen, unpublished) and continued throughout this study. Thus, known maternal age potentially ranged from

4 (i.e., age at first parturition) to 9 years at the beginning of the study, and from 4 to 19 years at the end. Data on the oldest ages (14-, 15-, and 16-year-olds) were combined into a 14+ age category (Chapter 3).

Pupping dates were converted to day of year, taking into account the leap years 1988, 1992, and 1996. To test for effects of changing demography, cohort year was categorized into two 5-year periods: 1987 to 1991, when pup production was essentially stable; and 1992 to 1996, when pup production was in rapid decline (Figure 2.1).

Mass of pups at weaning was estimated by weighing a subset of pups at, or near weaning, as described in Chapter 5. Rate of mass gain of pups was estimated by dividing mass gained during lactation by the length of the lactation period.

To document population trends within and among seasons, weekly counts on the study area were made beginning in 1991. An experienced observer surveyed the north beach of the island in late afternoon, and counted adult males, adult females, juveniles, and pups. Since seals in the water were not included, the observer would not be able to count every seal present on the island during a particular week. It was, however, expected that trends within a season would be noticeable, such as the disappearance of females from the beach after weaning. At the end of each study season, and for each category, the highest count was called the “maximal count.” Annual trends of maximal counts were assumed to represent annual trends within the population as a whole.

Statistical analyses were performed using SPSS statistical software. Means are reported with standard errors (SE). The significance level for all tests was $\alpha = 0.05$.

Results

Count data

Beginning in 1991, there was a fairly steady decline in maximal counts of pups (Figure 2.3). Numbers of females remained stable until 1993, then also began to decline.

Numbers of juveniles and adult males declined between 1991 and 1996.

Pupping date and maternal age

Observed births occurred from May 11 to June 16 (Table 2.1). Among years, the briefest observed pupping period was 17 days in 1987 (May 11 to May 27), and the longest was 34 days in 1995 (May 13 to June 16). Observed dates of pupping were influenced by when observations began and ended in each year. In most years, observations began after a small number of pups had been born. However, sampling encompassed the main part of the pupping season in each year, thus mean pupping dates are reasonably accurate. In 1987, observations ended before the end of the pupping season, thus the brief observed period of pupping was inaccurate, and mean pupping date may have been negatively biased.

Mean date of pupping was essentially stable around May 22 (day 142) from 1987 through 1991 (Table 2.1; Figure 2.4). After 1991, pupping started to occur at progressively later dates; in 1992 and 1993, mean pupping date was May 26, and in 1996, mean pupping date was May 31. Pupping date and year were positively correlated over the period 1987 to 1996 ($r = 0.49$, $n = 676$, $p < 0.001$).

Pupping date was significantly correlated with maternal age ($r = 0.36$, $n = 91$, $p = 0.001$). This relationship, however, appeared to be due to increasingly later pupping dates (Figure 2.5), and increasingly older parturient females (Figure 2.2). In 1987-91, mean

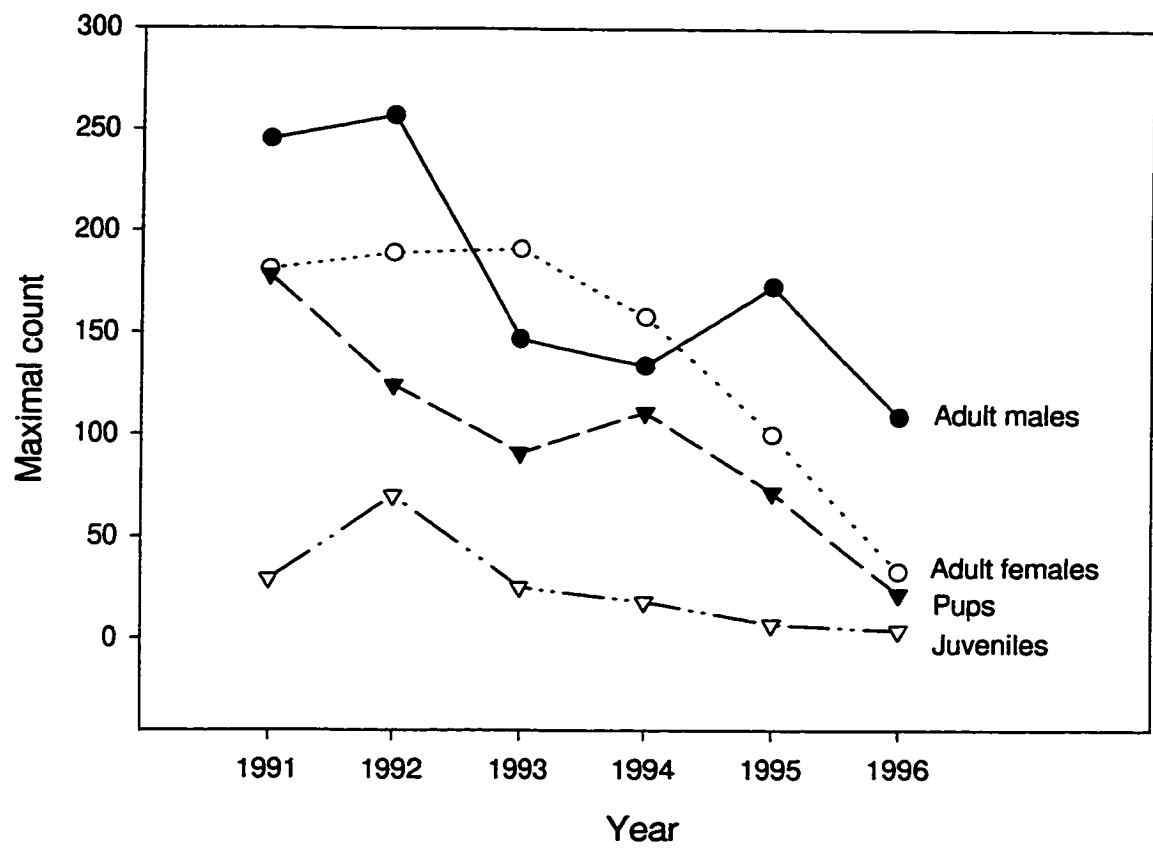


Figure 2.3. Maximal numbers of harbour seals counted on the study area, 1991-1996.

Table 2.1. Summary of annual pupping dates¹ of harbour seals observed on Sable Island ($n = 676$).

Year	Mean	SE	n	Earliest observed birth ²	Latest observed birth	Range (days)
1987	May 20 ³	0.4	57	May 11	May 27 ³	17 ³
1988	May 25	0.4	70	May 18	June 7	21
1989	May 22	0.7	60	May 11	June 6	27
1990	May 22	0.7	46	May 13	June 1	20
1991	May 20	0.5	53	May 11	May 28	18
1992	May 26	0.4	92	May 18	June 7	21
1993	May 26	0.5	96	May 14	June 6	24
1994	May 27	0.5	82	May 16	June 12	28
1995	May 31	0.7	84	May 13	June 16	35
1996	June 1	0.8	36	May 24	June 10	18
All	May 26	0.2	676	May 11	June 16	23

¹ Data are cross-sectional (i.e., each female is represented only once).

² In each year, a small number of births occurred before sampling began, thus the earliest observed date was slightly later than the actual earliest pupping date for the population.

³ In all years but 1987, observations continued beyond the last birth, thus the latest observed date is representative of the population. In 1987, however, sampling was terminated before the end of the pupping season, thus latest date, mean date, SE, and range are negatively biased.

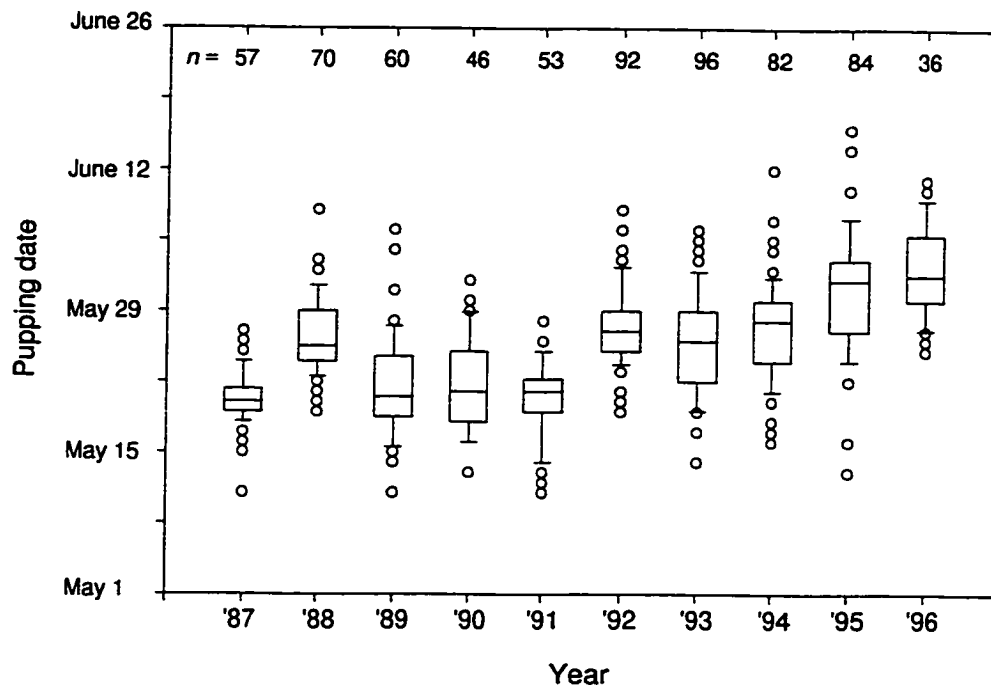


Figure 2.4. Distribution of pupping dates of harbour seals on Sable Island, 1987-1996 ($n = 676$). In 1987, observations ended early, so the latest observed pupping date was negatively biased. (Box-and-whiskers plot, as per Fig.2.2.)

Table 2.2. Comparison of life-history traits between periods of stable (1987-1991) and decreasing (1992-1996) population of harbour seals on Sable Island.

Trait	1987-1991 mean \pm S.E. (n)	1992-1996 mean \pm S.E. (n)	<i>p</i> t-test [d.f.]	<i>p</i> ANCOVA [d.f.]
Female				
Pupping date	May 22 \pm 0.3 (286)	May 28 \pm 0.3 (390)	<0.001 [674]	<0.001 ¹ [1, 88]
Age (yr)	6.4 \pm 0.30 (44)	10.0 \pm 0.52 (47)	<0.001 [89]	-
Parturition mass (kg)	85.3 \pm 0.70 (136)	84.8 \pm 0.84 (108)	0.64 [242]	0.25 ² [1, 72]
Lactation duration (d)	23.7 \pm 0.33 (87)	24.2 \pm 0.36 (88)	0.31 [173]	-
Weaning date	June 15 \pm 0.4 (87)	June 21 \pm 0.5 (88)	<0.001 [173]	<0.001 ³ [1, 97]
Pup				
Birth mass (kg)	10.8 \pm 0.1 (207)	11.0 \pm 0.9 (168)	0.14 [373]	0.74 ⁴ [1, 78]
Rate of mass gain (kg/d)	0.62 \pm 0.02 (48)	0.59 \pm 0.01 (68)	0.08 [114]	0.10 ³ [1, 97]
Weaning mass (kg)	24.6 \pm 0.38 (76)	25.1 \pm 0.37 (78)	0.37 [152]	0.60 ³ [1, 97]
Pup:female comparison				
Relative birth mass (%)	12.8 \pm 0.13 (136)	13.0 \pm 0.13 (108)	0.40 [242]	0.58 ¹ [1, 72]
Relative weaning mass (%)	29.8 \pm 0.48 (47)	29.7 \pm 0.43 (53)	0.92 [98]	-

¹ Controlling for maternal age

² Log parturition mass controlling for log maternal age

³ Controlling for parturition mass

⁴ Log birth mass controlling for log maternal age

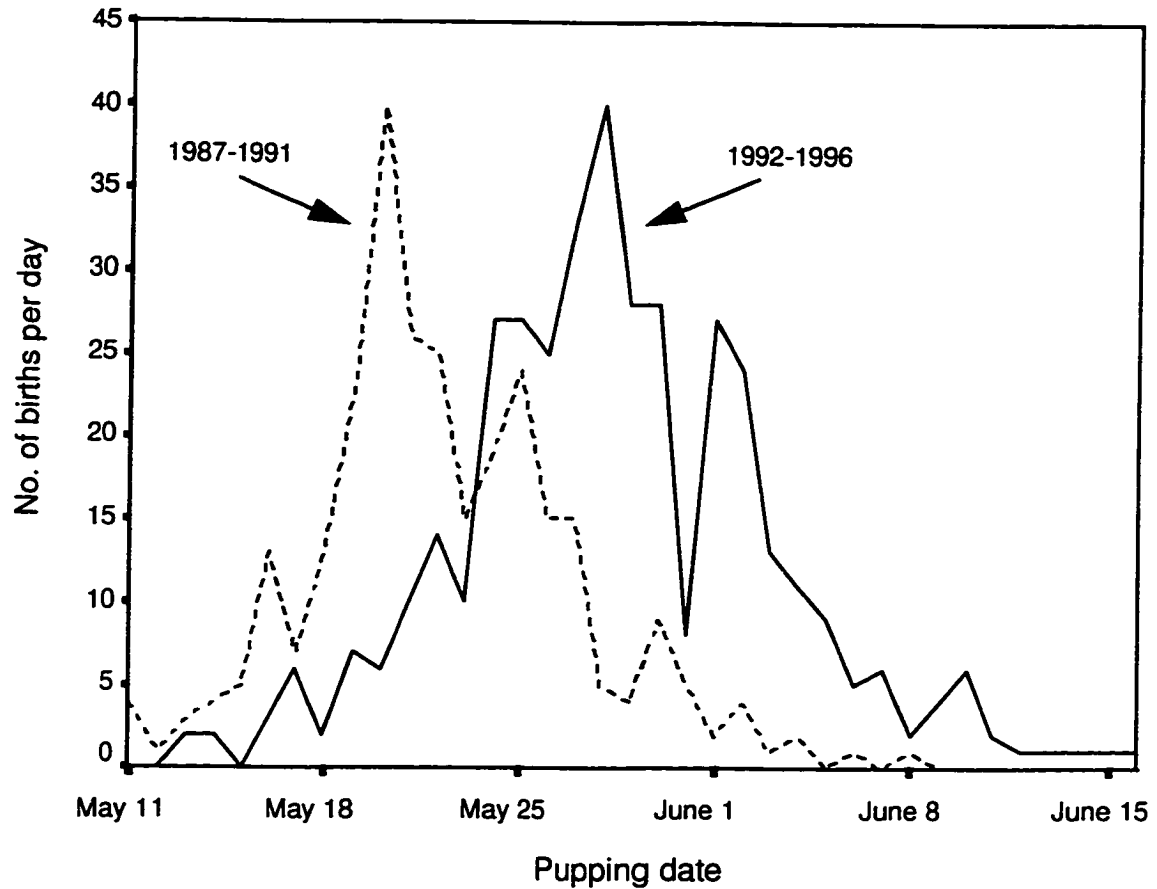


Figure 2.5. Comparison of pupping dates between periods of stable (1987-1991) and declining (1992-1996) production of harbour seal pups on Sable Island ($n = 676$).

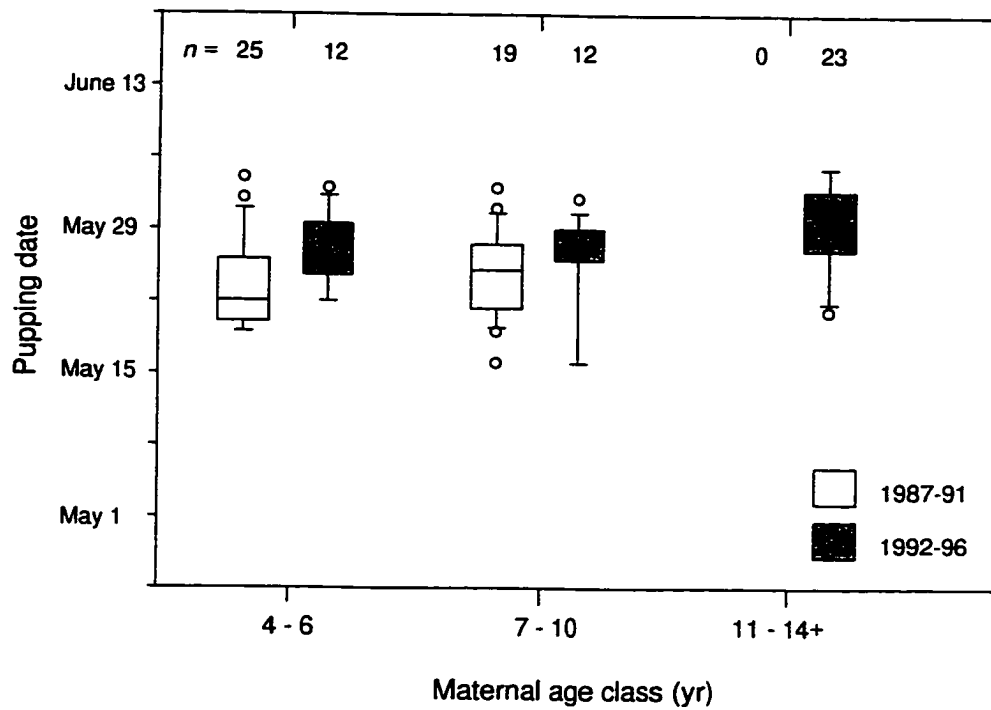


Figure 2.6. Relationship of timing of pupping to maternal age in periods of stable (1987-1991) and declining pup production (1992-1996). Note that no females of the 11-14+ age class were represented in the first period. (Box-and-whiskers plot as per Figure 2.4)

pupping date was May 22, and was May 28 in 1992-1996 (Table 2.2). Mean age of parturient females increased from 6.4 yr in the first period to 10.0 yr in the second.

Data were examined by maternal age class and period (Figure 2.6). Within each age class, mean pupping date was higher in the second period, whereas within periods there were no significant differences between mean pupping date of each age class (2-way ANOVA; period $p = 0.03$; age class $p = 0.11$). Thus, although mean pupping date was later in the second period, this was attributable to period rather than age class. The oldest age class was represented only in the second period, in which pupping dates were later (Figure 2.6). Thus the change in age structure gave the false impression that older females bore pups significantly later. I further explored the relationships among pupping date, maternal age, and period using longitudinal data. For 27 females of known-age that had two or more pups in each period, mean pupping date was 4 days earlier in first period compared with the second (mean dates May 24 and May 28, respectively). Again, the difference in mean pupping date was due to period rather than age (repeated-measures ANCOVA with mean age as a time-varying covariate: period $p = 0.01$; age $p = 0.18$). This corroborates the conclusion drawn from the cross-sectional data that period was more important than maternal age in determining pupping date.

Birth mass and parturition mass

Annual mean birth mass of pups ranged from a low of 10.1 in 1993 to a high of 11.4 in 1995 (Table 2.3; Figure 2.7a). Since log age was correlated with log birth mass ($r = 0.74$, $n = 81$, $p < 0.001$), as well as with log parturition mass ($r = 0.73$, $n = 75$, $p < 0.001$), and since maternal age increased over the study period, I controlled statistically for log age when looking for differences in annual means of each variable.

There was no significant interannual variation in mean birth mass. Mean parturition mass ranged from 78.9 kg in 1994, to 89.7 kg in 1995, but did not differ significantly by year (Table 2.3; Figure 2.7b). Annual mean birth mass was not significantly correlated with annual mean parturition mass (Spearman $r = 0.07$, $n = 10$, $p = 0.85$). Annual residuals of birth mass and parturition mass, expressed as percentage difference from the population means (Figure 2.8), were not correlated either (Spearman $r = 0.17$, $n = 10$, $p = 0.68$).

To test for effects of changing demography, mean birth and parturition masses were compared by period (Table 2.2). Mean birth mass was 10.8 kg in the first and 11.0 kg in the second. Mean parturition mass for each period was 85.3 kg and 84.8. Neither variable differed significantly between periods.

Traits associated with lactation and weaning

Mean rate of pup mass gain ranged from 0.56 kg/d in 1989 to 0.73 kg/d in 1992 (Figure 2.9a; Table 2.4). There was, however, no significant interannual variation in mean rate of pup mass gain. Mean weaning mass ranged from 23.7 kg in 1991 to 26.2 kg in 1992, and also did not differ significantly by year (Figure 2.9b; Table 2.4).

To test for effects of changing demography, mean traits of females and pups were compared between periods. Mean weaning mass and rate of pup mass gain did not differ, before or after controlling for parturition mass (Table 2.2; all $p > 0.05$). Mean lactation duration also did not vary by period. Mean wean date was significantly higher in the second period, as would be expected from the higher mean pupping date but similar duration of lactation (Table 2.2).

Table 2.3. Annual mean birth mass and parturition mass of harbour seals on Sable Island, 1987 to 1996 (mean \pm SE; sample size in parentheses).

Year	Birth mass (kg)	Parturition mass (kg)
1987	10.8 \pm 0.21 (39)	85.7 \pm 2.06 (10)
1988	10.8 \pm 0.18 (57)	87.4 \pm 1.52 (35)
1989	11.0 \pm 0.29 (30)	82.1 \pm 1.04 (24)
1990	10.6 \pm 0.23 (32)	88.1 \pm 1.65 (24)
1991	10.9 \pm 0.16 (49)	83.7 \pm 1.20 (48)
1992	11.1 \pm 0.15 (41)	84.7 \pm 1.27 (40)
1993	10.1 \pm 0.20 (32)	80.1 \pm 2.19 (19)
1994	11.0 \pm 0.30 (21)	78.9 \pm 2.16 (10)
1995	11.4 \pm 0.14 (51)	89.7 \pm 1.88 (19)
1996	11.2 \pm 0.14 (23)	87.9 \pm 1.56 (20)
ANCOVA <i>p</i> [d.f.]	0.246* [9, 70]	0.102* [9, 64]

* ANCOVA on log transformed data, controlling for log age

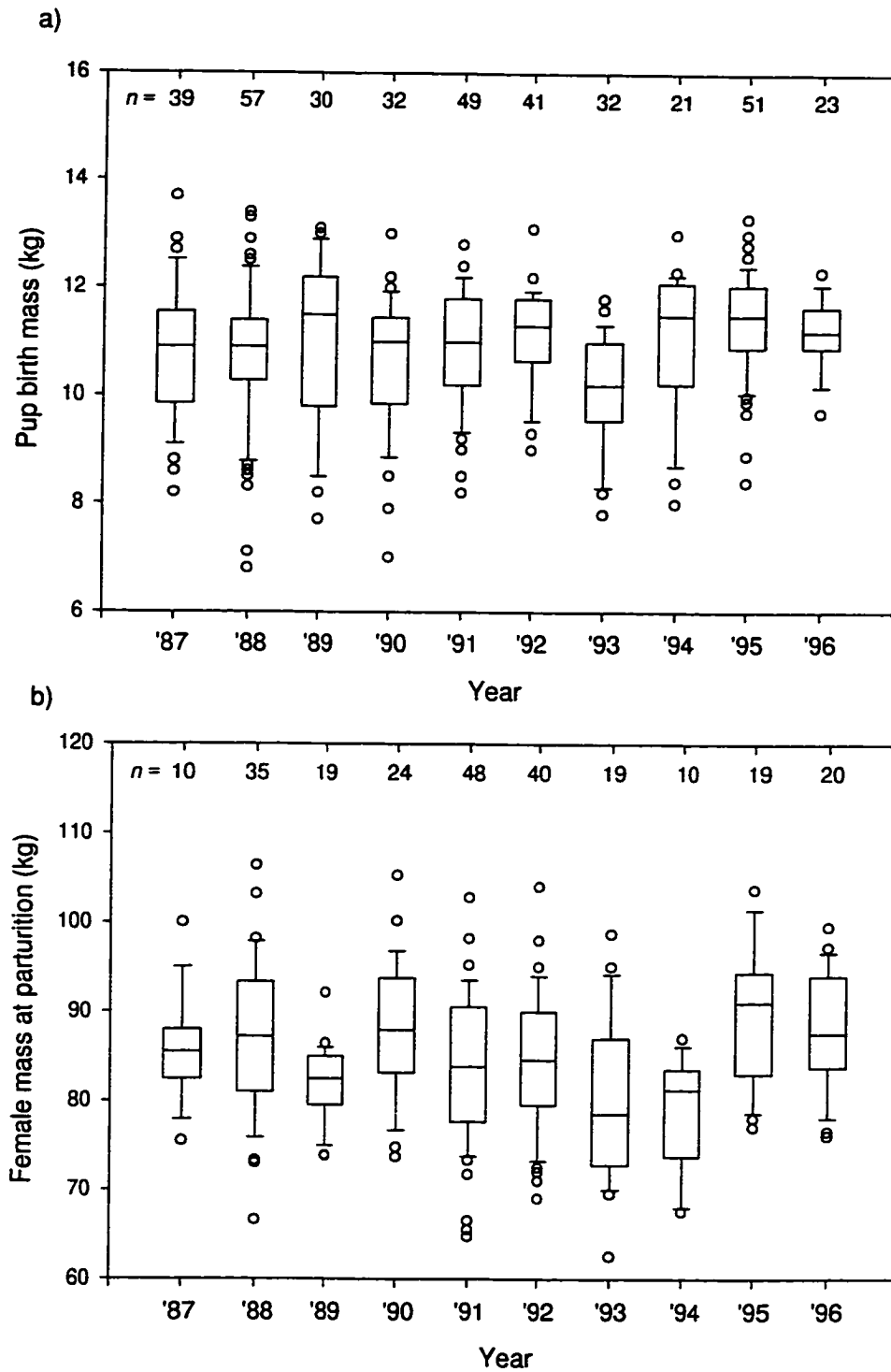


Figure 2.7. Interannual variation in a) birth mass ($n = 375$), and b) maternal mass at parturition ($n = 244$) of harbour seals on Sable Island, 1987 to 1996. (Box-and-whiskers plot, as per Figure 2.2)

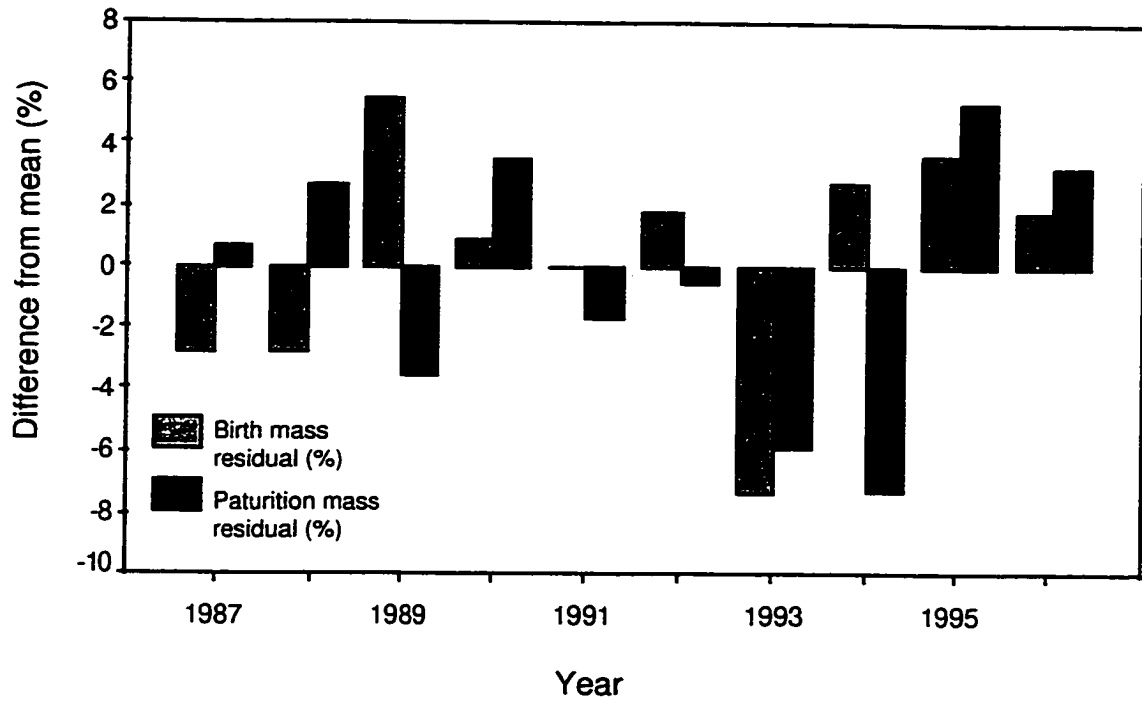


Figure 2.8. Annual differences from overall mean birth mass and mean parturition mass, expressed as percentages ($n = 244$ mother/pup pairs). Dashed vertical line represents point when the population began to decline (see text).

Table 2.4. Annual rate of mass gain and weaning mass of harbour seal pups on Sable Island, 1988 to 1996 (mean \pm SE; sample size in parentheses).

Year	Rate of mass gain (kg/d)	Weaning mass (kg)
1988	0.66 \pm 0.018 (16)	26.0 \pm 0.72 (23)
1989	0.56 \pm 0.038 (12)	24.1 \pm 0.50 (27)
1990	0.63 \pm 0.020 (9)	24.0 \pm 0.96 (15)
1991	0.63 \pm 0.051 (11)	23.7 \pm 0.99 (11)
1992	0.73 \pm 0.058 (3)	26.2 \pm 0.66 (6)
1993	0.57 \pm 0.017 (34)	24.7 \pm 0.48 (36)
1994	0.58 \pm 0.025 (22)	25.3 \pm 0.71 (26)
1995	0.62 \pm 0.061 (7)	25.6 \pm 1.81 (7)
1996	0.58 \pm 0.059 (2)	24.7 \pm 1.94 (3)
ANOVA <i>p</i> [d.f.]	0.071 [8, 107]	0.389 [8, 145]

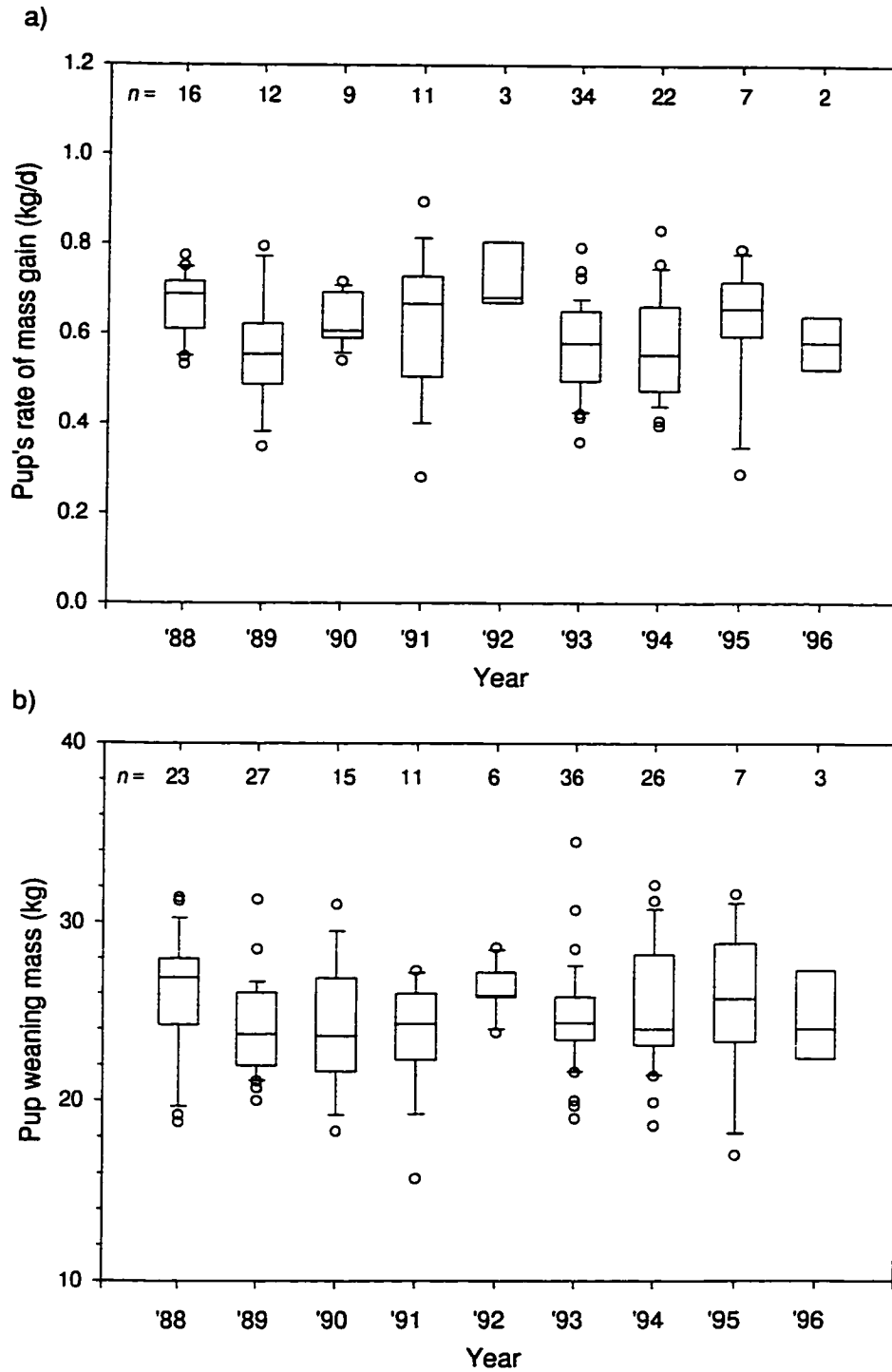


Figure 2.9. Annual distribution of a) rate of mass gain ($n = 116$), and b) weaning mass ($n = 154$) of harbour seal pups on Sable Island, 1988-1996. (Box-and-whiskers plot, as per Figure 2.2)

Reproductive effort

Similarly, energetic measures of maternal reproductive effort were compared by year and period. The ratio of birth mass to parturition mass is a measure of pre-natal reproductive effort known as relative birth mass (Chapter 3). Relative birth mass did not vary by year (ANCOVA controlling for maternal age, $F_{[9, 64]} = 1.3, p = 0.26$), or by period (Table 2.2). The ratio of weaning mass to parturition mass is a measure of overall reproductive effort known as relative weaning mass (Chapter 5). This measure of maternal investment also did not vary across years (ANOVA $F_{[8, 91]} = 1.7, p = 0.11$) or between periods (Table 2.2).

Discussion

Changing demography

There was a fairly steady decline in the number of harbour seal pups born on Sable Island after 1991. Concurrently, maternal age distribution of known-aged females shifted to older ages. The increase in age of parturient females resulted from few young females giving birth in later years. This trend was not due to a bias in data collection because almost every breeding female was captured in the last few years of the study. The trend reflects a lack of recruitment of young females to the breeding population. It is possible that young females had higher mortality, or emigrated elsewhere. Alternatively young females may have been less able to carry a fetus to term in later years. Severe population crashes are common in populations of large mammals (Young 1993) and dramatic declines in pinniped populations have been observed that cannot be accounted for by direct or indirect exploitation (Loughlin et al. 1992). Natural die-offs of carnivores tend

to be due to diseases (Harwood and Hall 1990; Young 1993), yet there are no signs of disease in this population. Unfortunately, there are no ongoing studies elsewhere in eastern Canada to address the possibility of emigration.

Increased mortality or emigration could be caused by changes in prey distribution or competition with other species (Pianka 1976). A candidate for competition is the grey seal (*Halichoerus grypus*), whose population on Sable Island has been increasing by about 13% per year for several decades (Mohn and Bowen 1996). Analyses of stomach and scat contents have shown dietary overlap in the two species, both inshore (Bowen and Harrison 1996) and on Sable Island (Bowen and Harrison 1994; W. D. Bowen unpubl.). Studies on domestic mammals have shown that nutrition in the latter stages of pregnancy has the greatest effect on fetal growth and mass of newborns (Sadleir 1969; Robinson 1977). However, no appreciable changes in birth mass of the pups or the condition of parturient females were detected over this study, so increased competition or shifts in prey distribution may be occurring away from Sable, before the pupping season. An alternative explanation is predation by sharks on young females. Sharks are predators of seals in eastern Canada (Boulva and McLaren 1979; Brodie and Beck 1983) and shark predation on harbour seal pups near Sable Island increased over the study period (W. D. Bowen unpubl.).

The other appreciable change over the study period was the shift in pupping dates, as indicated by cross-sectional and longitudinal data. The observed trend towards later pupping dates did not appear to be caused by increased maternal age. In many mammals, photoperiod controls the timing of birth (Follett 1982). In pinnipeds, including harbour seals (Temte 1994), photoperiod is thought to initiate embryonic implantation, and all

females in a population should implant at about the same time to ensure synchronized reproduction (Boyd 1991). Seasonal patterns of photoperiod would not have changed over the study period, thus other environmental features, such as changes in ocean temperature or nutritional stress, are more likely to be responsible for the changes in pupping date.

Changes in ocean temperature, which are often correlated with changes in fish and invertebrate distribution, have been documented on the Scotian Shelf over the study period (Drinkwater 1996). Pupping date can be influenced by food availability through changes in gestation length. In Antarctic fur seals (*Arctocephalus gazella*), pupping dates were delayed due to longer pregnancies in years of low food availability (Boyd 1996). If this were the case in harbour seals, the steadily increasing pupping dates observed after 1991 may indicate decreasing food availability for pregnant females. This too could have been caused by changes in prey distribution and/or competition with the expanding population of grey seals. It is noteworthy that in Antarctic fur seals, the number of young born was reduced in years where births were late on average (Lunn and Boyd 1993). This suggests that nutritional stress changes the timing of birth and reduces the probability that females will carry a fetus to term (Boyd 1996). This pattern is similar to that seen in harbour seals on Sable Island after 1991.

Interannual variation

Despite the observed changes in pupping date and maternal age structure, there was no significant variation in parturition mass or birth mass by year or period. This stability may be partially explained by the fact that Sable Island is a pupping site, and thus comparable to a maternity ward (W.D. Bowen, pers. comm.). The only females sampled

were successful females, whose condition may have surpassed a critical threshold that allowed them to carry a viable fetus to parturition (Arnbom et al. 1994). Females that did not bear pups simply would not appear in the data set. There was also no significant variation in rate of mass gain during lactation or weaning mass. By definition, these data also represented only females that had weaned their pups successfully.

The lack of interannual variability was noted in the earlier work of Muelbert and Bowen (1993), who found that weaning mass and lactation duration of harbour seals on Sable Island did not differ between 1988 and 1989. The longer time frame of the present study illustrates the consistency of pup mass at birth and weaning in harbour seals. In many animals, survival increases with body size (Guinness et al. 1978; Clutton-Brock 1988) and weaning mass of mammals is likely to be under strong selective pressure (Lee et al. 1991).

The lack of interannual variation in pup traits shows that pups were not significantly affected by any interannual environmental fluctuations. This could have resulted from a lack of fluctuation, or from the ability of females to buffer their offspring from the types of variation that occurred. Buffering by females is a more likely explanation, given the arguments above for nutritional stress potentially leading to delayed pupping dates. Furthermore, changes in ocean temperature have been documented on the Scotian Shelf over the study period, with deep waters warming, and surface waters cooling after 1991 (Drinkwater 1996).

The lack of variation in pup traits between the early and late periods shows that the shifts in maternal age structure and pupping date did not affect pup traits. Also, since pupping date has no significant effect on birth mass of harbour seals (Chapter 3), or

weaning mass (Chapter 5), the shift in pupping dates should not have altered relationships between maternal traits and offspring traits. The similarity of energetic measures of prenatal and postnatal reproductive effort among years, and between periods is evidence of a consistent relationship between parturition mass of females and mass of pups at birth and weaning. These points allowed me to pool data from all years to analyze maternal effects (Chapters 3-5).

Summary

After 1991 there was a steady decline in the number of harbour seal pups born on Sable Island. Overall, numbers of adult males and females and juveniles declined over the same period. The decline in numbers of adult females was due to reduced recruitment of young females to the breeding population. The cause for the decline in recruitment of young females is unknown, but may include differential emigration and/or mortality, or an inability to carry a fetus to term in later years.

Pupping dates became later after 1991, possibly because of reduced food availability due to a shift in prey distribution or competition with grey seals.

From 1987 to 1996 mean annual birth mass, rate of pup mass gain, and weaning mass did not vary significantly. The lack of interannual variation suggests strong selective pressure on these life-history traits of pups or a capacity of female harbour seals to buffer the young from the observed environmental variation.

CHAPTER 3

MATERNAL EFFECTS ON TRAITS OF NEWBORN

HARBOUR SEALS

Introduction

An organism's phenotype results from complex interactions between its genotype and the environment (Bernardo 1996). A female can, however, directly influence offspring phenotype independently of genotype (Arnold 1994). For example, in domestic animals, birth mass can be affected by the female's nutritional intake (Willis and Wilson 1974; Robinson 1977). Such influences are known as maternal effects.

Maternal age can also affect offspring traits, even after traits correlated with maternal age, such as body mass, are statistically adjusted (Bernardo 1996). Age likely reflects behavioural and physiological changes in the female, which in turn can affect offspring (Forslund and Pärt 1995). Age effects are stronger among young females than old females (Forslund and Larsson 1992). For example, in birds it is well established that reproductive performance improves with age among young females, then levels out in middle age, and, in some cases, declines in old age (Curio 1983; Rockwell et al. 1993; Forslund and Pärt 1995). This is similar to the pattern seen in many large mammals, such as northern elephant seals, *Mirounga angustirostris*, and red deer, *Cervus elaphus* (Clutton-Brock et al. 1988; Le Boeuf and Reiter 1988; Sydeman et al. 1991). Most evidence for maternal age effects comes from long-term studies on birds and mammals (Clutton-Brock et al. 1988; Newton 1989; Rockwell et al. 1993). With the exception of

northern elephant seals (Le Boeuf and Reiter 1988) and Antarctic fur seals, *Arctocephalus gazella* (Boyd 1996), there are few long-term life-history studies on pinnipeds. Here I present results of a 10-year study on female harbour seals, *Phoca vitulina*.

Birth mass is a phenotypic characteristic of offspring that is positively correlated with probability of survival in some mammals (Clutton-Brock et al. 1982). Birth mass varies with maternal mass at parturition within (Costa et al. 1988; Iverson et al. 1993) and across species (Blueweiss et al. 1978; Oftedal 1985). However, other factors, such as age, parity, pupping date, and offspring sex can also affect birth mass in mammals (Guinness et al. 1978; Reiter et al. 1981). The effects of such variables, particularly maternal age and mass, are usually studied in isolation (Boyd and McCann 1989; Lee et al. 1991; Arnborn et al. 1993).

In general, both maternal age and condition are likely to affect offspring life-history traits. In addition, their relative effects may change throughout an animal's lifetime. Thus, I examined the effects of maternal age and parturition mass on traits of newborns, over a range of maternal ages, and within three age-classes of females. I predicted that maternal age would be correlated with birth mass among young females because increasing age, and thus experience, could lead to behavioural or physiological changes in the female that would increase birth mass. After several reproductive events, experience would not be expected to add further benefits (Forslund and Pärt 1995). Condition, measured here as parturition mass, was predicted to affect birth mass in older females.

Maternal mass at parturition appears to be a good measure of general condition in harbour seals, as it reflects the amount of absolute energy stores available to the female at

pupping. Percentage body fat is similar among post-parturient harbour seals (approximately 30% of body mass) and is independent of body mass (Bowen et al. in prep.). Parturition mass is also a convenient measure of condition since, by definition, it is always taken at the same point in each female's reproductive cycle, and is therefore useful for comparisons among and within females.

For animals that continue to grow after maturity, such as pinnipeds, life-history theory predicts trade-offs between growth and reproduction (Gadgil and Bossert 1970; Roff 1992). Female harbour seals 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). Since young females continue to grow after sexual maturity, they will need to devote some energy toward growth. Thus, young females may have a smaller proportion of energy to allocate towards reproduction than have older females, and offspring may be correspondingly smaller. In long-lived species with a high probability of survival after sexual maturity, there are also allometric grounds for expecting young females of smaller body size to invest less in offspring and more in growth (Reiss 1989). I predicted that reproductive investment would be lowest among younger females, since they have greater growth requirements than older females. After age 10, reproductive investment should level off. The ratio of "mass of young / mass of female" has been used as an index of maternal reproductive investment in mammals (Robbins and Robbins 1979; Kovacs and Lavigne 1986). One problem with using this approximation for mammals is that it does not consider lactation (Roff 1992), which is energetically expensive (Oftedal 1985). To avoid this problem, one can separate reproductive investment into pre- and post-natal. I consider the ratio "mass of young / mass of female" as a measure of prenatal reproductive

investment.

Pinnipeds typically bear single, precocial offspring (Bonner 1984). Newborn harbour seals are more precocious than most other phocids, being larger relative to the size of the female, more active, and usually born without a fetal coat. They enter the water within hours of birth (Lawson and Renouf 1985), whereas most other phocids do not begin to swim until after weaning. Their advanced development is also reflected in the shedding of the fetal coat, or lanugo, in utero (Ofstedal et al. 1991); most phocid species maintain their lanugo for a period after birth (Ling and Button 1975). Large relative size (hence low surface-to-volume ratio) and shedding of fetal lanugo may be adaptations for early entry into cold water (Ofstedal et al. 1991). On Sable Island, most newborn harbour seals with extensive lanugo are born early in the season and are small in body size (Boulva 1975; Bowen et al. 1994).

In this study I examined relationships of maternal age, mass, experience, and pupping date to traits of newborns, including birth mass and state of development (reflected in lanugo pelage at birth) using cross-sectional and longitudinal data. In addition, I investigated patterns of prenatal reproductive investment in female harbour seals as examples of large, iteroparous, mammals that continue to grow after maturity.

Methods

Data collection

Data were collected in May and June from 1987 to 1996 on Sable Island, a vegetated sand bar off 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 which were captured by hand or with hoop nets. A pup was considered to be newborn if it was still wet with birth fluids; if fresh blood was on the pup's coat or birth site; or if it had difficulty holding its head up and moved with an awkward "gait" (Bowen et al. 1994). Pup sex was recorded, and an individually numbered Rototag was inserted in the webbing of the hind flipper. The percentage of lanugo covering the entire body was estimated visually .

When mothers of newborn pups were present, they were captured with a hand-held net fastened between two aluminum poles, and tagged (Bowen et al. 1992a). To facilitate recognition of individuals from a distance, mother-pup pairs were marked on their backs with identical symbols using a fast-drying fluorescent paint (V-285, Lenmar Inc., Baltimore MD). Females and pups were weighed using a spring-balance scale suspended from a mobile all-terrain vehicle. Pups were weighed to the nearest 0.1 kg, on a 50-kg scale, and females to the nearest 0.5 kg on a 200-kg scale.

Maternal age was known in cases where the female was first tagged as a pup and the tag was retained to the time of recapture. Pup tagging first began in 1978 by the Department of Fisheries and Oceans (W. T. Stobo and W. D. Bowen unpubl.) and continued throughout this study. Known maternal age potentially ranged from 4 to 9 years at the beginning of this study, and from 4 to 19 years at the end; no females gave

birth before they were 4 years of age.

Statistical techniques

Two types of data were available for analyses: cross-sectional, in which each female was represented only once; and longitudinal, in which individual females were studied over time. To create cross-sectional data sets, data for each female were chosen randomly from only one pupping season. Pups whose mothers were not known were considered to have distinct mothers, and were included in cross-sectional data. Cross-sectional data were analyzed rather than the larger, complete data sets in order to meet the assumptions of independence required for regression analysis and analysis of variance, and thus avoid problems caused by serial correlation (Laird and Ware 1982).

Longitudinal data were analyzed using univariate and multivariate techniques. One advantage of multivariate data is that there is no need to make assumptions about the correlation structure between repeated measures on the same females. Repeated measures ANCOVA on multivariate data accounted for serial correlations and some forms of non-independence of data (Laird and Ware 1982).

Pupping dates were converted to day of year, taking into account the leap years 1988, 1992, and 1996. Only masses recorded within 24 hours of birth were included. Mass of pups was defined as “birth mass” and mass of females was defined as “parturition mass.” Body mass measured on the day after birth was extrapolated by subtracting a daily mass gain of 0.5 kg for pups ($n = 71$) and adding a daily mass loss of 1.7 kg for females ($n = 52$) (Bowen et al. 1994). Data from all years were pooled (Chapter 2). One extreme birth mass/maternal age outlier was removed from the data set. (This data point was a 12-year old female that bore a newborn that weighed only 7.3 kg.

This birth mass was atypical of the pups of 12-year olds (mean: 10.7 ± 1.1 kg, $n = 17$), and was removed from the data set since it was smaller than the mean birth mass minus 3 standard deviations for all 12-year-old females. The reason for this atypical birth mass is unknown.)

At the oldest maternal ages, data were not available for both pup sexes, i.e., within 15-year-olds ($n = 6$) there were no data on male pups, and among 16-year-olds ($n = 1$) there were no data on female pups. For this reason, data on 14-, 15-, and 16-year-olds were combined into a 14+ age category.

To meet the assumption of linearity required for regression analyses, ANOVA, and ANCOVA, data were transformed as necessary. In regression analyses on lanugo coverage, the raw amount of percentage lanugo was used. For categorical analyses, such as ANCOVA, pups were categorized as having no lanugo (0-5%), moderate (6-49%), or extensive (50-100%) (Bowen et al. 1994). Similarly, age and log age were treated as a continuous variables in regressions and as covariates in ANCOVAs. For categorical analyses of age, females were grouped into three age classes: 4 to 6; 7 to 10; and 11 to 14+ yr. The first class included females with little or no prior maternal experience (they would have produced only from 0 to 2 pups previously). The second class included moderately experienced females (3 to 5 pups), while the third class included experienced, females (> 5 pups). Only females in the first and second groups were still growing, since little growth occurs in females after age 10 (Boulva and McLaren 1979; McLaren 1993).

Path analyses were conducted to explore possible causal relationships between maternal effects and traits of newborn pups, and to determine the relative strengths of relationships. For these analyses, a subset of data ($n = 74$) was used, in which each case

was complete for all 5 variables examined (maternal age, parturition mass, pupping date, birth mass, and percentage lanugo). This assured an equal sample size along each path, making comparisons between paths meaningful. Path models were constructed *a priori*, based on hypothesized causal order. Paths were considered uni-directional to allow unique estimation of parameters (Klem 1995). Standardized partial-regression coefficients were used as path coefficients, and were obtained from multiple regressions on each endogenous variable (Wilkinson et al. 1996). If a path coefficient was not significantly different from zero, the model was trimmed by removing the path, and the multiple regression was run again to re-estimate the parameters (Klem 1995). 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 is shown in path diagrams as a percentage at the end of a thick arrow (Klem 1995).

Statistical analyses were performed using SPSS statistical software. Means are reported with standard errors (SE). Correlation coefficients are Pearson's r , unless stated otherwise. The significance level for all tests was $\alpha = 0.05$. All statistics, figures, and tables refer to cross-sectional data sets unless stated otherwise.

Results

Mean pupping date, birth mass, maternal age, and parturition mass

Pupping dates were known for 1,136 pups, of which 676 were known or assumed to be from different females. Mean pupping date was May 26 (Table 3.1). Birth mass was measured for 617 pups, of which 375 were from different females. Birth mass ranged between 6.5 and 14.2 kg, averaging 10.9 kg (Table 3.1). There was no significant difference between the birth mass of pups weighed prior to suckling (i.e., within a few hours of birth; $n = 26$) and those weighed within 24 hours of birth ($n = 349$) (ANOVA, $F_{[1, 374]} = 0.66, p = 0.42$).

For pups with known birth mass, maternal age ranged from 4 to 16 years, with a mean of 8.4 ± 0.36 years ($n = 81$). Parturition mass was measured 424 times in 244 individual females. Mean parturition mass was 85.1 ± 0.54 kg ($n = 244$), and ranged from 62.5 to 106.4 kg. Parturition mass increased with maternal age non-linearly (Figure 3.1). Parturition mass was measured in 75 females of known-age. Log maternal age was positively correlated with log parturition mass ($r = 0.73, n = 75, p < 0.001$), and accounted for 54% of the variation in log parturition mass. Mean parturition mass increased progressively within the 3 maternal age classes (75.6, 83.8, and 90.1 kg, for young, intermediate-aged, and older females, respectively) and was significantly different by maternal age class (Table 3.1).

Table 3.1. Effect of maternal age class on life-history traits at birth in harbour seals (sample size in parentheses; degrees of freedom in square brackets).

Variable	All females	Maternal age class			<i>p</i> ANOVA or ANCOVA
		Young (4 - 6 yr)	Intermediate (7 -10 yr)	Older (11-14+ yr)	
Pupping date	May 26 ± 0.2 (676)	May 25 ± 0.7 (37)	May 25 ± 0.8 (31)	May 29 ± 0.9 (23)	0.107 ¹ [2, 87]
Birth mass (kg)	10.9 ± 0.06 (375)	9.3 ± 0.25 (30)	11.0 ± 0.16 (27)	11.7 ± 0.15 (24)	<0.001 ² [2, 71]
Maternal mass at parturition (kg)	85.1 ± 0.54 (244)	75.6 ± 1.19 (24)	83.8 ± 1.10 (27)	90.1 ± 1.37 (24)	<0.001 [2, 72]
Relative birth mass (%) (pup:female mass)	12.9 ± 0.09 (244)	12.1 ± 0.30 (24)	13.2 ± 0.27 (27)	13.1 ± 0.26 (24)	0.010 [2, 72]

¹ Two-way ANOVA with period (Chapter 2)

² ANCOVA of log birth mass on age class, controlling for log parturition mass

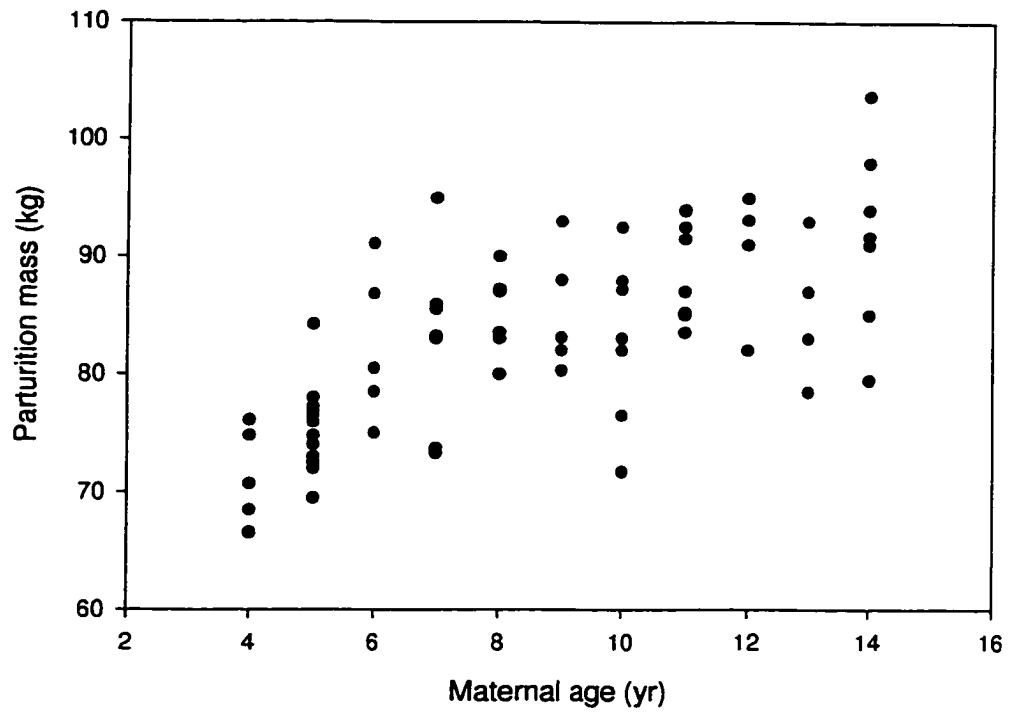


Figure 3.1. Parturition mass and age of parturient female harbour seals on Sable Island ($n = 75$).

Pupping date in relation to other traits

Pupping date was not significantly related to birth mass of males ($r = 0.11$, $n = 175$, $p = 0.14$), females ($r = 0.10$, $n = 200$, $p = 0.15$), or both sexes combined ($r = 0.09$, $n = 375$, $p = 0.08$). Pupping date was also not significantly related to parturition mass for mothers of male pups ($r = 0.13$, $n = 118$, $p = 0.16$), female pups ($r = -0.04$, $n = 126$, $p = 0.69$), or both sexes combined ($r = 0.04$, $n = 244$, $p = 0.57$).

Pupping date was not related to sex of pup. Pupping date and sex were recorded for 1001 pups, from 545 different females. Overall, mean birth date of male pups was 1 day earlier than that of females (May 25 \pm 0.4 d, $n = 251$, versus May 26 \pm 0.4 d, $n = 294$), however, this difference was not significant after controlling for year effects (Chapter 2) on birth date (2-way ANOVA, year $p < 0.001$, pup sex $p = 0.08$, interactions $p = 0.65$). In addition, pupping date did not differ significantly within years by sex of pup (Table 3.2) even though males were born on average at least 1 day earlier than females in 7 years out of 10.

Pupping date as an individual trait

Many females tended to pup around the same time each year (Figure 3.2). In the longitudinal data set, there were 30 females of known-age that produced from 4 to 7 pups ($n = 144$ cases). Among females, mean pupping dates were not equal (ANOVA, $F_{[29, 114]} = 3.5$, $p < 0.001$). Twenty percent consistently gave birth before the mean pupping date (May 26) while thirty percent gave birth later. The remainder bore pups before and after the mean pupping date of the population (Figure 3.2).

Table 3.2. Mean pupping date by year and pup sex for harbour seals on Sable Island, 1987-1996.

Year	<i>n</i>	Male	Female	<i>t</i> -test <i>p</i>
1987	54	May 20	May 20	0.96
1988	69	May 25	May 26	0.57
1989	54	May 21	May 22	0.50
1990	44	May 21	May 22	0.21
1991	53	May 20	May 21	0.43
1992	45	May 26	May 27	0.21
1993	65	May 26	May 26	0.43
1994	72	May 27	May 29	0.18
1995	53	May 29	May 28	0.50
1996	36	May 31	June 2	0.35
All	545	May 25	May 26	0.08*

* *p* for pup sex in a 2-way ANOVA, with year and pup sex as factors (year $p < 0.001$).

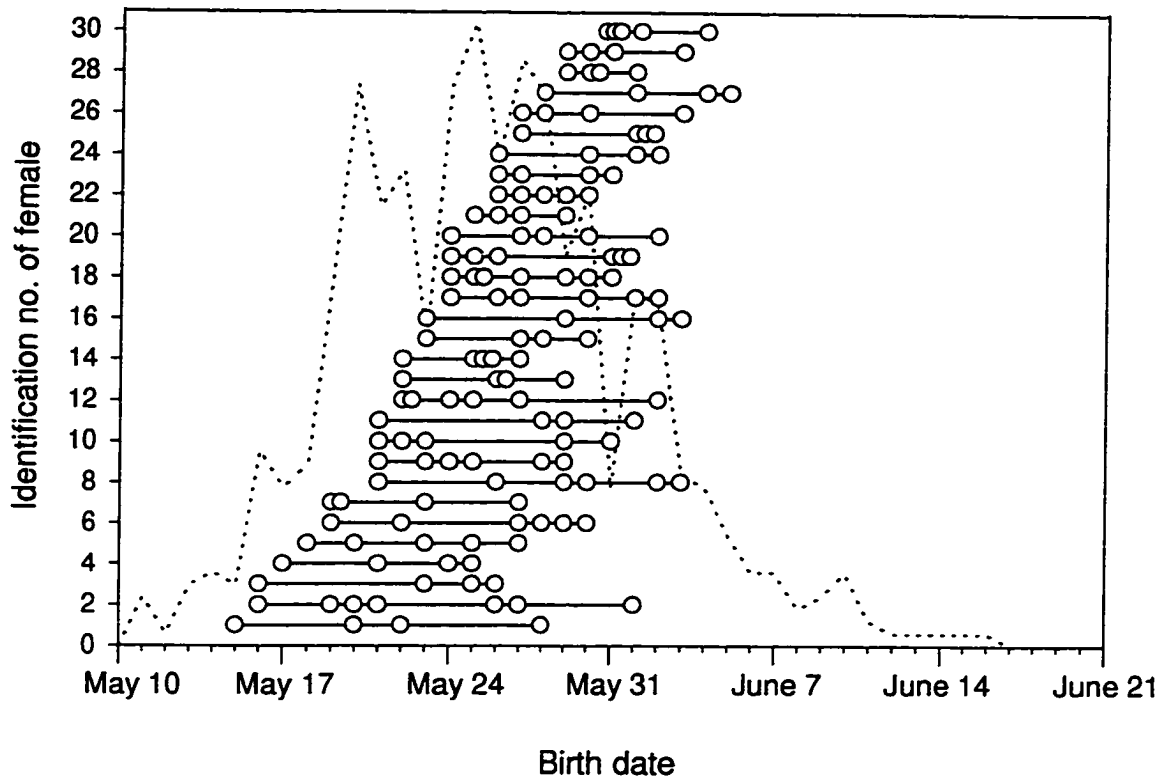


Figure 3.2. Seasonal distribution of pupping dates for 30 female harbour seals that produced 4 or more pups between 1987 and 1996 on Sable Island. Overlapping symbols indicate pups born on the same day in different years. Dotted line shows frequency distribution of births within the population, 1987-1996

Based on the first and last recorded births during the study, the possible range of pupping dates was 36 days. Each female covered a narrower range than this: the greatest range in pupping dates within an individual was 16 days (over 7 years), while the lowest range was 3 days (over 6 years). Some females were more variable than others.

Differences in ranges of maternal age did not explain this variability since variance in pupping date was not significantly correlated with variance in maternal age ($r = -0.06$, $n = 30$, $p = 0.79$). Two general patterns of variation in pupping date were observed among the 30 females: stable, and increasing (Figure 3.3).

Birth mass in relation to other traits

Pup birth mass increased with parturition mass and maternal age. The relationship between birth mass and parturition mass was non-linear (Figure 3.4a). Log parturition mass was positively correlated with log birth mass ($r = 0.45$, $n = 244$, $p < 0.001$), and accounted for 20% of the variation in log birth mass. This correlation was stronger for female pups ($r = 0.50$, $n = 126$) than for male pups ($r = 0.41$, $n = 118$), but was not significantly different by pup sex ($p > 0.50$). The relationship between birth mass and maternal age was also non-linear (Figure 3.4b). Log maternal age was positively correlated with log birth mass ($r = 0.74$, $n = 81$, $p < 0.001$), and accounted for 55% of the variation in log birth mass. Again, this correlation was stronger for female pups ($r = 0.79$, $n = 38$) than for male pups ($r = 0.72$, $n = 43$), but not significantly so ($p > 0.20$). Mean birth mass increased with maternal age even after controlling for parturition mass (ANCOVA on log-transformed data, $F_{[10, 63]} = 6.9$, $p < 0.001$). Conversely, birth mass was not correlated with parturition mass after controlling for maternal age (partial correlation on log-transformed data; $r = 0.16$, $n = 72$, $p = 0.18$.)

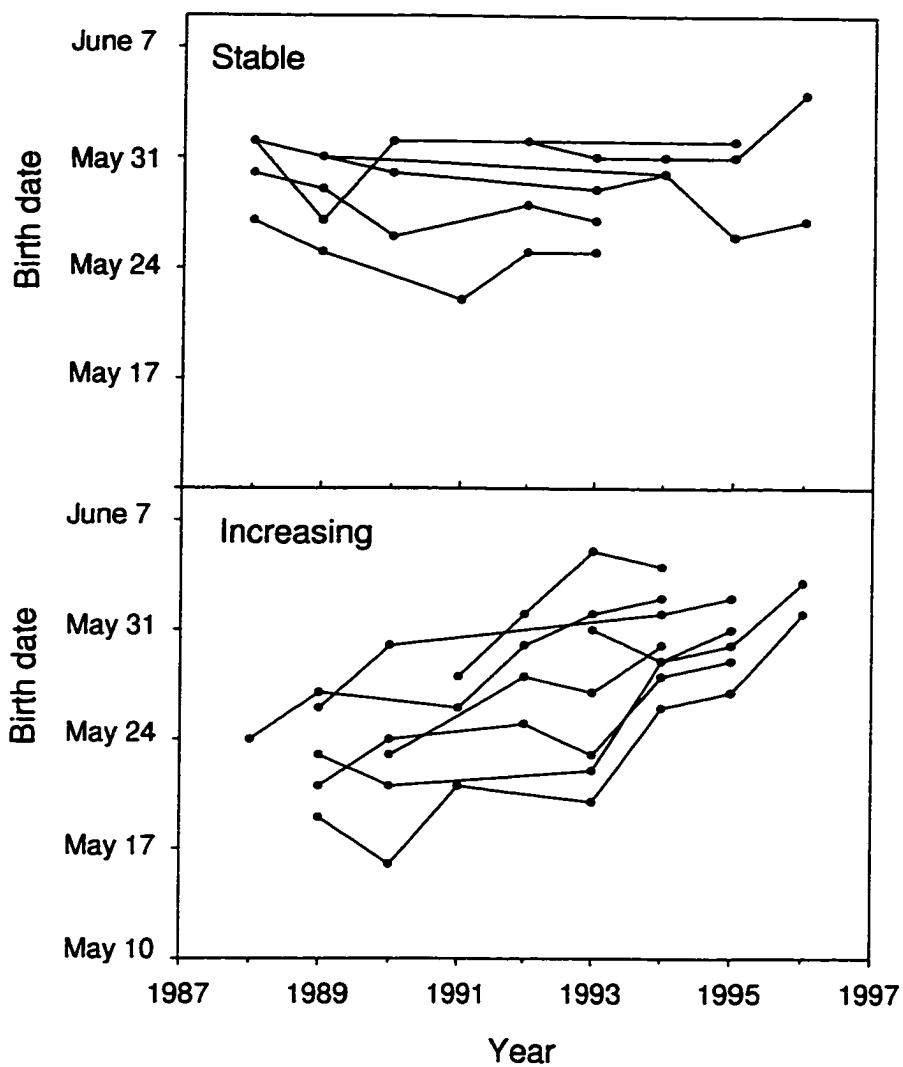


Figure 3.3. Two general patterns of variation in pupping dates of female harbour seals on Sable Island, 1987-1996.

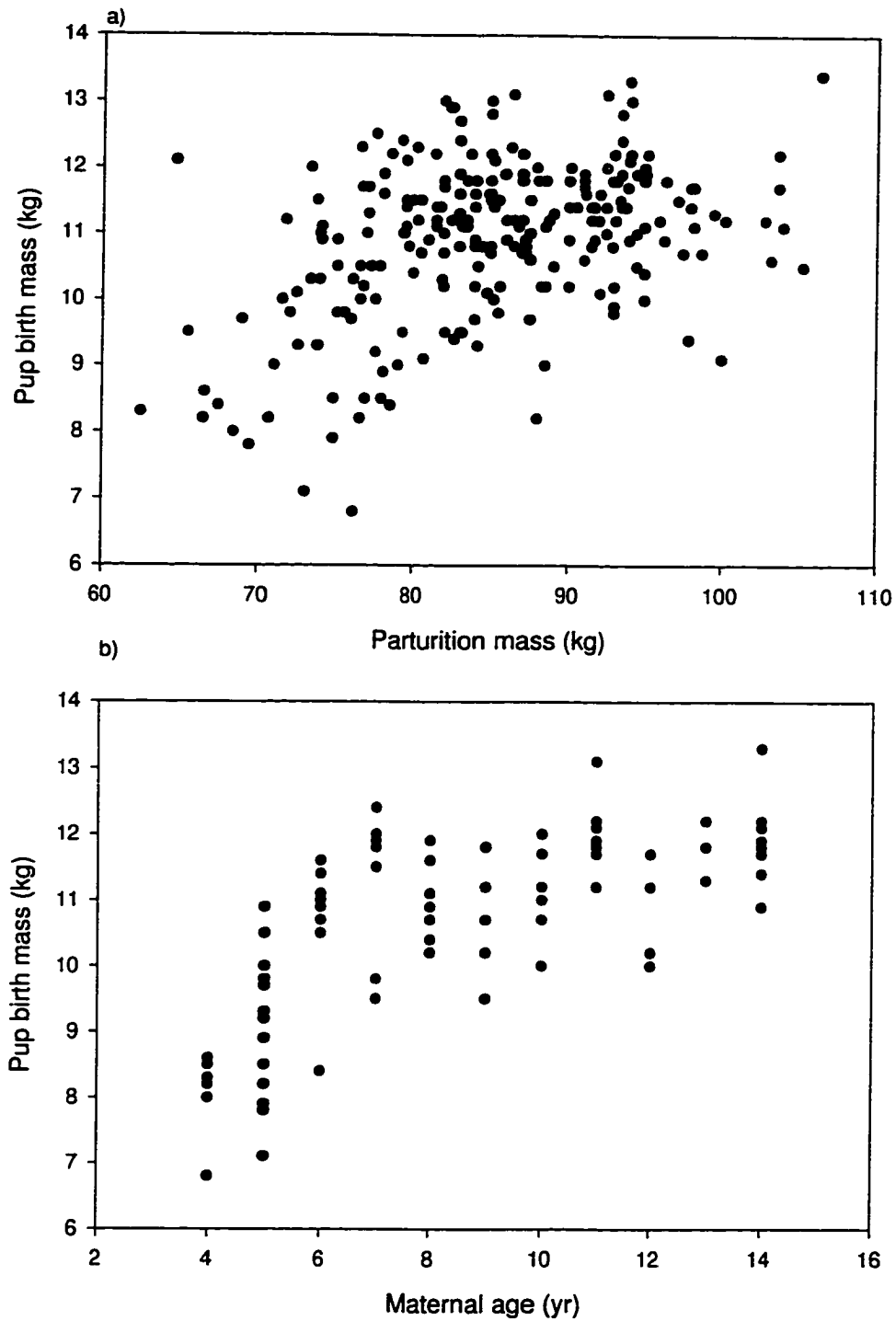


Figure 3.4. Relationships between a) pup birth mass and female parturition mass ($n = 244$), and b) pup birth mass and maternal age ($n = 81$), for harbour seals on Sable Island.

Mean birth mass was lowest for pups of the youngest females (9.3 kg), while those of the intermediate and oldest age classes were higher and similar (11.0 and 11.7 kg, respectively) (Table 3.1). Mean birth mass was significantly different among age classes even after controlling for parturition mass.

Males were significantly heavier than females at birth (11.1 ± 0.09 kg, $n = 175$, versus 10.7 ± 0.09 kg, $n = 200$) (t -test, $p = 0.009$).

Maternal effects on fetal coat

Most pups (84%) were born without lanugo. Most pups with $\geq 50\%$ lanugo were born to young females and had low birth mass (Figure 3.5). They were also mainly born early in the season (within the first two pupping date quartiles; Figure 3.6). Means of pupping date, birth mass, parturition mass, and maternal age were all lowest for pups with extensive lanugo (Table 3.3). The means of these traits increased for pups with moderate lanugo, and then again for pups without lanugo (Table 3.3).

In the cross-sectional data, pups with extensive lanugo were limited almost exclusively to the youngest maternal age class. Among known-age females whose parturition mass was recorded, there were 13 pups with more than extensive lanugo born to young females, 1 pup born to an intermediate-aged female, and none born to the oldest females. Parturition mass of the intermediate-aged female bearing the pup with extensive lanugo was 71.7 kg. This was substantially lower than the median parturition mass for the intermediate maternal age class (83.8 ± 1.1 kg).

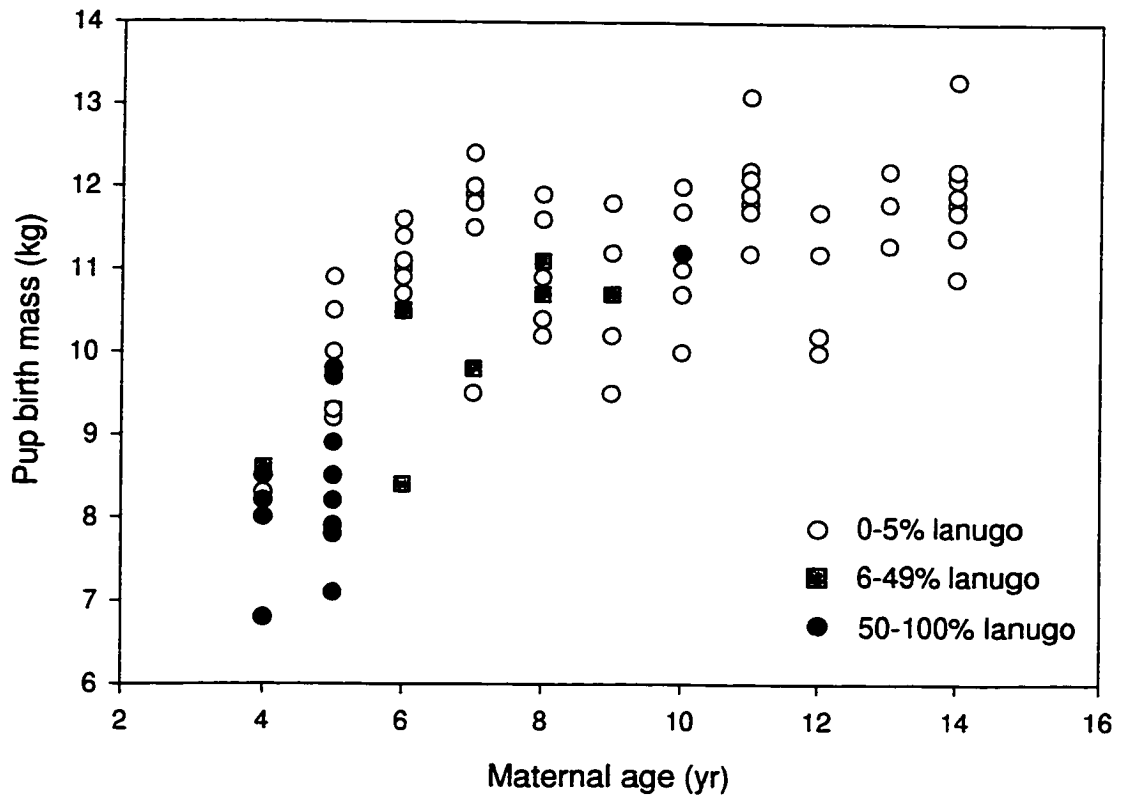


Figure 3.5. Birth mass and maternal age of harbour seals born with low ($n = 56$), moderate ($n = 8$), and extensive lanugo ($n = 14$).

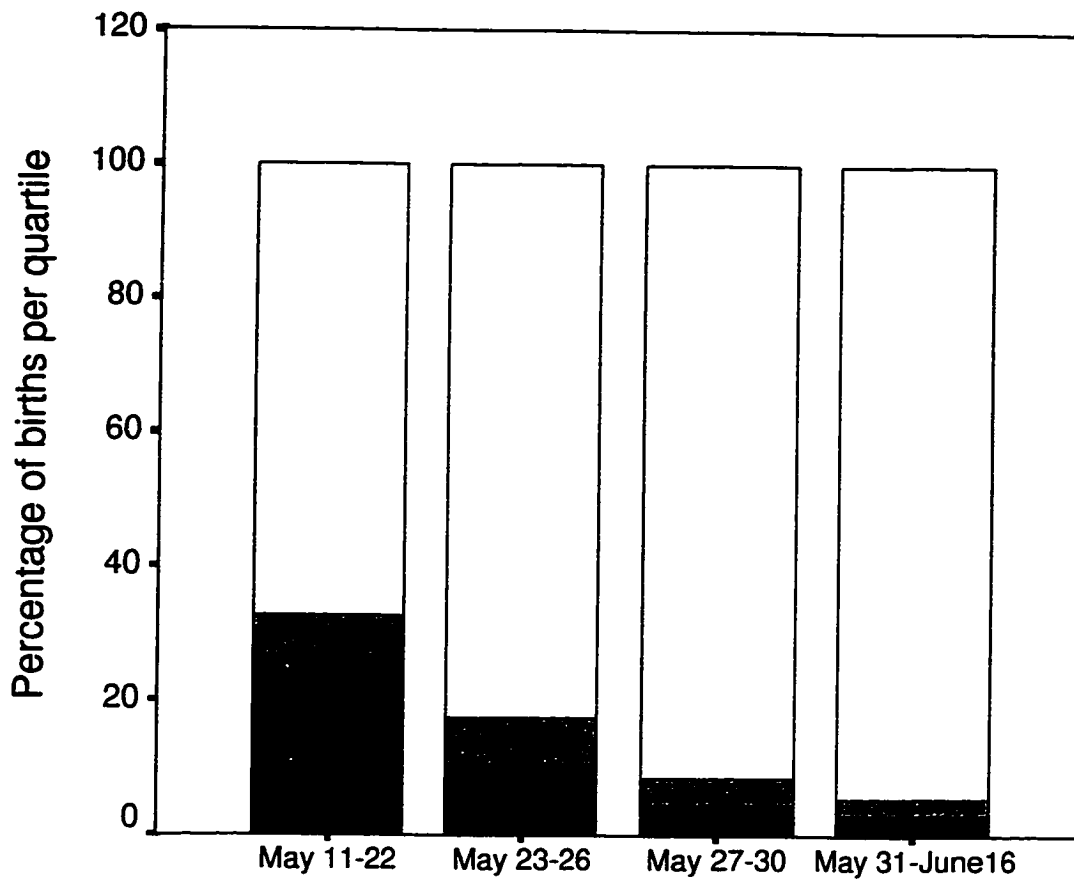


Figure 3.6. Percentage of harbour seals born within each birth-date quartile with extensive (50-100%; black), moderate (5-49%; grey), and no lanugo (0-4%; white) ($n = 573$).

Table 3.3. Relationship between lanugo coverage and other variables for harbour seals (mean \pm SE, sample size in brackets).

Variable	Lanugo coverage		
	Extensive (50 - 100%)	Medium (6 - 49%)	Low (0 - 5%)
Pupping date	May 22 \pm 0.3 (66)	May 25 \pm 1.0 (28)	May 27 \pm 0.6 (480)
Pup birth mass (kg)	9.0 \pm 0.17 (43)	10.0 \pm 0.23 (22)	11.2 \pm 0.06 (267)
Parturition mass (kg)	75.0 \pm 1.35 (24)	82.3 \pm 2.06 (15)	86.5 \pm 0.56 (194)
Maternal age (yr)	5.6 \pm 0.58 (18)	6.6 \pm 0.93 (8)	9.4 \pm 0.44 (58)

Individual females showed no tendency to produce pups of a particular lanugo class. Most females that bore more than one pup had pups with no lanugo (89% of 209). Twenty-five females (11%) had pups with lanugo (Table 3.4). For 17 of these females, the percentage lanugo decreased from one pup to the next, and in the remainder, percentage lanugo increased. There were two intermediate-aged females of known parturition mass that bore pups with extensive lanugo. When the pup with extensive lanugo was born, each female's parturition mass was low compared to her mean parturition mass (Figure 3.7).

Path analysis of maternal effects on newborn traits

Path analysis was used to examine possible causal relationships and to determine the relative influence of maternal age, parturition mass, and pupping date on pup birth mass and percentage lanugo. I hypothesized a model with 8 paths (Figure 3.8a). I postulated that maternal age could have direct effects on parturition mass, as well as on birth mass and percentage lanugo. Age could also have indirect effects on birth mass through parturition mass, and on percentage lanugo through birth mass. Parturition mass and pupping date could have direct effects on birth mass and percentage lanugo, and indirect effects on percentage lanugo through birth mass. I did not hypothesize a relationship between maternal age and pupping date, or between parturition mass and pupping date, due to earlier analyses that indicated non-significant relationships after controlling for the effects of increasing birth date over the study period (Chapter 2).

The main assumption of path analysis is that the relationships between linked variables are linear. Non-linear effects must be accounted for in the unexplained variance, or by transformations of the variables (Sokal & Rohlf 1995). I therefore used log-transformed data on maternal age, parturition mass, and birth mass in the model.

Table 3.4. Percentage lanugo coverage on pups of 25 known-age harbour seal females captured in 2 or more years on Sable Island, and bearing at least 1 pup with lanugo. In the first 17 cases, lanugo decreased or remained stable, while in the last 8 cases, lanugo coverage increased at least once.

Female no.	Maternal age (yr)										
	4	5	6	7	8	9	10	11	12	13	14+
952	100	40	0					0			
998	100			5							
1003	100			0	0						
1012	90	50	0								
994	75					0	0	0			
954	20				0		0				
987		100			20	0	0				
1011		95	30		0						
990		90	0		0			0	0	0	
945		75	0	0							
947		50		30							
941			100	25	4						
991			5	0	1						
950				90	0	0	0	0	0		
959				5			0		0	0	
949					5			0			
967					2					0	0
1008	0	4	25								
996		0		10	0						
1000		15	4	10	0	0					
944			20		0	80	0				
992			0		75	0	5				
953					0	20					
965					0			4	0	0	0
980							10			80	0

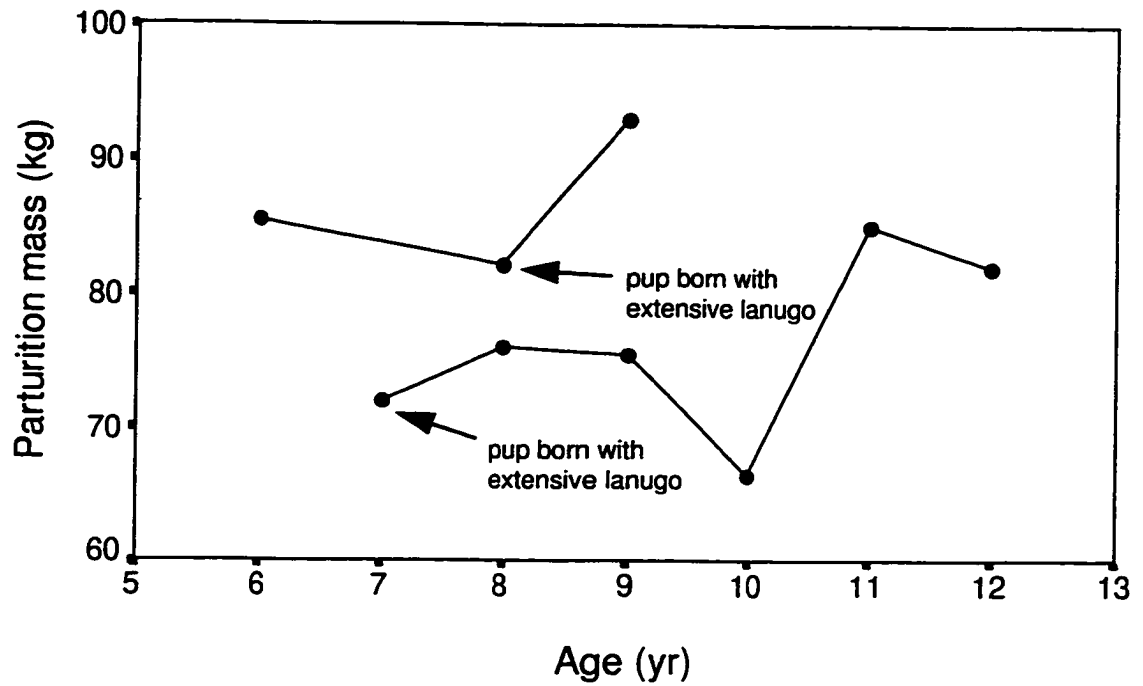


Figure 3.7. Longitudinal parturition masses of two female harbour seals that bore pups with extensive lanugo while of intermediate age (7-10 years). Dashed lines represent mean parturition mass of each female.

Data on percentage lanugo were not transformed due to null values, and data on pupping date were not transformed either. The variables were all significantly correlated with one another, except for pupping date (Table 3.5).

In the overall model, all maternal ages and both pup sexes were examined together (Figure 3.8a). Pupping date was not significantly related to birth mass or lanugo and was dropped entirely from the model. Two other paths were not significant: the path between parturition mass and birth mass, and that between age and percentage lanugo. Eliminating these made the model simpler, with only 4 paths (Figure 3.8b). The path strength between age and birth mass (0.75) was similar to that of age on parturition mass (0.73). These were the strongest paths in the model. Parturition mass had a direct effect on percentage lanugo (-0.23), but no significant effect on birth mass. The indirect effect strength of age on percentage lanugo (-0.65) (Appendix 3.1) was stronger than the direct effect of parturition mass on percentage lanugo (-0.23) (Table 3.6). There was a strong negative effect of birth mass on percentage lanugo (-0.64).

The amounts of unexplained variance for each endogenous variable were 36% for percentage lanugo, 44% for birth mass, and 46% for parturition mass (Figure 3.8b). Sources of unexplained variance may include pup sex and unquantified individual maternal effects. Since path analysis can include only interval or ordinal data (Klem 1995), it was not possible to use dummy variables for pup sex or maternal ID in the model.

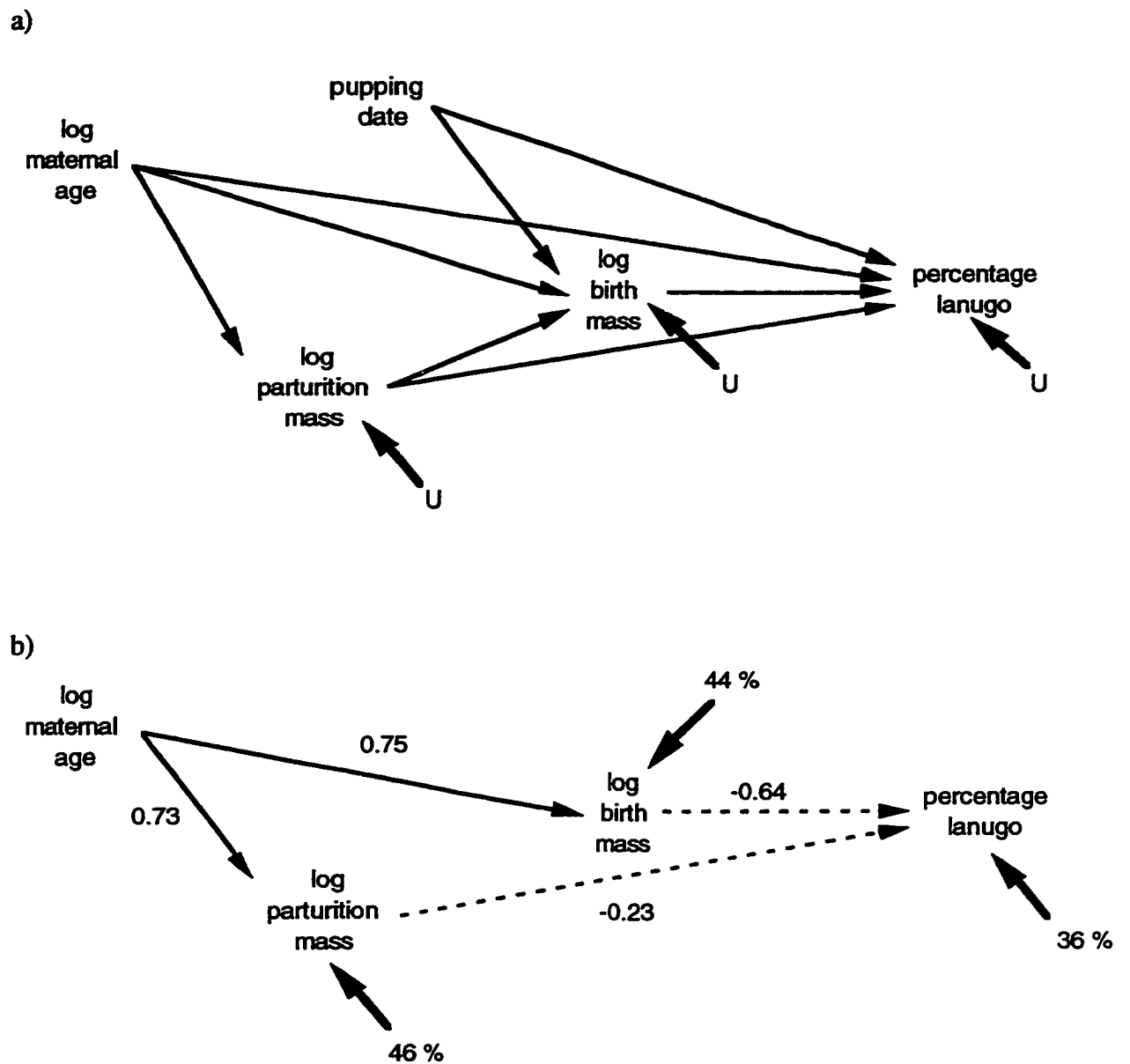


Figure 3.8. Path model linking life-history traits of harbour seal mothers and pups at birth: a) hypothesized full model, b) trimmed model. Model includes both pup sexes and all maternal ages ($n = 74$). Unexplained variance is linked to each endogenous (dependent) variable by a thick arrow, and is represented as the letter "U" or as a percentage. Dashed lines represent negative paths.

Table 3.5. Bivariate correlation matrix (Pearson's r) for life-history traits used in path analyses ($n = 74$).

Trait	Log maternal age	Log parturition mass	Birth date	Log birth mass	Percentage lanugo
Log maternal age	-				
Log parturition mass	0.73**	-			
Pupping date	0.27*	0.18	-		
Log birth mass	0.75**	0.62**	0.07	-	
Percentage lanugo	-0.67**	-0.63**	-0.21	-0.78**	-

* $p < 0.05$

** $p < 0.01$

Table 3.6. Effect strength¹ of variables in the three path models containing compound paths (Figures 3.8b to 3.9b). (NS = not significantly different from 0)

Exogenous variable	Endogenous variable		
	Log maternal age	Log parturition mass	Log birth mass
<i>Overall path model (Fig. 3.8b)</i>			
Log maternal age	-		
Log parturition mass	0.73	-	
Log birth mass	0.75	NS	-
Percentage lanugo	-0.65	-0.23	-0.64
<i>Male pup model (Fig. 3.9a)</i>			
Log maternal age	-		
Log parturition mass	0.76	-	
Log birth mass	0.71	NS	-
Percentage lanugo	-0.66	-0.33	-0.57
<i>Female pup model (Fig. 3.9a)</i>			
Log maternal age	-		
Log parturition mass	0.71	-	
Log birth mass	0.84	NS	-
Percentage lanugo	-0.69	NS	-0.82

¹ 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 (calculations in Appendix 3.1).

To test for differences due to pup sex, the model was re-estimated for each sex, across all maternal ages. In the model for male pups ($n = 41$), all the same paths were significant as in the overall model (Figure 3.9a). The effect strengths of the model on male pups were similar to the overall model (Table 3.6), as were the amounts of unexplained variance. In the model for female pups ($n = 33$), the path between age and birth mass was stronger (0.84), and the unexplained variance was reduced to 29% (Figure 3.9b); this is the strongest path coefficient and the lowest unexplained variance in all path models presented here. The path between parturition mass and percentage lanugo was not significant in the female pup model. Birth mass alone explained as much of the variance in female percentage lanugo (67%) as did birth mass and parturition mass in the model for male pups (66%). The effect strength of age on percentage lanugo was similar for both sexes (male: -0.66; female: -0.69; Table 3.6).

To see whether the model was valid for all ages, the model was re-estimated for the 3 maternal age classes (Figure 3.10). The model was appropriate only for the youngest maternal age group (4- to 6-yr-olds, $n = 24$). It had the same final form (Figure 3.10a) as the model for all ages, except the link between parturition mass and percentage lanugo was not significant. The path coefficients were smaller, and the unexplained variances greater. For the intermediate age class (7- to 10 yr, $n = 26$), the only significant path was between parturition mass and percentage lanugo (Figure 3.10b). The significance of the path was, however, only marginal ($p = 0.046$), and the unexplained variance of percentage lanugo was high (84%). No paths were significant in the model for the oldest females (11 - 14+ yrs, $n = 24$).

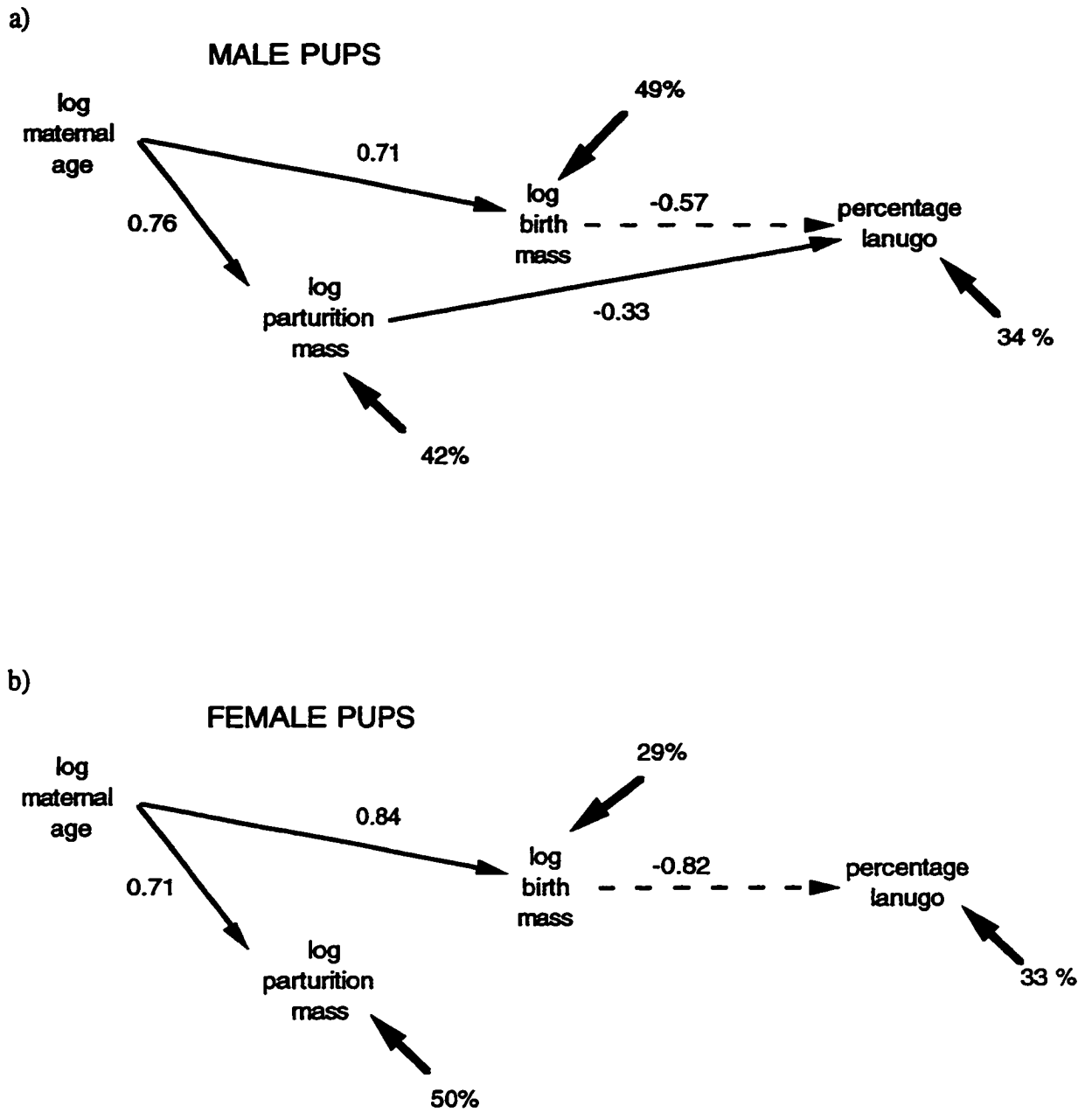


Figure 3.9. Trimmed path models of maternal effects at birth in harbour seals by pup sex: a) male pups ($n = 41$), and b) female pups ($n = 33$). Percentage unexplained variance is linked to each endogenous (dependent) variable by a thick arrow. Dashed lines indicate negative paths.

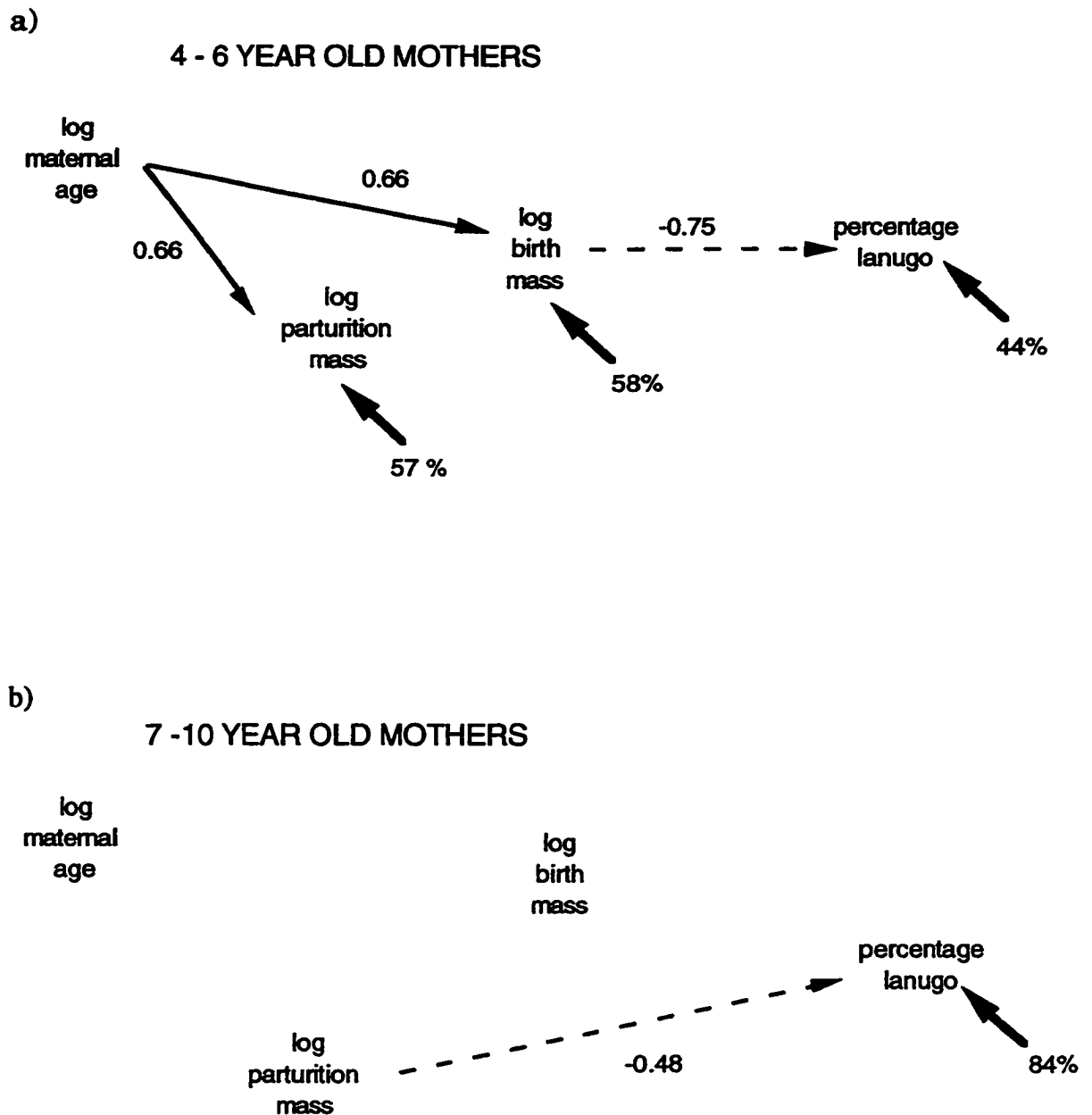


Figure 3.10. Trimmed path diagrams of maternal effects at birth in harbour seals by maternal age class: a) mothers aged 4 to 6 years ($n = 24$), and b) mothers aged 7 to 10 years ($n = 26$). (In the model for mothers ≥ 11 yrs old ($n = 24$) no paths were significant.)

Prenatal reproductive investment

Birth mass of pups ranged from 8.9% to 18.7% of maternal mass at parturition (mean, $12.9 \pm 0.09\%$, $n = 244$). There were no trends over the pupping season as relative birth mass was not significantly correlated with pupping date ($r = -0.04$, $n = 244$, $p = 0.53$). Relative birth mass was positively correlated with maternal age ($r = 0.26$, $n = 75$, $p = 0.025$) and differed between the three maternal age classes; the youngest females had the lowest relative birth mass (12.1%), while relative birth mass was higher and equal in the other two age classes (13.2% and 13.1%, respectively; Table 3.1). Relative birth mass was significantly higher for male pups than female pups ($13.2 \pm 0.14\%$, $n = 118$, versus $12.6 \pm 0.12\%$, $n = 126$) (t -test, $p = 0.002$).

Age versus experience

Harbour seals usually give birth each year following maturity (Bigg 1969), so maternal experience increases with maternal age. This makes it difficult to distinguish between the influences of experience (parity) and age. To test whether age *per se* was an important determinant of birth mass for pups of young females, I compared parturition mass and pup birth mass of primiparous 4- and 5-year olds ($n = 6$ and 14, respectively). Mean parturition mass of 4-year-old females was significantly lower than that of 5-year-old females (70.5 ± 1.7 versus 75.7 ± 1.0 kg) (t -test, $p = 0.01$). Mean birth mass was lower among primiparous 4-year-olds than primiparous 5-year-olds (8.1 ± 0.2 kg, versus 9.0 ± 0.3 kg), but this was not significantly different after controlling for parturition mass (ANCOVA, $F_{(1, 17)} = 1.4$, $p = 0.25$). Relative birth mass in each group was 11.5% and 11.8% respectively, and these were not significantly different (t -test, $p = 0.66$).

To test for an influence of experience, while controlling for age, I compared parturition mass and birth mass for pups of primiparous 5-year old females ($n = 14$), with those of 5-year-olds with one year's prior experience ($n = 3$). Mean parturition mass for the two groups were 75.7 ± 1.0 kg and 80.5 ± 1.6 kg, and were marginally significantly different (ANOVA, $F_{[1, 15]} = 4.6$, $p = 0.048$). After controlling for parturition mass, mean birth mass did not differ between the two groups (ANCOVA, $F_{[1, 14]} = 1.1$, $p = 0.32$). Relative birth mass was slightly higher but not significantly different in the 5-year-olds with prior experience (12.6% versus 11.8%) (t -test, $p = 0.47$).

A separate approach to look for effects of experience was to compare primiparous females with multiparous females while controlling statistically for age. I assumed that all females older than 5 were multiparous and so pooled data on them ($n = 57$) and compared them with pooled primiparous 4- and 5-yr-olds ($n = 18$). Log parturition mass did not differ between the two groups after controlling for log age (ANCOVA, $F_{[1, 72]} = 2.5$, $p = 0.117$). However, log birth mass was lower among the primiparous females after controlling for log age and log parturition mass (ANCOVA, $F_{[1, 71]} = 16.3$, $p < 0.001$).

Discussion

Maternal effects on traits of newborns

Pupping date, maternal age, and parturition mass had different influences on the extent of lanugo on newborns and on pup mass at birth. Pupping date did not significantly affect pup birth mass or percentage lanugo, and thus cannot be considered a maternal effect on newborn harbour seals. Maternal age and parturition mass were, however, significant maternal effects.

In bivariate analyses, log maternal age explained 55% of the variation in log birth mass, while log parturition mass explained only 20%. This effect of parturition mass is low compared to other species of pinnipeds. For example, maternal mass explained more than 50% of the variation in birth mass in grey seals, *Halichoerus grypus* (Iverson et al. 1993) and Antarctic fur seals (Costa et al. 1988). In fact, the overall path model suggests that parturition mass does not affect birth mass in harbour seals, but simply covaries with it through effects of age (Figure 3.8b). Age affected birth mass and parturition mass equally. On the other hand, both age and parturition mass affected percentage lanugo. Both relationships were negative, reflecting the observation that younger and smaller females were more likely to have pups with low birth mass and extensive lanugo (Bowen et al. 1994).

The relationships between pup traits and maternal traits changed with maternal age. This has been documented in other mammals. Dobson and Michener (1995) compared path analyses of different age classes of female Richardson's ground squirrels and found that the influence of maternal characteristics on offspring traits, including neonate mass, varied with age. My comparison of path models between the three maternal age classes (Figure 3.10) supports the hypothesis that, among young females, age is an important factor influencing offspring birth mass and state of development. In the model on 4 to 6 year-olds, age had an equal and positive effect on both birth mass and parturition mass. As in the overall model, parturition mass did not significantly influence pup traits among young females, but simply covaried with birth mass. However, within the intermediate age group, the effect of age was no longer significant. There was a small, but statistically significant effect of parturition mass on percentage lanugo,

suggesting that condition can affect the state of pup development in intermediate-aged females. For the oldest females, neither age nor condition significantly affected the newborn traits that I studied. These path models support the hypothesis that experience, reflected by age, is important over the first few reproductive events. After that, condition, reflected by increasing parturition mass, is more influential. At higher ages and heavier masses both variables lost their influence.

What mechanisms might lead to increasing birth mass with age (after controlling for parturition mass)? As mentioned earlier, there are likely to be trade-offs between growth and reproduction. Since young females are still growing, they may have a smaller proportion of energy to allocate towards current reproduction. If this is so, offspring should be relatively smaller. In addition there may be limitations on the amount of nutrients that a female can give to her growing fetus. In mammals, the maternal environment can be critical for fetal growth (reviewed by McKeown et al. 1976). In some species, such as guinea-pigs (*Cavia parcellus*) and humans, the reserves of the uterus are limited, and neonate mass is more related to size of the female than to that of the male parent. In other species, such as some breeds of sheep, the reserves of the uterus are abundant and impose no constraints on fetal growth; in these cases, birth mass is determined by fetal genes, and is related to the size of both parents. This argument could apply to species that continue to grow after beginning to reproduce. While the female is young and small, transfer of nutrients in utero may be reduced relative to older females. After reaching full-size, nutrient transfer in utero might become more than sufficient to meet fetal needs, and maternal age and mass would no longer influence birth mass. This could explain the seemingly random variation in pup birth mass for females older than 10

yr and greater than the median mass of 85.0 kg (Figure 3.4). This variation is clearly not related to maternal age or maternal mass, but could be related to variation in paternal genes and other unmeasured factors.

Maternal age versus maternal experience

Age alone was not an important determinant of birth mass among young females, as evidenced by the comparison of primiparous 4- and 5-year olds. The fact that females of different ages, but equal experience, had pups of similar birth mass suggests that experience is more important than age *per se*. This suggests that age is nothing more than a convenient metric, representing underlying behavioural and physiological components.

Although the mean birth mass of pups was not significantly different between 5-year old females with no prior experience and those with 1 year's experience, it is possible that the small sample size of the latter ($n = 3$) is responsible for the lack of significance. It is noteworthy that in the experienced category, females were 6% heavier and pups were 13% heavier, thus prenatal reproductive investment was higher. These patterns are consistent with the hypothesis that birth mass and reproductive investment are positively influenced by maternal experience among young animals. Further studies with greater sample sizes are needed to address this question directly in harbour seals. There is some additional support for the positive effects of experience. Birth mass was lower in primiparous than multiparous females after controlling for age and parturition mass. This was also the case in northern fur seals (Trites 1991). The author concluded that females were physiologically altered by their first pregnancy, and he hypothesized that after the first parturition, higher numbers of intrauterine blood vessels led to improved fetal provisioning.

Prenatal investment

The relative birth mass of 12.9% is high compared with other phocids which average 9.0% (12 species; Bowen 1991), and is exceeded only by bearded seals, *Erignathus barbatus* (13.4%) (Bowen 1991). Among mammals, relative birth mass varies from 0.3% in the polar bear (*Ursus maritimus*), to 63% for the guinea pig (McKeowen et al. 1976), and the general pattern is for larger species to bear relatively smaller offspring (Leitch et al. 1959). The average offspring or litter mass for mammals with parturition masses similar to harbour seals is between 5.2 and 8.7% of maternal mass (McKeowen et al. 1976). Thus, a female harbour seal has high prenatal investment relative to comparable mammals in general, and to other phocids in particular. Newborn harbour seals are more active and precocious than most comparably sized mammals, beginning to swim within hours of birth (Lawson and Renouf 1985; Oftedal et al. 1991), thus, high relative birth mass may be an adaptation to earlier activity (McKeowen et al. 1976). It is also likely to be an adaptation to earlier entry into the water than most other pinnipeds (Oftedal et al. 1991).

I hypothesized that while female harbour seals were still growing, trade offs with current growth would limit prenatal reproductive investment, and lead to lower relative birth mass than in older, larger females. I expected that relative birth mass would increase as adult growth decelerated, and then increase again after adult growth stopped. Relative birth mass was lowest among young females and increased between the young and intermediate-aged females, as expected. It did not, however, increase between intermediate and older females. This similarity between intermediate-aged, growing females and non-growing, older females does not support the hypothesis that investment will increase after growth has finished.

The pattern of increasing investment with age differed from other phocids and most mammals. Relative birth mass usually declines with maternal age (Deutsch et al. 1994) or maternal mass (Millar 1977; Kovacs and Lavigne 1986). The fact that prenatal reproductive investment increased after the first few reproductive events in harbour seals, then leveled off, suggests that young harbour seals are particularly limited in the amount of resources they can put toward gestation. Physiological constraints, such as the ability to deliver nutrients to the fetus in utero (McKeowen et al. 1976), could be important limitations to birth mass of pups in young females. In harbour seals, relative birth mass is still high compared with other phocids and mammals, as discussed, but appears to be limited for young females.

Perhaps this difference in patterns of investment can be explained by the fact that, in many aspects, harbour seals are atypical phocids. They are one of the smallest phocid species, but slightly larger than most otariid species (Boness et al. 1994). They exhibit a strategy of maternal care that is intermediate between otariids and phocids, feeding rather than fasting during lactation (Bowen et al. 1992a; Boness et al. 1994; Boness and Bowen 1996). The small body mass of harbour seals is thought to be critical in the evolution of this foraging, since they have a limited ability to store reserves throughout lactation (Boness et al. 1994). This study suggests that small body mass is also a limiting factor during gestation for young females.

Fetal coat

Most pups were born without lanugo. Pups with extensive lanugo were mainly born early in the season to young females. On average, pups with extensive lanugo weighed 20% less than pups without lanugo. Since low birth mass can be related to high

mortality in some mammals (Calambokidis and Gentry 1985; Trites 1990) these patterns are consistent with the idea that extensive lanugo is indicative of an under-developed pup of low quality (Bowen et al. 1994). In the earlier study, among 10 females that bore at least 1 pup with lanugo, percentage lanugo decreased in almost all cases (Bowen et al. 1994). There were more instances in the present study (9 out of 25) of lanugo coverage increasing in subsequent pups. Although these cases were still the minority, they illustrate that extensive lanugo on a pup is not limited to a female's first reproductive event. Limited observations suggest that, among intermediate-aged females, relatively poor condition, reflected by low parturition mass, can lead to extensive lanugo (Figure 3.7).

Path analyses indicated that among young females, maternal age, and not condition, affected the amount of lanugo coverage. The effect of age was not significant among intermediate-aged or older females. The path model on intermediate-aged females suggested that condition influenced lanugo. This was supported by the observation that an intermediate-aged female that gave birth to a extensive lanugo pup weighed substantially less than the median of its age class.

Patterns in pupping date

As in most other pinnipeds (Bonner 1984), female harbour seals on Sable Island synchronize their reproduction, giving birth within a period of 3 to 4 weeks. Such reproductive synchrony must be maintained by selection. Within the pupping season, however, there were no significant relationships between pupping date and maternal age or parturition mass. In many mammals, birth date is related to survival of offspring (Festa-Bianchet 1988; Iason 1989). For instance in red deer, calves born early or late in the

season have a lower chance of surviving the summer than those born in peak season (Guinness et al. 1978), and in northern elephant seals, females that bear pups early in the season are more successful (Reiter et al. 1981). Based on the lack of relationships between pupping date and maternal age or mass within the season, I hypothesize that on Sable Island selection for pupping date acts similarly on all female harbour seals, regardless of age or mass.

Each female's range of pupping dates over the study period was narrower than that of the population as a whole, and mean pupping dates were different among individuals. Boyd (1996) made similar observations using longitudinal data on 21 Antarctic fur seals, noting that some females gave birth early in the season while others gave birth later. Data presented in Figure 3 of Boyd's publication (1996) indicate that 24% of females gave birth before the mean pupping date for the population, 43% after, and 33% both before and after. The author suggested that the tendency to give birth at specific times of the year indicated a range of responses to photoperiod, and that this response might be genetically determined, as in wild rodents (Desjardins et al. 1986).

Sex differences

On average, males were born one day earlier than females. This relationship was not significant after considering interannual variation. Relationships of birth date to natal sex ratio are variable in other mammals. In Antarctic fur seals natal sex ratio is not related to birth date (Boyd and McCann 1989), but males tend to be born earlier in the season than females in grey seals (Coulson and Hickling 1964; Anderson and Fedak 1987) and red deer (Clutton-Brock et al. 1982).

In polygynous, species in which adult males are larger than females, large size

usually confers reproductive advantages to males, and males usually have higher reproductive potential than females and greater variability in reproductive success (Clutton-Brock et al. 1982; Le Boeuf et al. 1989). In such species, sexual-selection theory predicts that evolution would favour greater parental investment in male offspring (Trivers and Willard 1973; Maynard-Smith 1980), and male newborns typically weigh more than females (Clutton-Brock et al. 1982). This pattern is seen in phocids (Le Boeuf et al. 1989; McCann et al. 1989) and otariids (Boyd and McCann 1989). In the present study, male pups averaged 3.7% heavier than females, and relative birth mass was 5% greater. Greater birth mass may be a factor leading to sexual dimorphism in adult harbour seals. However, most of the growth leading to sexual dimorphism in pinnipeds occurs during growth spurts long after weaning (McLaren 1993), and therefore after the period of maternal investment (Bowen et al. 1992b). The relationship between birth mass and adult mass is unknown in harbour seals (and for other pinnipeds) thus the biological significance of differential birth mass is unclear.

Summary

Pupping date was not a significant maternal effect on birth mass in harbour seals.

Contrary to studies of other mammals, in which pupping date within the pupping season is related to offspring survival, there was no tendency for older or larger females to give birth early. I hypothesized that the lack of relationships between pupping date and maternal age or mass suggests that selection on pupping date affects all females similarly.

In harbour seals, maternal effects of age were stronger than parturition mass on pup birth mass. In fact, parturition mass had no significant effect on birth mass, but simply

covaried with age. Age effects were strongest among young females, weak for intermediate-aged females, and insignificant for older females. It appeared that, among young females, age itself is was not as important as reproductive experience in determining offspring birth mass. Experience could lead to behavioural improvements, such as increased foraging ability during pregnancy, or physiological improvements, such as improved intrauterine transfer of nutrients to the fetus. Such effects of experience may to apply to mammals in general.

Pups with extensive lanugo usually had low birth mass, and were born early in the season to young light females. Over all ages, maternal age had an indirect negative effect on percentage lanugo through its effect on birth mass, while parturition mass had a direct negative effect. Among intermediate-aged females, only parturition mass affected percentage lanugo, suggesting a role for condition, but not age, after the first few reproductive events.

Prenatal reproductive investment, measured as the ratio between birth mass and maternal mass, was 12.9%. This is high for mammals and pinnipeds alike, and may be an adaptation to earlier activity than comparably sized terrestrial mammals, and early entry into cold water. Investment increased from young females to intermediate-aged females, then leveled off. This suggests that young female harbour seals are limited in the amount of resources they can deliver to a growing fetus, and may reflect a trade-off between growth and reproduction, and limitations due to small body mass.

There were differences in pup traits by pup sex. Male newborns weighed 3.7% more than females, and prenatal reproductive investment, measured as relative birth mass, was 5% greater for male pups. Overall, males were born one day earlier, but this

relationship was not significant after considering interannual variation. It is unknown whether greater absolute and relative birth mass of males lead to increased adult size, survival, or reproductive success of males.

Appendix 3.1. Calculations of the effect strength of variables of compound paths in path model (Figures 3.8 to 3.10). The strength of a compound path is the product of each path coefficient. The effect strength of one variable on another is the sum of the direct path between them (if any) plus the products of any compound paths connecting the two variables (Klem 1995).

Figure 3.8b. Trimmed model, across all ages and both sexes.

$$\text{Effect of log age on percentage lanugo} \quad (0.75 \times -0.64) + (0.73 \times -0.23) = - \mathbf{0.65}$$

Figure 3.9. Trimmed models, for male and female pups.

Males:

$$\text{Effect of log age on percentage lanugo} \quad (0.71 \times -0.57) + (0.76 \times -0.33) = - \mathbf{0.66}$$

Females:

$$\text{Effect of log age on percentage lanugo} \quad 0.84 \times -0.82 = - \mathbf{0.69}$$

Figure 3.10a. Trimmed model, for 4-6 yr-old females.

$$\text{Effect of log age on percentage lanugo} \quad 0.66 \times -0.75 = - \mathbf{0.50}$$

CHAPTER 4

MATERNAL EFFECTS ON NATAL SEX RATIO

IN HARBOUR SEALS

Introduction

In polygynous species in which males are larger than females, male reproductive success is often affected by male-male competition (Clutton-Brock et al. 1982). Larger males are more likely to gain access to females by displacing smaller males in aggressive encounters (Le Boeuf 1974). Large body size also confers an energetic advantage to animals that fast (Lindstedt and Boyce 1985), which is the case for most male pinnipeds during the breeding season (Bartholomew 1970). Trivers (1972) hypothesized that in a polygynous mating system, mothers should invest more in male than female offspring, since a son could benefit more from additional investment, and a son in good condition could potentially produce more descendants. Evidence for differential investment might include higher birth mass, weaning mass, or growth rate, reflecting greater resource allocation by the mother (Maynard Smith 1980; Clutton-Brock et al. 1982).

Another form of differential investment could be a skewed sex ratio. Trivers and Willard (1973) hypothesized that in species whose reproductive success is related to their size or condition, and where this relationship differs between sexes, mothers should vary offspring sex in relation to their own body condition. According to theory, large, older mothers should produce more males whereas small, young mothers that are still growing should produce more females. This prediction comes from the expectation that a

son in good condition at the end of the period of maternal investment should outreproduce a daughter in similar condition, whereas a daughter should outreproduce a son if both are in poor condition (Trivers and Willard 1973).

The hypothesis that females will adjust offspring sex ratio toward the sex that will have the greatest effect on their own fitness has generated great interest among behavioural ecologists. There is abundant evidence of skewed sex ratios with respect to maternal condition among invertebrates (Charnov 1982), however the evidence among polygynous, sexually dimorphic mammals has been mixed. Among species in which adult males are larger, there are examples of the predicted female-biased sex ratios for young mothers, or mothers in poor condition, but also of male-biased sex ratios, and unbiased sex ratios (reviewed by Clutton-Brock and Iason 1986; Byers and Moodie 1990). Reviewers have criticized some of these studies because of their small sample sizes, and for claiming that trends are supportive of theory despite a lack of statistical significance (Clutton-Brock and Iason 1986).

Pinnipeds are considered good study candidates with which to test predictions of differential investment (Kovacs and Lavigne 1986; Le Boeuf et al. 1989). Within the two main families of pinnipeds—the Otariidae and Phocidae—there are varying degrees of sexual size dimorphism. In all otariid species, adult males are larger than females (Alexander et al. 1979), reaching up to 5 times larger in northern fur seals, *Callorhinus ursinus* (Gentry 1981). In most phocid species, adult males are also larger than females, ranging from 1.1 to 10 times larger (Bryden 1972; Kovacs and Lavigne 1986). All otariids, and many phocids, have polygynous mating systems (Boness et al. 1993). In pinnipeds, parental care is provided solely by females, and ends after lactation, which is

brief in phocid seals compared with other mammals (Bonner 1984; Bowen 1991). These features facilitate studies of parental energetic investment in offspring.

Evidence for a skewed sex ratio with respect to maternal condition is weak in phocids. One of the few examples of positive evidence is the southern elephant seal, *Mirounga leonina* (Arnbom et al. 1994). Southern elephant seals are polygynous and extremely size dimorphic, with adult males weighing up to 10 times as much as females (Bryden 1972). Large body size in adult males confers a fighting advantage necessary to maintain high dominance status, which is associated with high reproductive success (McCann 1981; Modig 1996). Arnbom et al. (1994) found that the birth sex ratio in southern elephant seals was related to maternal body condition (measured as mass), but not to maternal age. Females below a threshold mass of 380 kg gave birth exclusively to female pups. As only 9 females below this suggested threshold were studied, more data are needed to confirm this result. Furthermore, in northern elephant seals, *Mirounga angustirostris*, a closely related species in which males are also much heavier than females, and large males tend to dominate mating (Le Boeuf and Reiter 1988), there was no relationship between natal sex ratio and maternal mass (Le Boeuf et al. 1989). There was also no relationship between birth sex ratio and maternal age in northern elephant seals (Reiter et al. 1981; Le Boeuf et al. 1989).

Compared with these phocid species, adult harbour seals, *Phoca vitulina*, show a lower degree of size dimorphism between the sexes. At the beginning of the breeding season in eastern Canada, mean male mass is 108 kg (Walker and Bowen 1993), and mean female mass is 85 kg (Chapter 3); thus adult males weigh 1.3 times as much as females. This lower degree of dimorphism may be related to the fact that harbour seals

mate aquatically, rather than terrestrially (Coltman et al. in press (c)). In the aquatic environment, agility could be a more important factor leading to successful mate competition than large size (Le Boeuf 1991), thus sexual selection on size may be lower in aquatically breeding species (Coltman et al. in press (c)).

Regardless of the reason for lower size dimorphism in harbour seals than in larger phocids, body size appears related to reproductive success. Large males spend less time foraging during the mating season, and more time engaged in shallow dives, which are usually associated with aggressive behaviour and advertising displays to females (Coltman et al. 1997). In addition, large males expend more energy during the mating season than small males. This may translate into a mating advantage since reproductive effort is correlated with mating success in other phocids (Coltman et al. in press (c)). Males engage in fights during the breeding season (Sullivan 1981; Walker and Bowen 1993), and there is genetic evidence for a low level of polygyny in harbour seals (Coltman et al. in press (b)). It is reasonable, therefore, to expect some level of differential maternal energy investment in harbour seals. Here I examine natal sex ratio. Differential birth mass is explored elsewhere (Chapter 3), as are sex ratio at weaning and differential growth rate and weaning mass (Chapter 5).

Evidence suggests little differential investment in phocid seals. Nonetheless, harbour seals appear to exhibit features for which theory predicts differential effects. Therefore, I used my data to examine the predictions that offspring sex ratio should vary with parturition mass and with maternal age. In addition, I examined the assumptions of adaptive sex ratio theory to see whether the assumptions apply to pinnipeds.

Methods

Data were collected in May and June from 1987 to 1996 on Sable Island, a vegetated sand bar off 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, newborn pups on the beach were captured by hand or with hoop nets as described in Bowen et al. (1992a). Sex was recorded for 1001 pups. When mothers of newborns were present, they were captured and weighed to the nearest 0.5 kg on a 200-kg scale suspended from a mobile all-terrain vehicle.

Mass of females was measured within 24 hours of parturition in 424 cases, and defined as “parturition mass.” The age of females was known in 251 females that had retained individually numbered tags from annual pup tagging programs conducted by the Department of Fisheries and Oceans beginning in 1978 (W. T. Stobo and W. D. Bowen, unpubl.). Both maternal age and parturition mass were known for 178 females.

At the oldest maternal ages, data were not available for both pup sexes, i.e., among 15-year-olds ($n = 6$) there were no male pups, and among 16-year-olds ($n = 1$) there were no female pups. For this reason, data on 14-, 15-, and 16-year-old females were combined into a 14+ age category.

Kolmogorov-Smirnov tests were used to test for differences in the distribution of variables. Logistic regression models were tested to predict pup sex based on maternal age alone, maternal mass alone, and maternal age and mass together. Pup sex was treated as a binomial response variable, with females coded as 0 and males as 1 (Arnbom et al. 1994). Predictor variables were treated as continuous. Data were analyzed using SPSS statistical software. Means are reported with standard errors (SE). The significance level

for all tests was $\alpha = 0.05$. Sex ratios are presented as percentage of males.

Results

The overall natal sex ratio was 468 males to 533 females, or 46.7% males. This was marginally different from equality ($\chi^2 = 4.2, p = 0.04$). Within years, however, the sex ratio did not differ significantly from equality (Table 4.1). The ratio was close to deviating from unity only in 1993, when there were 41.7% males (Table 4.1).

Mean parturition masses of mothers of male and female pups were 84.8 ± 0.55 kg ($n = 209$) and 85.0 ± 0.56 kg ($n = 215$), respectively, and were not significantly different (t -test, $p = 0.77, d.f. = 422$). There was no significant difference in the distributions of parturition mass by pup sex (Kolmogorov-Smirnov, $p = 0.77$).

To examine the influence of parturition mass on offspring sex, mass was divided into five 10-kg groups, ranging from 60-69 kg, to 100-109 kg. Sex ratio was not significantly different from equality in any mass category (Table 4.2). In a coarser categorization of females into large and small, based on the median mass of 84.9 kg, sex ratio did not differ from unity in either category (Table 4.2).

A logistic regression model predicting pup sex by maternal parturition mass was not significant ($\chi^2 = 0.08, n = 424, p = 0.77$), and correctly predicted only 51% of cases.

Table 4.1. Natal sex ratio of harbour seals on Sable Island, 1987 to 1996 ($n = 1001$).

Year	Male <i>n</i>	Female <i>n</i>	% males	Chi-square <i>p</i>
1987	32	26	55.2	0.43
1988	45	54	45.5	0.37
1989	45	54	45.5	0.37
1990	42	41	50.6	0.91
1991	48	50	49.0	0.84
1992	56	49	53.3	0.49
1993	58	81	41.7	0.05
1994	65	78	45.5	0.28
1995	54	65	45.4	0.31
1996	23	35	39.7	0.12
Overall	468	533	46.7	0.04*

* $p < 0.05$

Table 4.2. Natal sex ratio of harbour seals on Sable Island, 1987-1996, by parturition mass category ($n = 424$).

Parturition mass category (kg)	Male <i>n</i>	Female <i>n</i>	% males	Chi square <i>p</i>
60 - 69	4	8	33.3	0.25
70 - 79	55	50	52.4	0.63
80 - 89	96	95	50.3	0.94
90 - 99	48	55	46.6	0.49
100 - 109	6	7	46.2	0.78
Small (≤ 84.9 kg)	108	106	50.5	0.89
Large (≥ 85.0 kg)	101	109	48.1	0.58
All females of known mass	209	215	49.3	0.77

The predicted values for pup sex at each mass ranged between 0.47 and 0.51. Since predicted values from a logistic model can be interpreted as probabilities (Wright 1995), at any mass a mother had an approximately equal chance of having a pup of either sex. Contrary to theory, the prediction of this logistic model was for smaller mothers to have male pups, and larger mothers to have female pups, but the model was not significant, and the prediction clearly did not properly represent the data (Figure 4.1).

Age of mothers of male and female pups averaged 8.4 ± 0.50 ($n = 121$) and 9.0 ± 0.26 yr ($n = 130$), respectively. These did not differ significantly ($p = 0.09$, $d.f. = 249$). There was also no significant difference in the distribution of maternal age by pup sex (Kolmogorov-Smirnov, $p = 0.46$).

To investigate the influence of maternal age on offspring sex, I examined sex ratio at each maternal age, and by the three maternal age classes examined elsewhere in this thesis (young, 4-6 yr; intermediate, 7-10; and older 11-14+ yr). Sex ratio did not vary by maternal age, or age class (Table 4.3). In addition, a logistic regression model was tested to predict pup sex based on maternal age. The model was not significant ($\chi^2 = 2.9$, $n = 251$, $p = 0.09$). It correctly predicted only 54% of the cases. Contrary to theory, the prediction of this logistic model was for younger mothers to have male pups, and older mothers to have females; however the model was not significant, and the prediction did not properly represent the data.

To examine the simultaneous effects of maternal age and mass on pup sex, a logistic model was tested using both variables as predictors. The predictive strength of this model with two variables was better than the previous models with only one variable however, it was still not significant ($\chi^2 = 3.0$, $n = 178$, $p = 0.22$).

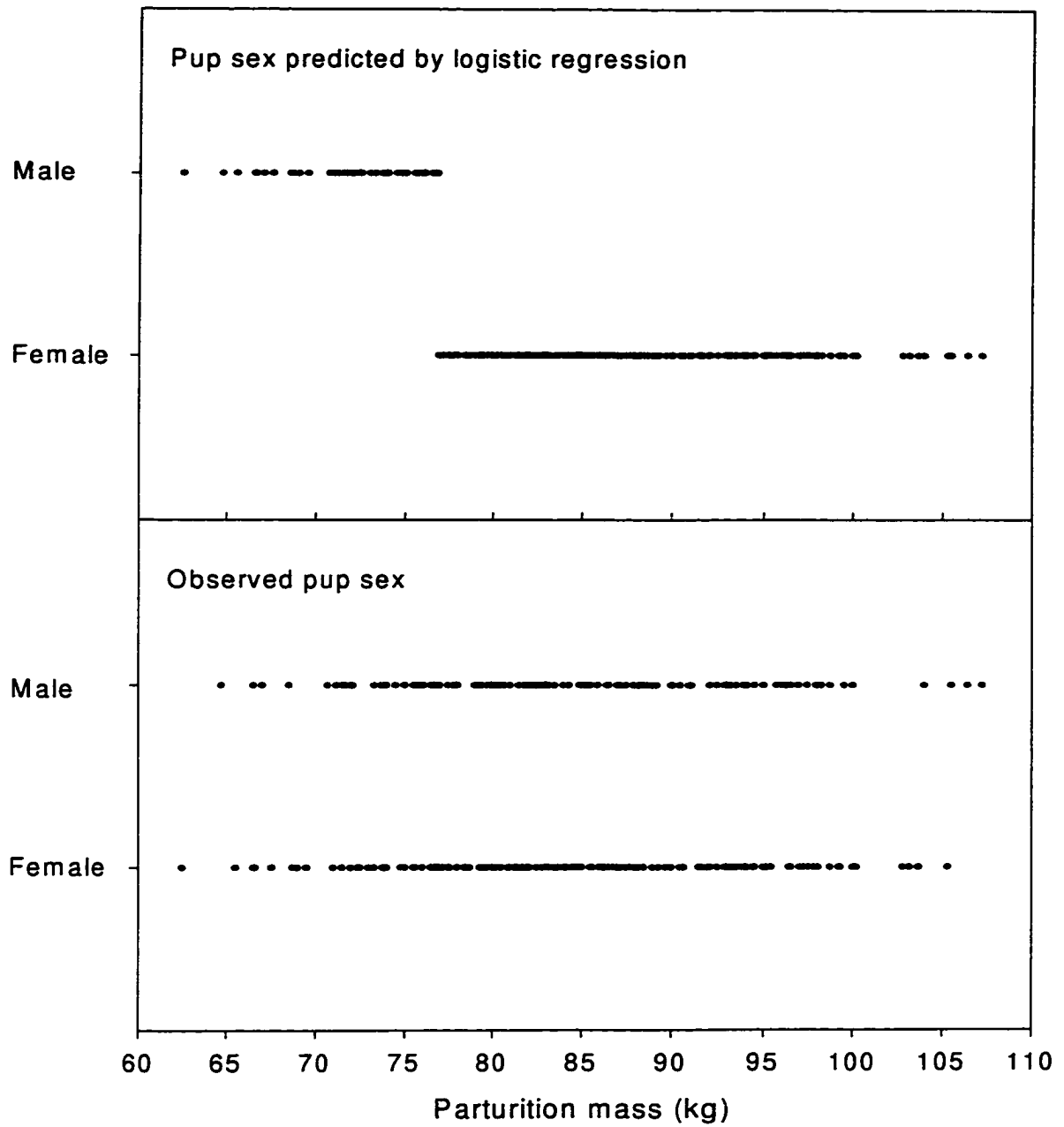


Figure 4.1. A comparison of pup sex as predicted by logistic regression versus observed data with respect to maternal parturition mass. The logistic regression was not statistically significant.

Table 4.3. Natal sex ratio of harbour seals on Sable Island, 1987-1996, by maternal age and maternal age class ($n = 251$).

Maternal age (yr)	Male (n)	Female (n)	% males	Chi-square p
4	6	4	60.0	0.53
5	10	16	38.5	0.24
6	16	12	57.1	0.45
7	19	13	59.4	0.29
8	17	14	54.8	0.59
9	11	13	45.8	0.68
10	15	16	48.4	0.86
11	9	10	47.4	0.82
12	7	13	35.0	0.18
13	7	8	46.7	0.80
14 ⁺	4	11	26.7	0.07
Young (4 - 6)	32	32	50.0	1.00
Intermediate (7 - 10)	62	56	52.5	0.58
Older (11 - 14+)	27	42	39.1	0.07
All known-age females	121	130	48.2	0.57

Discussion

Trivers and Willard (1973) predicted that even though certain conditions could theoretically lead to deviations from a 50:50 sex ratio, these deviations should tend to cancel out in the population. The sex ratios of equality in harbour seals each year are consistent with this prediction. Sex ratio theory also predicts that females should bias offspring sex according to their ability to invest in that offspring. Contrary to theory, none of these trends were seen in harbour seals.

Young females were no more likely to produce female pups than were older females, which on average had more energy to invest in offspring due to greater parturition mass (Chapter 3). Sex ratio did not deviate from unity at any maternal age or within any maternal age class, and age was not a significant predictor of pup sex in logistic regression. Similar results were found in northern elephant seals, where sex ratio did not differ from unity for young or old females (Le Boeuf et al. 1989), and in southern elephant seals where age was not a significant variable in a logistic regression on pup sex (Arnbom et al. 1994). It appears that maternal age does not significantly affect pup sex in the phocid seals studied to date.

Similarly, light harbour seal females were no more likely to produce female pups than were heavy females. Sex ratio did not vary within any parturition mass category, and maternal mass was not a significant predictor of pup sex in logistic regression. This latter result is contrary to findings on southern elephant seals, in which females below a threshold mass of 380 kg gave birth exclusively to female pups (Arnbom et al. 1994). This difference may be due to the greater sexual dimorphism in elephant seals and the relatively greater advantage that male size may confer on mating success in southern

elephant seals compared with the aquatically mating harbour seals. Alternatively, the elephant seal findings may be a statistical artifact of small sample size, as only 9 females below the suggested threshold were studied. Work on the closely related and highly sexually dimorphic northern elephant seal showed no relationship between birth sex ratio and parturition mass (Reiter et al. 1981; Le Boeuf et al. 1989). While there was a tendency for larger female grey seals, *Halichoerus grypus*, to produce more sons, this was not significant (Anderson and Fedak 1987). Thus, results of the present study support the more common finding that parturition mass does not affect sex ratio in phocid seals.

In otariid seals, males are usually heavier at birth and tend to grow slightly faster than females (Trillmich 1996). Adult males are polygynous, and are substantially larger than females (Boness et al. 1993). Male body size has not yet been proven to be important to reproductive success in otariids due to inherent measurement difficulties (Ono and Boness 1996), however size is believed to influence fighting ability and fasting duration during the mating season (Boyd and Duck 1991). There is reason, therefore, to expect differences in sex ratio according to maternal age and condition in otariids as well. There is some indirect evidence for a relationship between maternal condition and pup sex in California sea lions, *Zalophus californianus*. The proportion of male pups declined during the 1982-1983 El Niño, when female condition was assumed to decrease due to reduced prey availability (Ono and Boness 1991). Otherwise, evidence in otariids does not support the theory of adaptive sex ratios. In a study of 7,000 fetuses of northern fur seals over 16 years, there was no difference in sex ratio for females of different ages or between primiparous and multiparous females (Trites 1991). Similarly, there was no significant relationship between maternal size and pup sex in California sea lions (Ono

and Boness 1996), or maternal mass and pup sex in northern fur seals (Macy 1982, cited in Ono 1997) and Antarctic fur seals, *Arctocephalus gazella* (Costa et al. 1988).

In other mammals, most data do not reveal female biased-sex ratios for small or young mothers (Clutton-Brock and Iason 1986). For example, in red deer (*Cervus elaphus*), although there was evidence for higher allocation of body reserves to male offspring, sex ratios did not differ significantly between mothers of different ages; between hinds that were barren the previous year and those that had successfully raised a calf; or between females occupying habitats of different quality (Clutton-Brock et al. 1981). In a more recent study, Reimers and Lenvik (1997) examined the sex of fetuses in a large sample of semi-domestic reindeer, *Rangifer tarandus* ($n = 1,525$). There was no significant difference in maternal mass between mothers of male versus female fetuses. In addition, sex ratio was not different from equality overall (50.0% males), or within three age classes. The authors also fitted a logistic regression model with fetal sex as the binomial response variable and maternal mass, maternal age, and mass-by-age interactions as predictor terms. As with my logistic regression models on pup sex of harbour seals, their model was not significant.

Why might harbour seals and other pinnipeds not conform to the theory of adaptive sex ratios? It is important to note that theory of Trivers and Willard (1973) is based on three basic assumptions, each of which must be examined. The first assumption is that the condition of offspring at the end of the period of parental investment is correlated with condition of the mother during parental investment. This appears to be true for harbour seals, as parturition mass was positively correlated with weaning mass (Chapter 5).

The second assumption is that differences in condition at the end of parental investment endure into adulthood. This is uncertain for pinnipeds. There is no evidence that birth mass or weaning mass of phocids are related to adult body size (McCann et al. 1989). Most of the growth leading to sexual dimorphism in pinnipeds occurs long after weaning, with male growth spurts occurring near sexual maturity (McLaren 1993). In ungulates, Reimers and Lenvik (1997) point out that female weaning mass explains only 10% of the variation in adult body mass since heavy calves are likely to breed earlier and subsequently weigh less as adults.

The third assumption is that slight advantages in body size or condition are relatively more beneficial to male reproductive success than to female reproductive success. Male reproductive success is more variable than female success in pinnipeds (Le Boeuf and Reiter 1988; Boness et al. 1993), however, the relative importance of body size to reproductive success of males and females is not clear. Although reproductively successful males tend to be large, size is just one of several variables determining success in male elephant seals (Le Boeuf and Reiter 1988; Deutsch et al. 1994) and male harbour seals (Coltman et al. in press (a)).

Thus, there are insufficient data to determine whether two of the three assumptions of adaptive sex ratio theory apply to pinnipeds. If future studies show that the assumptions do not apply to phocids, then unbiased sex ratios cannot be considered as evidence against the theory of Trivers and Willard (1973). On the other hand, if all three assumptions apply, it will be possible to reject the theory for pinnipeds. Present evidence indicates that sex ratio does not vary with maternal age or mass in phocid or otariid seals.

Summary

Sexual selection theory predicts that in sexually dimorphic and polygynous species, females in good condition should invest more in male offspring. One way this can be accomplished is for older or larger mothers to vary the sex ratio towards males (Trivers and Willard 1973). In harbour seals, there was no evidence for deviations in sex ratio by maternal age or parturition mass, and this is in agreement with most evidence for phocid and otariid seals. Data on pinniped sex ratios that do not support the theory of Trivers and Willard (1973) cannot, however, be considered as negative evidence until it is known whether pinnipeds meet the assumptions of the theory.

CHAPTER 5

MATERNAL EFFECTS ON OFFSPRING TRAITS OF HARBOUR SEALS DURING LACTATION

Introduction

Offspring phenotype can be influenced directly by maternal phenotype, independently of genotype (Bernardo 1996). Such influences are known as maternal effects (Arnold 1994). Maternal effects can be behavioural or physiological, and may vary with maternal age (Forslund and Part 1995; Bernardo 1996). Maternal effects operate only during the period of maternal care. In mammals, this period usually consists of three phases: gestation, lactation, and post-weaning care. In pinnipeds, however, maternal care ceases at weaning (Bonner 1984), limiting the influence of maternal effects to gestation and lactation. This makes studies of maternal effects simpler in pinnipeds than other mammals.

Mammals produce energy-rich milk to provision offspring, making lactation the most expensive period of maternal energy investment (Millar 1977; Oftedal 1985). During lactation, females may either fast or forage. Until recently it was thought that pinniped strategies of maternal care were determined by phylogeny, with the family Phocidae fasting throughout lactation, and the Otariidae foraging during lactation (Bonner 1984; Costa 1991). While it is true that all otariids forage during lactation, recent evidence has shown that some small-bodied phocid species forage during lactation as well (Hammill et al. 1991; Lydersen and Kovacs 1993; Boness et al. 1994).

Harbour seals, *Phoca vitulina*, are phocids that forage during lactation (Bowen et al. 1992a; Boness et al. 1994). Lactation lasts approximately 24 days (Muelbert and Bowen 1993), a typical duration for phocids (Boness and Bowen 1996). In contrast, lactation lasts dramatically longer in otariids, ranging from 117-540 days (Table 1, Boness and Bowen 1996). The foraging cycle of harbour seals is, therefore, a strategy of maternal care that is intermediate between otariids and most phocids (Boness et al. 1994; Boness and Bowen 1996).

For species that fast throughout lactation, the energy a female can invest in offspring will be limited by her energy reserves at parturition (Iverson et al. 1993; Deutsch et al. 1994). In contrast, in species that forage during lactation, females supplement initial energy stores, and thus can invest additional energy towards offspring nourishment. The proportion of supplemental energy obtained will be determined mainly by the time spent foraging, and by foraging ability or efficiency.

Foraging species fast before beginning to forage (Bonner 1984), and maternal mass and age may affect foraging efficiency and timing. Mass at parturition can dictate when foraging begins, with smaller females beginning to forage sooner, due to earlier exhaustion of initial energy stores (Thompson et al. 1994; Bowen et al. in prep.). Foraging efficiency might also be affected by maternal size and mass through morphological constraints (e.g., dive duration). Maternal age is likely to influence foraging efficiency through learning (DesRochers 1992). In general, age is more strongly correlated with pups traits at younger ages than at older ages because young females and their offspring can benefit most from increasing maternal experience (Curio 1983;

Forslund and Larsson 1992; Sydeman and Nur 1994). Both maternal age and parturition mass are, thus, expected to affect energy intake of foraging females. Energy intake in turn will affect life-history traits of offspring during lactation.

Weaning mass and growth rate during lactation are important offspring traits, as they are correlated with probability of survival of young mammals (Clutton-Brock et al. 1982). In pinnipeds, pups fast for a period after weaning, and lose mass before they begin to forage independently (Worthy and Lavigne 1987; Arnbohm et al. 1993; Muelbert and Bowen 1993). Thus, weaning mass may be critical in providing sufficient stores for survival to nutritional independence. Low rates of mass gain by pups during lactation tend to be associated with reduced survival in red deer, *Cervus elaphus* (Clutton-Brock et al. 1982) and grey seals, *Halichoerus grypus* (Coulson and Hickling 1964).

In pinnipeds, there is evidence that maternal mass and age affect pup traits. Weaning mass varies with maternal mass at parturition both within species (Arnbohm et al. 1993; Iverson et al. 1993) and among (Lee et al. 1991) species. Weaning mass also varies with maternal age in northern elephant seals, *Mirounga angustirostris* (Reiter et al. 1981). Rate of pup mass gain is related to parturition mass in pinnipeds, including grey seals (Anderson and Fedak 1987; Iverson et al. 1993) and southern elephant seals, *Mirounga leonina* (McCann et al. 1989).

In phocid species that fast throughout lactation, there is a strong relationship between maternal parturition mass and pup weaning mass, since maternal energy reserves at parturition must support lactation (Arnbohm et al. 1993; Iverson et al. 1993; Deutsch et al. 1994). A weaker relationship is expected in species that feed during lactation, since

small females can supplement their energy reserves (Iverson et al. 1993). Other sources of variability associated with the lactational foraging cycle might include variation in local food supply, age- and size-related differences in foraging efficiency, and activity levels of females and pups.

The small body mass of harbour seals compared with other phocids is thought to be critical in the evolution of their foraging cycle, due to a limited ability to store reserves throughout lactation (Boness et al. 1994). On average, maternal body mass at parturition is around 85 kg (Chapter 3; Bowen et al. 1994); this is slightly larger than most otariids, and small for a phocid (Boness et al. 1994). Maternal foraging during lactation appears to occur in two other small-bodied phocids: ringed seals, *Phoca hispida*, and harp seals, *Phoca groenlandica* (Hammill et al. 1991; Lydersen and Kovacs 1993).

Within harbour seals, body mass may also influence maternal foraging behaviour. Harbour seals and other pinnipeds exhibit indeterminate growth, i.e., they continue to grow after sexual maturity. When this occurs, life-history theory predicts trade-offs between growth and reproduction (Gadgil and Bossert 1970; Roff 1992). Female harbour seals first give birth between 4 and 6 years of age, but continue to grow until about 10 (Boulva and McLaren 1979; Markussen et al. 1989). On average, young females (4-6 years old) weigh only 76 kg at parturition, whereas intermediate (7-10 yrs) and older (11-14+) females weigh 84 and 90 kg, respectively (Chapter 3). Percentage of body fat is similar among post-parturient harbour seal females (approximately 30% fat), independently of body mass (Bowen et al. in prep.). Thus, not only will absolute energy stores be smaller for young females, but trade-offs involving growth and reproduction

should be greater.

Several other points suggest that small females will be more energetically limited than large females. As maintenance metabolism scales allometrically with mass ($M^{0.75}$), smaller females will have a greater mass-specific metabolism (Costa 1991). Therefore, small females will have a smaller proportion of energy to devote to offspring. Together with the theory of trade-off between growth and reproduction, these points suggest that older, larger females should be able to invest relatively more in offspring during lactation.

To sum up, I predicted that relationships between maternal effects and pups traits during lactation will differ between pinniped species relative to strategies of maternal care. For example, effects of parturition mass and maternal mass loss on pup growth and weaning mass should be weaker in harbour seals than among phocid species that fast throughout lactation. After controlling for size, growth rates of harbour seal pups should be lower than for pups of fasting phocids, since harbour seal pups are more active than most phocid pups and experience intermittent fasting periods. Within harbour seals, I expected relationships between maternal mass loss and pup mass gain to be stronger for large females than small females part way through lactation, as small females should begin supplementing their energy stores sooner than large females. I expected to see effects of maternal age on pup traits (after controlling for parturition mass), due to the predicted trade-offs between growth and reproduction. I also expected age-related differences in pup traits due changes in maternal physiology and increased foraging efficiency, although I will be unable to address such physiological or behavioural aspects directly.

I examined the maternal life-history traits of age and parturition mass, as well as lactation duration and pupping date. I looked at their effects on pup traits during lactation, specifically weaning mass and rate of mass gain. I compared patterns found in harbour seals with other pinnipeds and related these to their intermediate strategy of maternal care. To examine relative effects of age and mass on offspring traits within harbour seals, I compared maternal mass classes and age classes. In addition, I examined patterns of reproductive investment in female harbour seals as examples of large, iteroparous mammals that continue to grow after maturity. The effects of maternal traits on newborns were examined in Chapter 3, but here I used path analysis to model the causal relationships among maternal traits and pup traits from birth through lactation and weaning. Sex differences in pup traits during lactation were also examined, with respect to theory on differential investment (Trivers and Willard 1973).

Methods

Data collection

Data on parturient female harbour seals and pups were collected in May and June from 1988 to 1996 on Sable Island, a vegetated sand bar off 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. Females and pups were studied at three stages in the cycle of maternal care: birth, mid lactation, and weaning.

Newborn harbour seals were sexed, weighed and then tagged in the webbing of the hind flipper with individually numbered Rototags (Chapter 3; Bowen et al. 1994).

When mothers of newborns were present, they were captured, weighed, and tagged (Chapter 3; Bowen et al. 1992a). To facilitate recognition of individuals from a distance, mother-pup pairs were marked on their backs with identical symbols using a fast-drying fluorescent paint (V-285, Lenmar Inc., Baltimore MD). Maternal age was known in cases where the female was first tagged as a pup and the tag was retained until the time of recapture. Pup tagging first began in 1978 by the Department of Fisheries and Oceans (W. T. Stobo and W. D. Bowen, unpublished), and continued throughout this study.

To study pup mass gain and maternal mass loss during mid lactation, a subset of mother-pup pairs was weighed around 15 days post-partum (dpp), or two-thirds of the way through the 24-day lactation period (Muelbert and Bowen 1993). To determine mass at weaning and mass change over the duration of lactation, another subset of females and pups was weighed near weaning. The occurrence of weaning was usually determined by one or more criteria: clear pup serum, no milk in the pup's stomach, absence of the female for more than 2 days, and loss of pup mass (Muelbert and Bowen 1993). Although pups were captured just prior to, and after, weaning it was seldom possible to capture females after they had weaned their pups. Pups were weighed to the nearest 0.1 kg, with a 50-kg spring-balance scale, and females to the nearest 0.5 kg using a 200-kg spring-balance scale.

Statistical techniques

Data from all years were pooled. Pupping dates and weaning dates were converted to day of year, taking into account the leap years 1988, 1992, and 1996. Only birth masses and parturition masses recorded within 24 hours of birth were used. Body

masses taken on the day after birth were extrapolated to birth and parturition masses, by subtracting the daily mass gain of 0.5 kg for pups, and adding a daily mass loss of 1.7 kg for females (Bowen et al. 1994; Chapter 3).

To study body mass and rate of mass change during mid lactation only data on females and pups weighed between 14 and 17 days post-partum were analyzed. Rate of pup mass gain and maternal mass loss rate were calculated as change in body mass, divided by the number of days post-partum (i.e., 14 to 17 d). To make comparisons of body mass in mid lactation meaningful, masses were extrapolated to 15-day masses using each pup's mid-lactation rate of mass gain, and each female's mid-lactation rate of mass loss. During lactation, phocids pups mainly gain mass in the form of fat (Bowen et al. 1985; Oftedal et al. 1993) rather than from growth of skeletal structure and musculature (Oftedal et al. 1987). Thus, I refer to rates of change in pup mass simply as "rate of mass gain" rather than "growth rate."

Only pups and females weighed within 4 days of weaning, and with lactation duration greater than 17 days, 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 (S.D.) days ($n = 52$; Muelbert and Bowen 1993). I defined premature weaning as any lactation duration less than this mean minus 2 standard deviations, and thus less than 18 days. Pups "weaned" before the 50th percentile of lactation duration, i.e., 12 days, were considered abandoned, rather than prematurely weaned, and were excluded from all analyses.

Body mass of pups just prior to weaning was extrapolated to pup weaning mass by

adding a daily mass gain of 0.5 kg/d. This late-lactation rate of pup mass gain was estimated from a subsample of 40 pups weighed just before weaning and again on the day of weaning. Pup mass just after weaning was extrapolated backward by adding 0.4 kg/day to account for post-weaning mass loss shortly after weaning (M. Muelbert, pers. comm.). Maternal mass just before the end of lactation was corrected to the day of weaning by subtracting 1.1 kg/d. This correction was determined from a subsample of 27 females for which there were two mass measurements in late lactation. Rates of pup mass gain and maternal mass loss during lactation were estimated linearly by dividing the change in body mass by lactation duration.

To meet the assumption of linearity required for regression analyses, ANOVA, and ANCOVA, data were transformed as necessary. Age and log age were treated as continuous variables in ANCOVAs and regressions. For categorical analyses of age, females were grouped into three age classes (4-6, 7-10, and 11-14+ yr) representing increasing levels of reproductive experience (Chapter 3). For categorical analyses of maternal mass, females were grouped into large and small mass classes, based on the median parturition mass of 85.0 kg (Chapter 3).

Path analyses were conducted to explore possible causal pathways between maternal effects and pup traits, and to determine the relative strengths of relationships. 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 uni directional 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). If a path coefficient was not significantly different from zero, the model was trimmed by removing the path, and the multiple regression was run again to re-estimate the parameters (Klem 1995). For each model, a subset of data was used, such 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 (Mitchell 1992; Dobson and Michener 1995). The amount of unexplained variation for 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 a thick arrow (Klem 1995).

Statistical analyses were performed using SPSS statistical software. Means are reported plus or minus one standard error (SE), and correlation coefficients are Pearson's r . The significance level for all tests was $\alpha = 0.05$. One outlier was removed from statistical analyses since maternal mass loss rate was greater than the mean by more than 3 standard deviations.

Results

Lactation duration and weaning date

Duration of lactation ranged from 13 to 31 days ($n = 196$). Twenty-three pups were weaned prematurely (i.e., between 12 and 18 days). The mean weaning mass of prematurely weaned pups was significantly lower than for successfully weaned pups (19.9 ± 0.7 , $n = 20$ versus $24.8 \text{ kg} \pm 0.3$, $n = 154$; t -test, $p < 0.001$; Figure 5.1). 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, $n = 100$; $p = 0.03$, $d.f. = 108$). There was no significant difference between the two groups in mean maternal age ($p = 0.42$, $d.f. = 78$), mean pupping date ($p = 0.45$, $d.f. = 196$), or mean birth mass ($p = 0.52$, $d.f. = 129$). Because of the strong differences in weaning masses of prematurely weaned pups, these pups were removed from the data set for all other analyses.

Among successfully weaned pups, lactation ranged from 18 to 31 days, with a mean of 23.9 ± 0.2 days ($n = 175$). Weaning dates ranged over 29 days, from June 3 to July 1 (mean, June 18 ± 0.4 d). Weaning date was correlated with pupping date (Figure 5.2). The standard deviations of pupping and weaning date were 4.8 and 5.4 days, respectively.

Lactation duration was positively correlated with weaning mass ($r = 0.29$, $n = 154$, $p < 0.001$) and weaning date ($r = 0.487$, $n = 116$, $p < 0.001$). Duration was negatively correlated with maternal age and rate of pup mass gain (Figure 5.3). In each case, however, these correlations explained relatively little of the variation in duration. There was no significant correlation between pupping date and lactation duration ($r = -0.14$, $n = 175$, $p = 0.06$). Lactation duration was not significantly correlated with parturition mass ($r = -0.07$, $n = 101$, $p = 0.48$), nor was it correlated with log birth mass, after controlling for the effects of log maternal age on lactation duration (partial $r = -0.05$, $n = 49$, $p = 0.74$). Lactation duration tended to decrease by age class, but did not differ significantly (Table 5.1); young females had a mean lactation duration of 25.3 days, whereas intermediate and older females averaged 24.5 and 23.1 days, respectively.

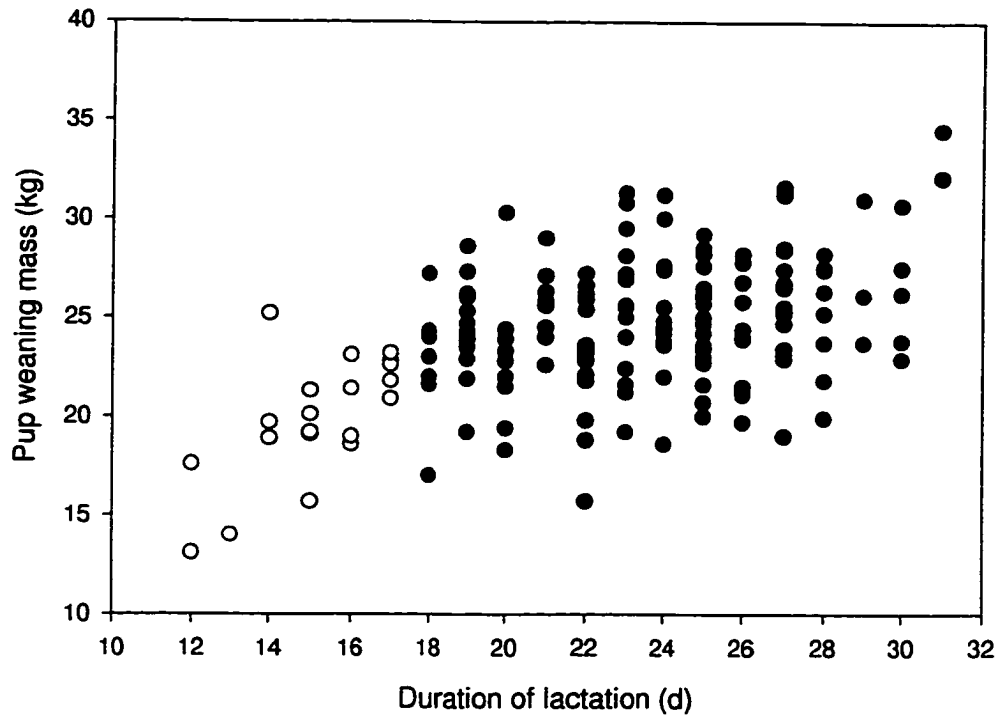


Figure 5.1. Weaning mass of prematurely weaned (open circles; $n = 21$) and successfully weaned (closed circles; $n = 154$) harbour seal pups on Sable Island, 1988-1996.

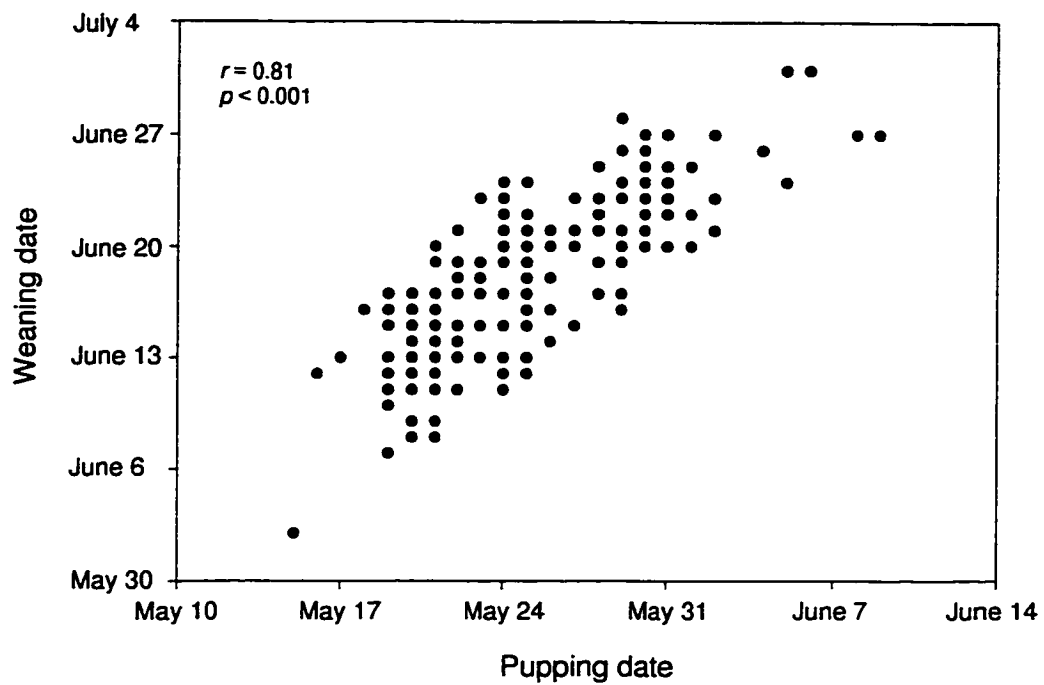


Figure 5.2. Weaning dates and pupping dates of harbour seal pups on Sable Island, 1988-1996 ($n = 175$).

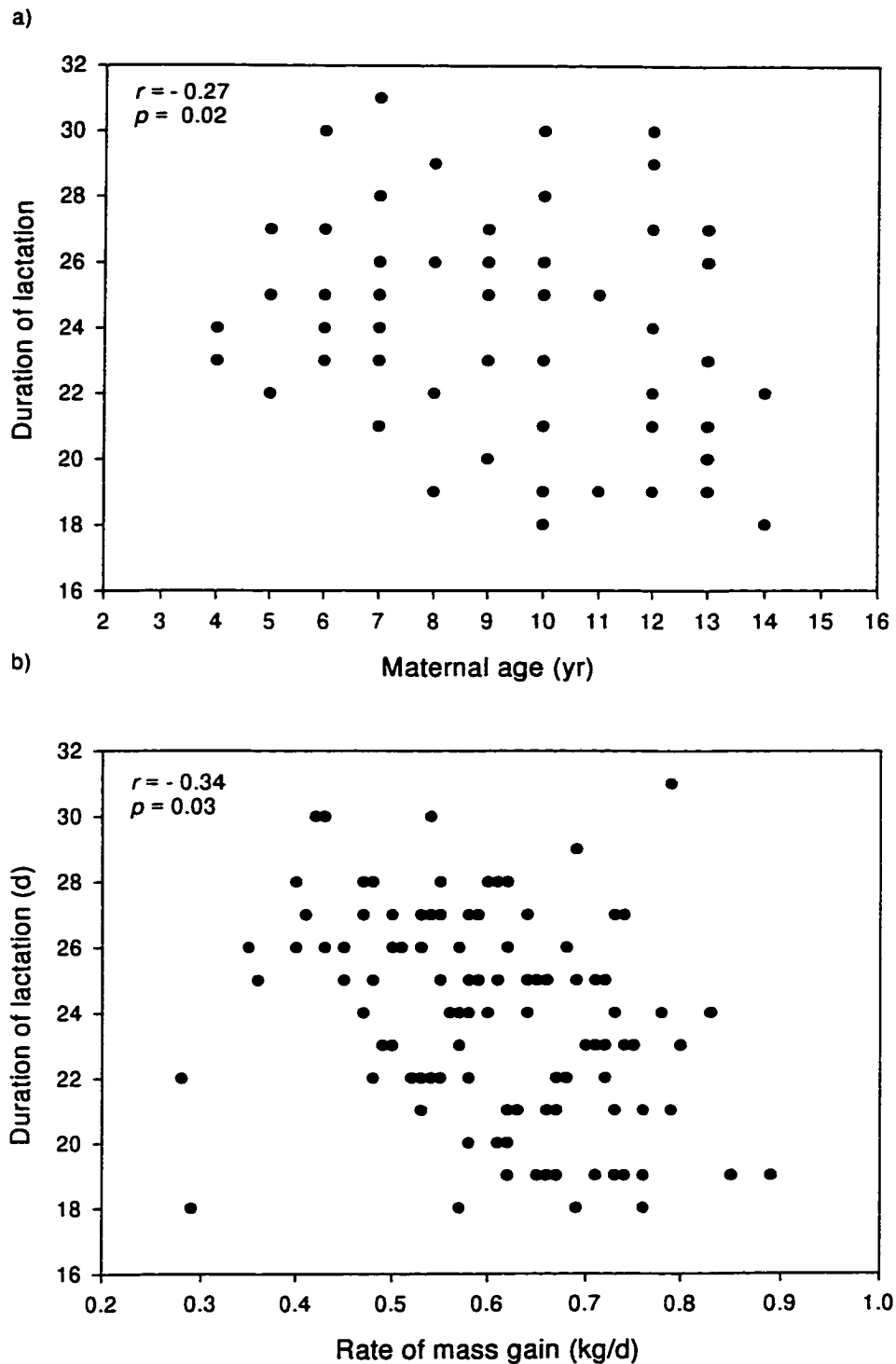


Figure 5.3. Duration of lactation of harbour seals in relation to a) maternal age ($n = 74$) and b) the rate of mass gain in pups ($n = 116$).

Table 5.1. Life history traits of harbour seal females and pups on Sable Island, overall and by maternal age class and mass class (sample size in parentheses; degrees of freedom in square brackets).

Variable	All females	Maternal age class			Maternal mass class		p	t-test
		Young (4 - 6 yr)	Intermediate (7 - 10 yr)	Older (11 - 14+ yr)	Small (≤ 85.0 kg)	Large (> 85.0 kg)		
Pup								
Birth mass ¹ (kg)	10.9 ± 0.06 (375)	9.3 ± 0.25 (30)	11.0 ± 0.16 (27)	11.7 ± 0.16 (24)	10.6 ± 0.12 (127)	11.3 ± 0.08 (117)	<0.001 ² [2, 71]	<0.001 [242]
Mass at 15 days post-partum (kg)	21.9 ± 0.23 (191)	18.5 ± 0.82 (14)	22.8 ± 0.49 (39)	24.0 ± 0.46 (25)	21.2 ± 0.33 (85)	22.9 ± 0.34 (68)	0.002 ³ [2, 70]	<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)	24.0 ± 0.36 (64)	26.3 ± 0.45 (36)	0.665 ³ [2, 47]	<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)	13.4 ± 0.33 (64)	15.2 ± 0.38 (36)	0.185 ³ [2, 47]	0.001 [98]
Lactation duration (d)	23.9 ± 0.24 (175)	25.3 ± 0.46 (18)	24.5 ± 0.57 (36)	23.1 ± 0.77 (20)	23.9 ± 0.35 (64)	23.5 ± 0.59 (36)	0.083 [2, 71]	0.560 [98]
Rate of mass gain (kg/d)	0.60 ± 0.011 (116)	0.54 ± 0.023 (13)	0.57 ± 0.026 (22)	0.59 ± 0.029 (17)	0.57 ± 0.015 (64)	0.66 ± 0.17 (36)	0.957 ³ [2, 47]	<0.001 [98]
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)	2.3 ± 0.04 (64)	2.4 ± 0.034 (36)	0.099 ³ [2, 47]	0.057 [98]
Female								
Maternal mass at weaning (kg)	54.9 ± 1.04 (33)	46.7 ± 1.79 (4)	52.9 ± 1.93 (4)	60.4 ± 3.25 (2)	51.7 ± 1.10 (14)	58.6 ± 1.40 (14)	0.001 ³ [2, 4]	0.001 [26]
Maternal mass loss (kg)	30.8 ± 0.94 (28)	31.9 ± 0.26 (3)	23.9 ± 0.82 (3)	29.4 ± 0.00 (2)	27.7 ± 1.15 (14)	33.8 ± 0.96 (14)	0.001 ³ [2, 4]	<0.001 [26]
Rate of maternal mass loss (kg/d)	1.42 ± 0.038 (28)	1.21 ± 0.033 (3)	1.28 ± 0.068 (3)	1.55 ± 0.00 (2)	1.28 ± 0.041 (14)	1.56 ± 0.035 (14)	0.152 ³ [2, 4]	<0.001 [26]
Maternal weaning mass to part'n mass (%)	64.3 ± 0.77 (28)	60.1 ± 0.56 (3)	69.2 ± 0.99 (3)	67.2 ± 1.19 (2)	65.2 ± 1.11 (14)	63.4 ± 1.04 (14)	0.001 [2, 5]	0.256 [26]

¹ Data from Chapter 3 ² ANCOVA of log birth mass on age class, controlling for log parturition mass ³ ANCOVA controlling for parturition mass

Pup mass at mid lactation and weaning

At 15 days post-partum, pups weighed between 13.3 and 29.1 kg, with an average mass of 21.9 ± 0.2 kg ($n = 191$). These pups had doubled their mean birth mass of 10.9 ± 0.1 kg in 15 days.

Eighty-eight pups were weighed on the day of weaning. Weaning masses were extrapolated for 20 pups weighed prior to weaning, and for 46 pups weighed after weaning. There was no difference in mean weaning mass among these three groups (ANOVA, $F_{[2, 151]} = 0.88$, $p = 0.42$), thus masses were pooled. Weaning mass ranged from 15.7 to 34.5 kg, with a mean of 24.8 (Table 5.1). On average, pups gained 14.2 kg, and weaning mass was 2.3 times birth mass (Table 5.1).

By 15 days post-partum, pups had reached 84.7% of their mass at weaning ($n = 83$). Age affected this percentage significantly; pups of young females ($n = 6$) had reached a significantly lower proportion of weaning mass ($75.5 \pm 3.7\%$) than had pups of intermediate-aged ($n = 16$) and older females ($n = 15$) ($86.3 \pm 1.6\%$ and $89.8 \pm 1.6\%$, respectively) (ANOVA on arcsine-transformed data, $F_{[2, 33]} = 7.2$, $p = 0.003$). The two older age classes did not differ significantly from one another.

Weaning mass was significantly correlated with parturition mass, but not with maternal age (Figure 5.4). As a maternal effect, parturition mass explained only a small amount of the variation in weaning mass ($R^2 = 26.3\%$). Weaning mass was positively correlated with log birth mass, even after controlling for the effect of log parturition mass on log birth mass (partial $r = 0.36$, $n = 97$, $p < 0.001$). Weaning mass was weakly correlated with lactation duration (Figure 5.5a).

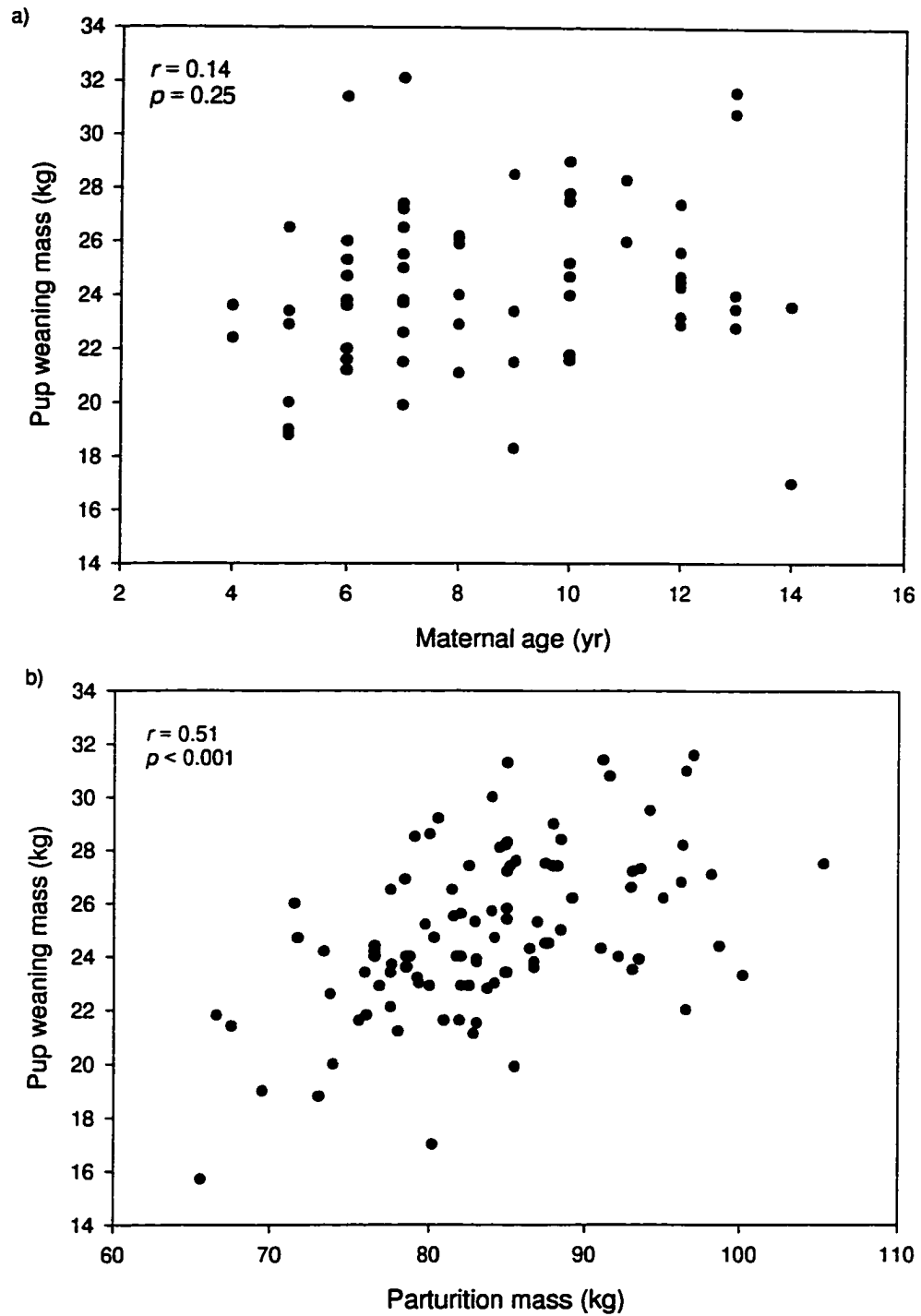


Figure 5.4. Weaning mass of harbour seal pups on Sable Island in relation to a) maternal age ($n = 65$), and b) parturition mass ($n = 100$).

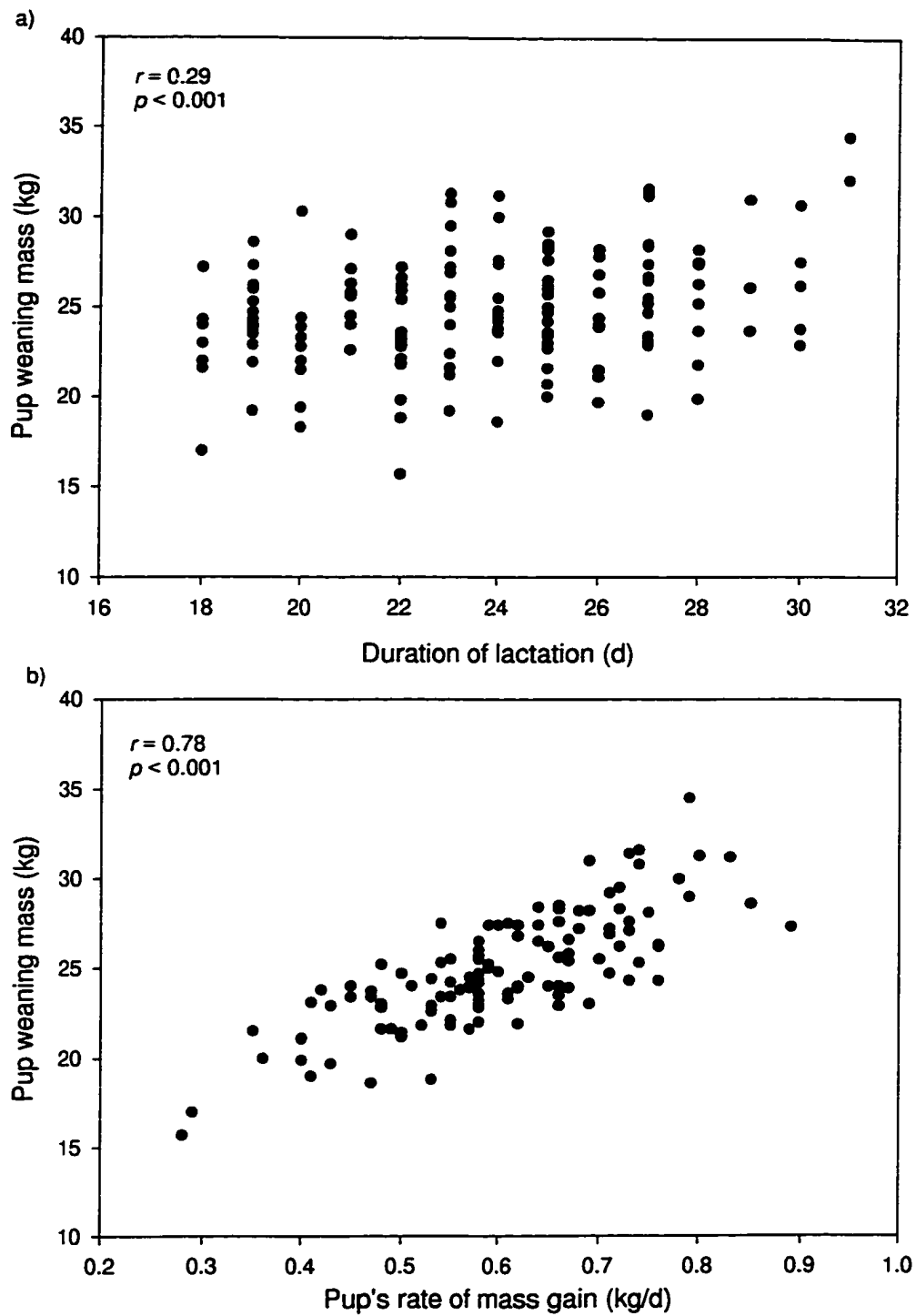


Figure 5.5. Weaning mass of harbour seal pups on Sable Island in relation to a) duration of lactation ($n = 154$), and b) rate of mass gain ($n = 116$).

Table 5.2. Rate of mass gain of harbour seal pups at mid lactation and over the entire lactation period, in relation to maternal age class and maternal mass class (sample size in parentheses; degrees of freedom in square brackets).

Maternal class	Mid lactation rate of mass gain (kg/d)	Overall rate of mass gain (kg/d)	<i>p</i> paired <i>t</i> -test
Age			
Young (4 - 6 yr)	0.56 ± 0.030 (14)	0.54 ± 0.023 (13)	0.735 [5]
Intermediate (7 - 10 yr)	0.74 ± 0.023 (39)	0.57 ± 0.026 (22)	< 0.001 [15]
Older (11-14+ yr)	0.78 ± 0.019 (25)	0.59 ± 0.029 (17)	< 0.001 [14]
ANCOVA <i>p</i> by age class [<i>d.f.</i>]	0.001 ¹ [2, 70]	0.957 ¹ [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>p</i> independent <i>t</i> -test by mass class [<i>d.f.</i>]	0.001 [151]	< 0.001 [98]	-
All females	0.69 ± 0.011 (191)	0.60 ± 0.011 (116)	< 0.001 [82]

¹ Controlling for parturition mass.

Rate of pup mass gain

At mid lactation the rate of mass gain of pups ranged from 0.25 to 1.07 kg/d, with a mean of 0.69 ± 0.011 kg/d ($n = 191$). The rate of mass gain was correlated with mass of females at parturition ($r = 0.32$, $n = 153$, $p < 0.001$). Pups of small females (i.e., below the median mass of 85.0 kg) gained mass at a slower rate than pups of large females (Table 5.2). Rate of mass gain in mid lactation was correlated with maternal age, even after controlling for parturition mass (partial $r = 0.37$, $n = 71$, $p = 0.001$). Rate of mass gain in mid lactation was significantly lower for pups of the youngest females than for pups of intermediate and older females (Table 5.2).

The sample size of mass gain over the entire lactation period was smaller than at mid lactation ($n = 116$ vs. 191). Over the entire lactation period, pups gained mass at a mean rate of 0.60 ± 0.011 kg/d, with a range from 0.26 to 0.89 kg/d. This overall rate of mass gain was strongly correlated with the mid-lactation rate of mass gain ($r = 0.72$, $n = 83$, $p < 0.001$). The overall rate of mass gain was, however, lower on average than mid-lactation rate of mass gain (0.60 versus 0.69 kg/d), suggesting that mass gain decelerated in late lactation (i.e., between 15 days post-partum and weaning). Maternal age appeared to influence this deceleration, since overall rates were equal to mid-lactation rates for pups of young females, but lower for pups of intermediate and older females (Table 5.2).

The overall rate of pup mass gain was strongly correlated with weaning mass (Figure 5.5b). This rate of mass gain was correlated significantly with maternal mass at parturition (Figure 5.6b). As seen in mid lactation, pups of small females gained mass at a significantly lower rate than pups of large females (Table 5.2). In contrast with mid

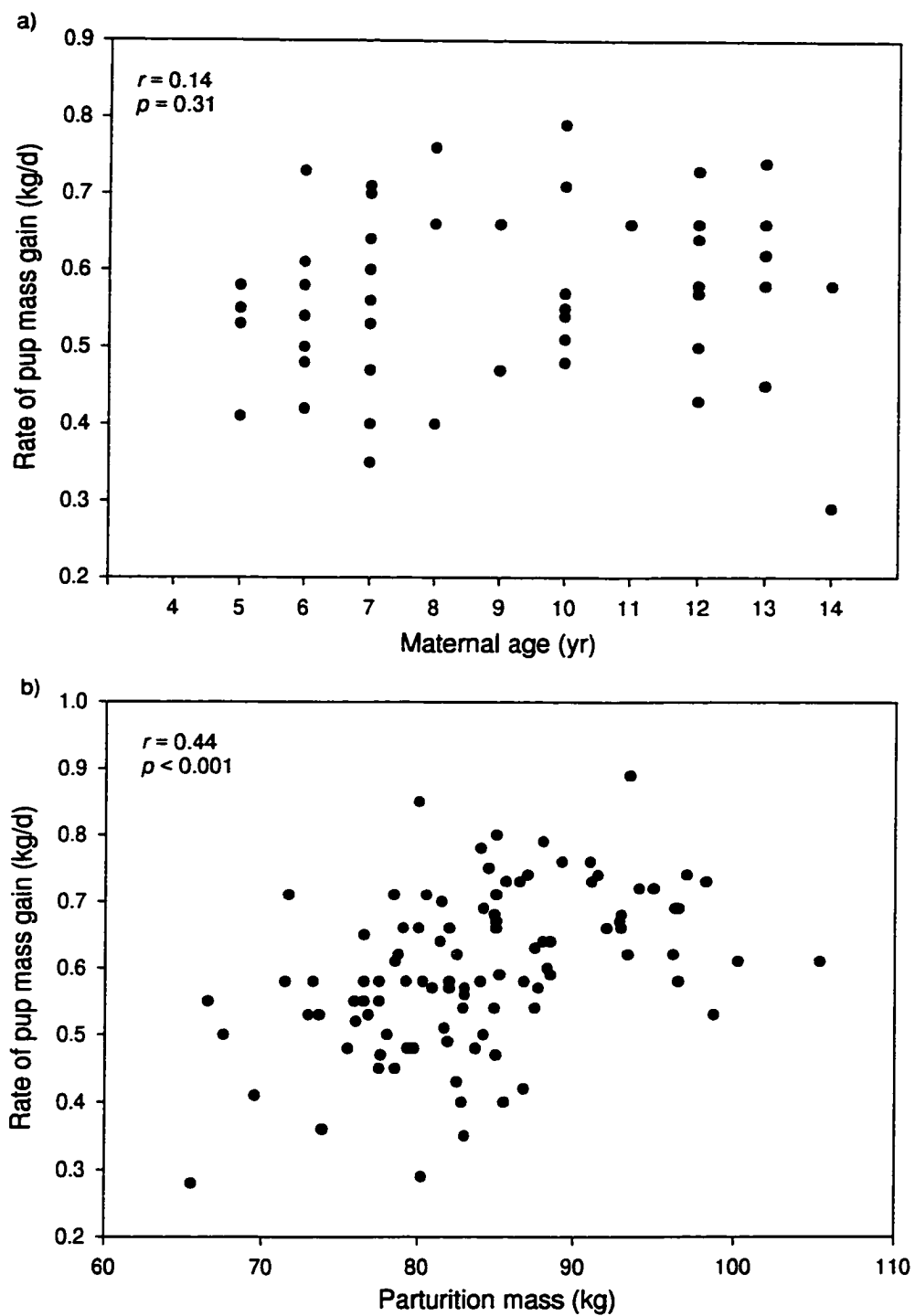


Figure 5.6. Rate of mass gain during lactation of harbour seal pups on Sable Island in relation to a) maternal age ($n = 52$), and b) parturition mass ($n = 100$).

lactation, however, at weaning there was no significant correlation between maternal age and rate of pup mass gain (Figure 5.6a). The overall rate of mass gain during lactation did not differ significantly by maternal age class (Table 5.2).

Maternal body mass and rate of mass loss

At 15 days post-partum, mean maternal mass was 62.2 ± 0.6 kg, and ranged from 47.1 to 77.7 kg ($n = 131$). The mean rate of female mass loss at mid lactation was 1.55 ± 0.02 kg/d ($n = 120$), and ranged from 0.73 to 2.00 kg/d. On average, at mid lactation females weighed 73% of parturition mass.

Maternal mass was measured on the day of weaning in only 4 cases. In another 28, females weighed less than 4 days prior to weaning, maternal mass at weaning was estimated by linear extrapolation. Maternal mass at weaning ranged from 42.4 to 68.0 kg, with a mean of 54.9 ± 1.03 ($n = 33$). Over the entire lactation period, females lost an average of 30.8 ± 0.94 kg ($n = 28$). Overall, females lost mass at a mean rate of 1.42 ± 0.038 kg/d ($n = 28$), ranging from 0.91 to 1.8 kg/d. (One female that lost 2.6 kg/d was an extreme outlier and was removed from all statistical analyses.) At weaning females averaged 64% of parturition mass.

Large females lost mass more quickly than small females (Table 5.1). Overall loss rate was strongly correlated with 15-day loss rate ($r = 0.84$, $n = 22$, $p < 0.001$). However, as with pup rate of mass gain, rates of maternal mass loss must have decelerated in late lactation since the mean overall loss rate (1.42 kg/d) was lower than the mean loss rate in mid lactation (1.55 kg/d) (paired t -test, $p = 0.001$, $d.f. = 21$). The overall rate of maternal mass loss accounted for 44.6% of the variation in the rate of pup

mass gain ($n = 28$, $p = <0.001$).

Initial maternal mass affected mass loss. By weaning, large females had lost more absolute mass than small females (33.8 versus 27.7 kg; Table 5.1). Relative to parturition mass, however, there was no significant difference in mass loss between the two mass classes (36.6% versus 34.8% for small and large females, $p = 0.26$). A similar pattern was seen in the larger sample size of female mass loss in mid lactation ($n = 120$). Large females lost significantly more mass by 15 days post-partum than small females (25.4 versus 21.9 kg; Table 5.1), but each group lost similar proportions of initial mass (27.6% versus 27.8% for small and large females; $p = 0.97$). At mid lactation, maternal mass loss was correlated with pup mass gain in larger females ($r = 0.32$, $n = 56$, $p = 0.017$), but not in small females ($r = 0.20$, $n = 64$, $p = 0.097$). At weaning, the correlation was stronger, and was significant for large and small mass classes ($r = 0.64$, $n = 14$, $p = 0.01$, and $r = 0.61$, $n = 14$, $p = 0.02$, respectively).

Maternal age affected maternal mass loss, even after controlling for parturition mass (Table 5.1). At weaning, young females had lost significantly more absolute and relative mass than females of intermediate or older ages (Table 5.1).

Mass transfer and energy investment during lactation

Maternal mass loss was positively correlated with pup mass gain by weaning (Figure 5.7). On average, females lost 30.8 ± 0.94 kg, and their pups gained 13.7 ± 0.53 kg ($n = 28$). The ratio of mass gain to mass loss (44.6%) can be considered as an index of mass transfer (Bowen et al. 1992a). Since most harbour seal females forage during lactation, the actual transfer efficiency must be less than this index. The mean index of

mass transfer did not differ significantly between large and small females (Table 5.3). Differences in the index of mass transfer were more pronounced by age class, however they did not differ significantly (Table 5.3). At mid lactation, the mean index of mass transfer was similar to that at weaning ($46.9 \pm 0.9\%$, $n = 119$), and did not differ by mass class (t -test $p = 0.10$), or age class (ANOVA $F_{[2, 66]} = 1.41$, $p = 0.25$).

Relative weaning mass (the ratio of pup weaning mass to female parturition mass) is an energetic measure of reproductive investment and is usually presented as a percentage (Bowen 1991). Relative weaning mass in harbour seals was 29.8%, and was greater for small than large females, but did not differ by age class (Table 5.3).

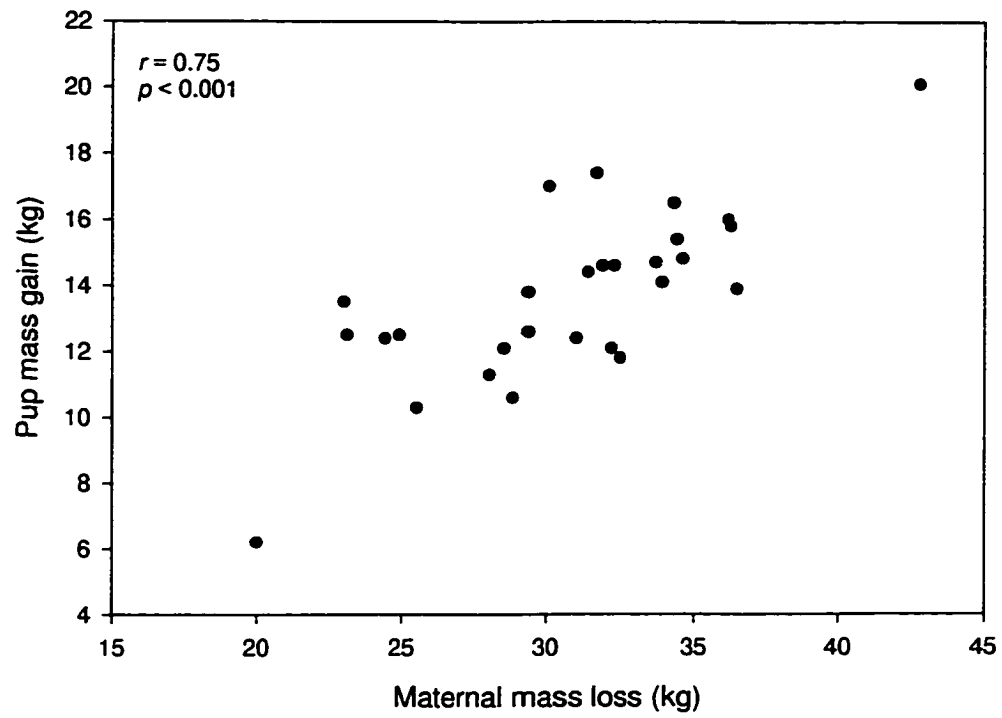


Figure 5.7. Mass gain during lactation of harbour seal pups in relation to maternal mass loss ($n = 28$).

Table 5.3. Comparative measures of pups and females, overall and by maternal age class and mass class (sample size in parentheses; degrees of freedom in square brackets).

Trait	All pairs	Maternal age class			ANOVA	P	Maternal mass class		P	t-test
		Young (4 - 6 yr)	Intermediate (7 - 10 yr)	Older (11-14+ yr)			Small (≤ 85.0 kg)	Large (> 85.0 kg)		
Pup/female comparisons										
Mass transfer index (%) (pup mass gain to maternal mass loss)	44.6 ± 1.22 (28)	45.6 ± 0.21 (3)	51.1 ± 5.50 (3)	44.9 ± 2.00 (2)	0.492 [2, 5]		44.4 ± 1.99 (14)	44.9 ± 1.48 (14)	0.829 [26]	
Relative weaning mass (%) (pup mass at weaning to parturition 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]	

Path analysis of maternal effects on pup traits

I formulated 2 path models to elucidate the inter-relationships between life-history traits of pups and females from birth through weaning. The first model included traits up to weaning, whereas the second concerned traits only to mid lactation . The weaning model is of most interest, since it encompasses the entire period of maternal investment. I developed the mid lactation model to explore the changes during lactation that were suggested in earlier analyses, and to take advantage of the larger sample size at mid lactation . For simplicity, I used the term “growth rate” instead of “rate of mass gain” in these models.

Weaning mass is related to birth mass, growth rate and lactation duration by the following equation.

$$\text{birth mass} + (\text{growth rate} \times \text{lactation duration}) = \text{weaning mass}$$

I constructed the path model such that each of these variables could have a direct effect on weaning mass (Figure 5.8a). Growth rate during lactation was hypothesized to affect lactation length, since a rapidly growing pup would be likely to be weaned in a shorter time. The maternal effects of age, parturition mass, and pupping date were hypothesized not to act directly on weaning mass, but indirectly through their effects on birth mass, growth rate, and lactation duration.

When the model was tested with the data ($n = 51$), seven paths were not significant, resulting in a simpler model containing 10 paths (Figure 5.8b). Pupping date had no significant effect on birth mass, lactation duration, or growth rate, and was dropped entirely from the model. Maternal age had no direct effect on growth rate, and parturition mass had

WEANING

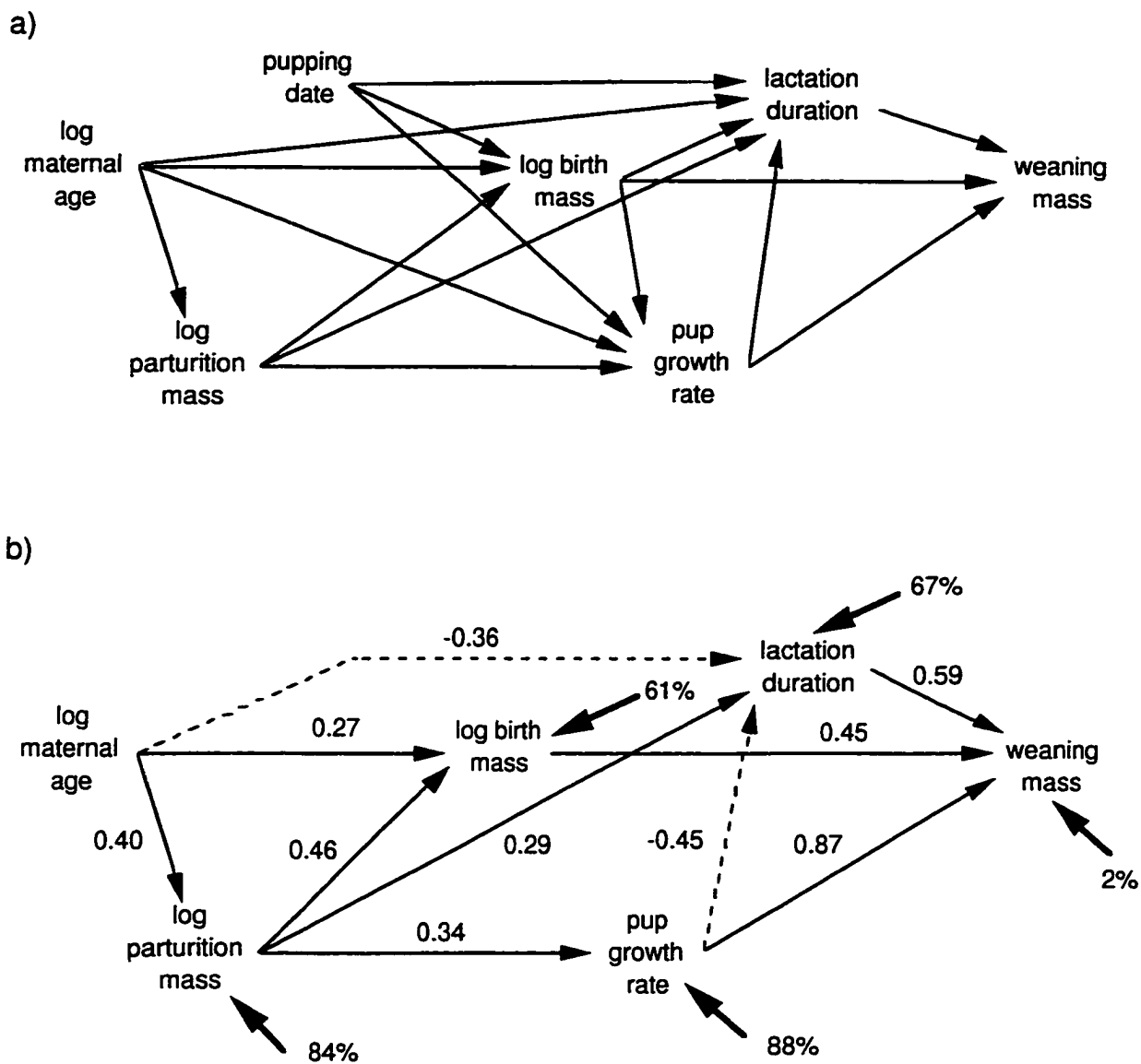


Figure 5.8. Path model linking traits of harbour seal mothers and pups during birth, lactation, and weaning: a) hypothesized full model, b) trimmed model. Solid lines represent positive paths, and dashed lines represent negative paths. Percentage of unexplained variance is linked to each dependent (endogenous) variable by a thick arrow ($n = 51$).

Table 5.4a. Correlation matrix for data used in path model on traits from birth through weaning (Figure 5.8b) ($n = 51$).

Variable	Log maternal age	Log parturition mass	Log birth mass	Growth rate	Lactation duration	Weaning mass
Log maternal age	-					
Log part'n mass	0.40**	-				
Log birth mass	0.46**	0.57**	-			
Growth rate	0.16	0.34*	-0.23	-		
Lactation duration	-0.32*	-0.01	-0.19	-0.41**	-	
Weaning mass	0.17	0.54**	0.54**	0.74**	0.15	-

* $p < 0.05$, ** $p < 0.01$

Table 5.4b. Effect strength¹ of variables in the path model on traits of harbour seal pups and females from birth to weaning (Figure 5.8b). (NS = not significantly different from zero.)

Dependent variable	Independent variable					
	Log maternal age	Log parturition mass	Log birth mass	Growth rate	Lactation duration	Weaning mass
Log maternal age	-					
Log part'n mass	0.40	-				
Log birth mass	0.45	0.46	-			
Growth rate	0.14	0.34	NS	-		
Lactation duration	-0.31	0.12	NS	-0.45	-	
Weaning mass	0.14	0.58	0.45	0.60	0.59	-

¹ 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. (For calculations see Appendix 5.1)

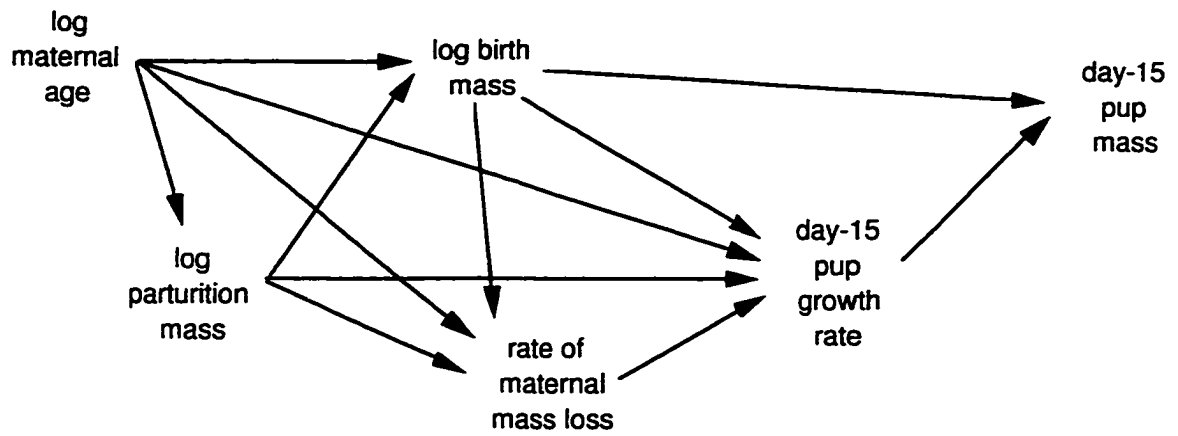
no direct effect on pupping date. Birth mass had no direct effects on lactation duration or growth rate. Birth mass and lactation duration had only direct effects on weaning mass, whereas growth rate had both a direct effect as well as an indirect effect through lactation duration. The strongest path in the model was between growth rate and weaning mass (0.87).

I calculated effect strengths based on all paths between each variable (Table 5.4b, Appendix 5.1). The effect strengths of growth rate, lactation duration, and parturition mass on weaning mass (0.60, 0.59, and 0.58, respectively) were similar, and were the strongest effects in the model. The effect strength of birth mass on weaning mass (0.45) was two-thirds that of the latter variables, whereas that of age (0.14) was less than one-quarter as strong. As expected, rate of pup mass gain was negatively related to lactation duration (-0.45). Age was also negatively related to lactation duration (-0.31), whereas parturition mass had a small but positive relationship with lactation duration (0.12). Both age and parturition mass had positive effect strengths on growth rate, but that of parturition mass (0.34) was more than twice that of age (0.14). Each had similar effects on birth mass (age, 0.45; parturition mass, 0.46).

In the mid lactation model ($n = 69$), the traits I considered were rate of maternal mass loss, offspring growth rate, and pup mass at 15 days post-partum. Again, I hypothesized that the effects of age and parturition mass would act on pup mass indirectly through intermediary traits (Figure 5.9a). I also hypothesized that the rate of maternal mass loss could be affected directly by birth mass, and by maternal age and mass.

MID LACTATION

a)



b)

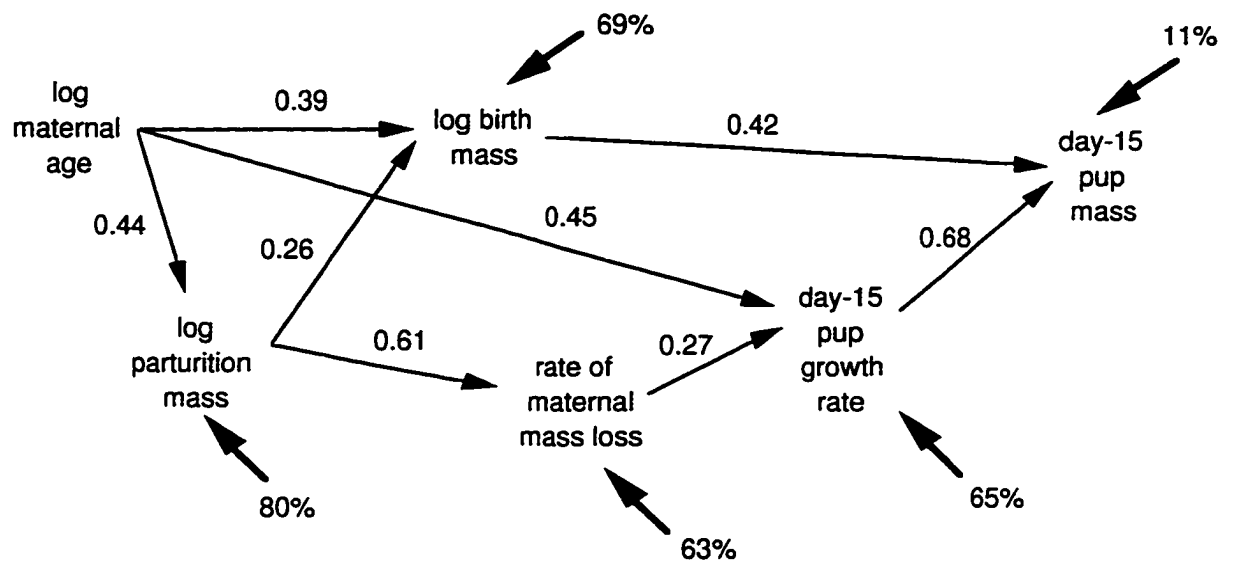


Figure 5.9. Path model linking traits of harbour seal mothers and pups from birth to mid lactation : a) hypothesized full model, and b) trimmed model. Percentage of unexplained variance is linked to each dependent (endogenous) variable by a thick arrow ($n = 69$).

Table 5.5a. Correlation matrix for data used in path model on traits from birth through mid lactation (Figure 5.8b) ($n = 69$)

Dependent variable	Independent variable					
	Log maternal age	Log parturition mass	Log birth mass	Maternal mass loss rate	Pup growth rate	Day-15 pup mass
Log maternal age	-					
Log part'n mass	0.44**	-				
Log birth mass	0.51**	0.43**	-			
Maternal mass loss rate	0.30*	0.61**	0.34**	-		
Pup growth rate	0.53**	0.41**	0.45**	0.41**	-	
Day-15 pup mass	0.58**	0.48**	0.72**	0.43**	0.87**	-

* $p < 0.05$, ** $p < 0.01$

Table 5.5b. Effect strength¹ of variables in path model on traits of harbour seal pups and females from birth to mid lactation (Figure 5.9b). (NS = not significantly different from zero.)

Dependent variable	Independent variable					
	Log maternal age	Log parturition mass	Log birth mass	Rate of maternal mass loss	Growth rate	Day-15 pup mass
Log maternal age	-					
Log part'n mass	0.44	-				
Log birth mass	0.50	0.26	-			
Rate of mass loss	0.27	0.61	NS	-		
Growth rate	0.52	0.16	NS	0.27	-	
Day-15 pup mass	0.57	0.22	0.42	0.18	0.68	-

¹ 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. (For calculations see Appendix 5.2)

Eight paths were significant (Figure 5.9b). As in the weaning model, the strongest path coefficient was between growth rate and pup mass (0.68), and this was the greatest effect strength as well (Table 5.5b). The second and third strongest effects (Table 5.5b) were those of maternal age on pup mass (0.57) and on growth rate (0.52). This result was very different from the weaning model, in which age had no direct path to growth rate (Figure 5.8b), and had only weak effects on weaning mass and growth rate (Table 5.4b). In the mid lactation model, parturition mass had weaker effects than maternal age on pup mass (0.22) and growth rate (0.16) (Table 5.5b). On the other hand, parturition mass had a much stronger effect on the rate of maternal mass loss (0.61) than did maternal age (0.27) (Table 5.5b).

Effects of pup sex

My final analyses compared life-history traits by pup sex (Table 5.6). At weaning, male pups weighed more on average than females (25.8 versus 24.1 kg), however this was not significantly different after controlling for birth mass (Table 5.6). Other traits, such as rate of mass gain, lactation duration, weaning date, and mass transfer index did not differ before or after controlling for covariates (Table 5.6). Mass-specific mass gain (mass gain divided by birth mass) and mass-specific rate of mass gain (rate of mass gain divided by birth mass) also did not differ by pup sex (Table 5.6).

Sex ratio at weaning did not differ from unity, overall or within any maternal age class or mass class (Table 5.7).

Table 5.6. Life-history traits of harbour seals on Sable Island, 1988-1996, by pup sex.

Trait	Male pups mean \pm SE (<i>n</i>)	Female pups mean \pm SE (<i>n</i>)	<i>p</i> <i>t</i> -test [<i>d.f.</i>]	<i>p</i> ANCOVA [<i>d.f.</i>]
Birth mass ¹ (kg)	11.1 \pm 0.1 (175)	10.7 \pm 0.1 (200)	0.009 [373]	0.001 ² [1, 241]
Weaning mass (kg)	25.8 \pm 0.38 (70)	24.1 \pm 0.34 (84)	0.001 [152]	0.106 ³ [1, 113]
Mass gain (kg)	14.8 \pm 0.42 (50)	13.8 \pm 0.32 (66)	0.059 [114]	0.056 ⁴ [1, 97]
Mass specific mass gain (kg/kg)	1.35 \pm 0.042 (50)	1.33 \pm 0.036 (66)	0.790 [114]	-
Rate of mass gain (kg/d)	0.63 \pm 0.018 (50)	0.58 \pm 0.014 (66)	0.052 [114]	0.191 ³ [1, 113]
Mass specific rate of mass gain (kg/d/kg)	0.057 \pm 0.00215 (50)	0.056 \pm 0.0014 (66)	0.740 [114]	-
Lactation duration (d)	23.8 \pm 0.37 (78)	24.0 \pm 0.37 (97)	0.658 [173]	0.530 ³ [1, 113]
Weaning date	June 18 \pm 0.6 (78)	June 19 \pm 0.5 (97)	0.103 [173]	0.504 ⁵ [1, 172]
Mass transfer index (%) (pup mass gain to maternal mass loss)	46.5 \pm 1.68 (13)	43.1 \pm 1.69 (15)	0.169 [26]	-
Relative weaning mass (%) (weaning mass to parturition mass)	30.8 \pm 0.46 (42)	29.0 \pm 0.41 (58)	0.004 [98]	-

¹ From Chapter 3. Includes data from 1987.² ANCOVA of log birth mass on pup sex, controlling for log parturition mass³ ANCOVA controlling for birth mass⁴ ANCOVA controlling for parturition mass⁵ ANCOVA controlling for pupping date

Table 5.7. Sex ratio at weaning by maternal age class and mass class.

Maternal class	Male (<i>n</i>)	Female (<i>n</i>)	Sex ratio (% males)	<i>p</i> chi-square
Age class				
Young (4 - 6 yr)	9	9	50.0	1.00
Intermediate (7 - 10 yr)	16	20	44.4	0.51
Older (11 - 14+ yr)	6	14	30.0	0.07
Mass class				
Small (≤ 85.0 kg)	25	39	39.1	0.08
Large (> 85.0 kg)	17	19	47.2	0.74
All females	78	97	44.6	0.15

Discussion

The two main goals of this study were: i) to examine how life-history traits of harbour seal females and pups relate to maternal care strategies in pinnipeds, and ii) to compare relative influences of maternal effects on offspring traits during lactation within harbour seals. In addition, I looked at sex differences in pup traits during lactation.

Relationships of lactation traits to strategies of maternal care

The mean rate of pup mass gain of 0.6 kg/d during lactation was very similar to estimates by Markussen et al. (1989; 0.5 kg/d) and Boulva and McLaren (1979; 0.6 kg/d). All estimates are lower than the estimate of 0.08 kg/d by Bowen et al. (1992), which was based on a sample of 13 large females (range 84 - 91 kg). Given the positive correlation between maternal mass and pup growth pups of larger females are expected to have a greater than average growth rate. The current study was more representative of the population due to its large sample size ($n = 116$) and wide range of maternal masses studied (65.5 - 105.3 kg). Previous studies used cross-sectional data on different individuals during lactation, whereas in this study, individual pups were followed longitudinally from birth to weaning, adding to the reliability of the estimate.

The rate of pup mass gain of other phocid species ranges from 0.76 kg/d in ringed seals to 7.1 kg/d in hooded seals, *Cystophora cristata* (Bowen 1991). Rate of mass gain in harbour seals is thus the lowest known rate for phocid pups. This may be partly due to the high activity levels of pups. This hypothesis is supported by the fact that the phocid species with the next lowest rates of pup mass gain (ringed seals and Hawaiian monk seals, *Monachus schauinslandi*) also begin to swim early in lactation (Bowen 1991).

Harbour seal pups also deposit less fat, and are considerably leaner at weaning (33% fat) than other phocids (> 40% fat; Bowen et al. 1992a; Muelbert and Bowen 1993). This occurs even though females deplete fat reserves by 79%, the greatest proportion reported for phocids (Bowen et al. 1992a). Harbour seal pups enter the water within hours of birth (Lawson and Renouf 1985; Oftedal et al. 1991), whereas most phocid pups do not begin to swim until after weaning (Bonner 1984). The highly aquatic nature of harbour seal pups may be responsible for the low rate of energy deposition (Bowen et al. 1992a). This hypothesis is supported by the fact that pups of Weddell seals, *Leptonychotes weddelli*, have comparably low body fat at weaning (37%, Tedman and Green 1987), and these pups also swim during lactation. An additional factor that may lead to low fat deposition in harbour seal pups may be the intermittent fasting that pups undergo while females are on foraging trips.

Otariid rates of pup mass gain are considerably lower than in phocids, ranging from 0.05 to 0.15 kg/d (Bowen 1991). Otariid pups undergo more true growth during lactation, reflected by lower fat deposition and more development of the skeleton and musculature (Oftedal et al. 1987). True growth in otariids contrasts with the fattening of most phocid pups (Bowen et al. 1985; Oftedal et al. 1993). The slow rate of mass gain of harbour seals, combined with low fat deposition, places their growth patterns intermediate between typical phocid and otariid growth patterns.

The rate of mass gain of harbour seal pups was weakly correlated with parturition mass ($R^2 = 19.9\%$). As predicted, this relationship was lower than in fasting phocids, such as grey seals ($R^2 = 48.8\%$, Iverson et al. 1993), and northern elephant seals ($R^2 =$

42.3%, Deutsch et al. 1994). There was a stronger relationship between the rate of pup mass gain and the rate of maternal mass loss in harbour seals ($R^2 = 44.6\%$). However, as predicted, the rate of maternal mass loss explained more of the variability in rate of pup mass gain in fasting phocid species. For example, loss rate explained 58% of pup mass gain in grey seals (Iverson et al. 1993), and 53% in northern elephant seals (Deutsch et al. 1994).

Parturition mass accounted for a small proportion of the variation in weaning mass of harbour seals ($R^2 = 26.3\%$). In contrast, parturition mass accounted for 55% of the variation in weaning mass in southern elephant seals (Arnbom et al. 1993) and 44% in northern elephant seals (Deutsch et al. 1994). At the other extreme, the Antarctic fur seal, *Arctocephalus gazella*, is an otariid that forages for about 117 days. Maternal body condition (measured as the ratio of mass to length) had no significant influence on pup mass near weaning ($n = 63$) (Doidge and Croxall 1989).

In phocids, weaning mass of pups is usually between 25% and 33% of parturition mass of females, with an average of $28.3 \pm 6.4\%$ for 10 species (Bowen 1991). Relative weaning mass of harbour seals (29.6%) fall within the typical phocid range. Most phocids, including harbour seals, weigh relatively less at weaning than most otariids (mean = 37.8% for 5 otariid species; Bowen 1991). Although otariids grow at slower rates, they are able to reach greater relative weaning mass than phocids due to their comparatively long period of lactation.

Among phocid species, weaning mass ranges from 2 to 5 times that at birth (Bowen 1991). Mean weaning mass of harbour seals was 2.3 times birth mass on Sable

Island, and was 2.4 times birth mass in British Columbia (Bigg 1969). Harbour seals are thus at the low end of the range for phocids, and this is probably related to the comparatively high activity levels of both females and pups, combined with intermittent fasting by pups. In otariids, the ratio of weaning mass to birth mass ranges from 2.3 to 4.4 (Bowen 1991). The low ratio of weaning mass to birth mass in harbour seals compared with otariids may be explained by the much briefer lactation period of harbour seals.

It is interesting to note that, compared with other phocids, harbour seal pups are unusually large at birth relative to maternal mass (Chapter 3; Bowen et al. 1985), but this relative difference disappears by weaning. This supports the hypothesis that relatively large mass at birth in harbour seals is an adaptation for entry into the cold marine environment shortly after birth (Oftedal et al. 1991).

Limitations of maternal body mass

The percentage of body mass lost by harbour seals during lactation (35%) is similar to relative mass loss within both fasting and foraging phocid species. During lactation, female northern elephant seals lose 39% of body mass (Costa et al. 1986), whereas female grey seals lose 40% (Iverson et al. 1993), and female Weddell seals lose 39% (Tedman and Green 1987).

Harbour seals differ from other phocids in that they deplete a greater proportion of fat reserves, even though they feed during lactation. Within the first 19 days of lactation, harbour seal females deplete 79% of their initial fat stores (Bowen et al. 1992a), the greatest level reported for phocids. Large phocid species such as hooded and northern

elephant seals use from 33% to 58% of stored energy (Bowen et al. 1987; Fedak and Anderson 1987). Since female harbour seals deplete such high proportions of energy stores, it seems unlikely that they could fast throughout lactation and still meet the increasing demands of a growing pup (Boness and Bowen 1996).

As predicted, at mid lactation maternal mass loss and pup mass gain were correlated for large females (i.e., those above the median mass of 85 kg at parturition), but not for small females. Thus, significantly more of the mass gain of pups could be attributed to maternal mass loss (i.e., energy stores) in larger than in smaller females. The relationship between maternal mass loss and pup mass gain may be weaker in small females because of foraging in early lactation. Thus, small females appear to begin foraging first. Studies using radio transmitters (Thompson et al. 1994) and time-depth recorders (TDRs) (Bowen et al. in prep.) support this interpretation.

The rate of pup mass gain appeared to decrease in late lactation. This deceleration of mass gain could result from behavioural or physiological changes associated with weaning, such as reduced suckling, reduced milk production (Martin 1984), or longer absences of the females. Decelerating mass gain could also be related to increased activity by females or pups. As lactation progresses, females spend significantly more time at sea, diving more often, and to deeper depths for longer periods (Boness et al. 1994; Bowen et al. in prep.). Since suckling occur only on land, increased foraging time would decrease the time that females are available for suckling. It would also increase energy costs for pups, if they accompany females. Both factors could lead to reduced rate of mass gain. In the Antarctic fur seal (an otariid species), pups whose mothers spent

more time onshore had greater weaning mass (Doidge and Croxall 1989).

There was a marked influence of maternal age class on whether the rate of pup mass gain changed during lactation. This may reflect different patterns of energy expenditure by small and large females. Pups of young females maintained their originally low rate of mass gain throughout lactation, whereas rate of mass gain of pups of intermediate-aged and older females appears to have dropped in late lactation. At mid lactation, rate of mass gain and pup mass were significantly lower for pups of young females, than for pups of intermediate-aged or older females. However, at weaning there was no significant effect of maternal age class on rate of mass gain, or on weaning mass. It is worth noting that, although not statistically different, lactation lasted 2 days longer for young females than old females. Late lactation (i.e., the period between mid lactation and weaning) may therefore be considered a “catch-up phase” for pups of young females, during which mass gain continues at lower rates for slightly longer. As a result, pups from each maternal age class had similar absolute mass gain during lactation, despite a slower start for pups of young females (Figure 5.10). Since young females were smallest, the slower initial rate of mass gain could result from smaller females producing less milk (Iverson et al. 1993), or depleting energy reserves sooner.

Index of mass transfer

In phocids, the efficiency of mass transfer of species that fast throughout lactation varies from 40% for grey seals (Iverson et al. 1993) to 63% in hooded seals (Kovacs and Lavigne 1992). In this study, the index of mass transfer (45%) fell within that range. Yet in other species that forage during lactation, the measure of mass transfer can be considerably greater, e.g., 76% in ringed seals (Hammill et al. 1991) and 86% in harp

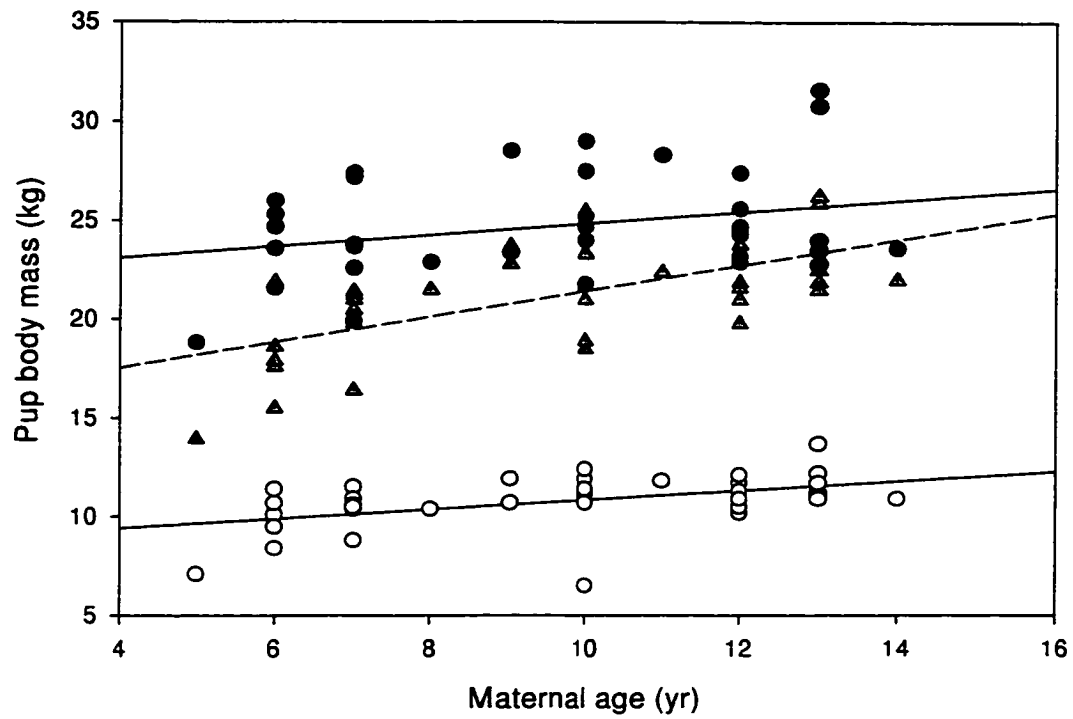


Figure 5.10. Body mass at birth (open circles), 15 days post-partum (triangles), and weaning (closed circles), for pups of 37 known-age females. Linear regression lines for each stage are shown.

seals (Lydersen and Kovacs 1993). These greater “transfer efficiencies” are explained by supplemental energy intake during lactation. It was thus surprising, on first inspection, to find that the index of mass transfer was so low in harbour seals. That it was so low may suggest that, overall, the additional activity associated with foraging is only sufficient to keep lactating harbour seals energetically on par with fasting phocids. Thus, harbour seals appear to forage out of necessity. Foraging may allow them to deliver essentially the same energy investment as the larger-bodied, fasting species. It does not appear to confer any energetic advantage, as would be implied by a comparatively greater index of mass transfer. The Weddell seal, another phocid species that forages during lactation, has a similar index of mass transfer (44%; Tedman and Green 1987).

Relative influence of maternal effects

In addition to exploring interspecific differences in strategies of maternal care, I set out to compare relative influences of maternal effects on offspring traits during lactation within harbour seals. Twelve percent of pups with known lactation duration were weaned prematurely. The only birth trait that differed between prematurely weaned pups and successfully weaned pups was parturition mass. This suggests that poor condition, rather than age (i.e., reproductive inexperience), is a cause of premature weaning.

Pupping date had no significant effects on any pup traits throughout lactation, just as it had no effects on pup traits at birth (Chapter 3). The only variable that was strongly correlated with pupping date was weaning date, and this was simply a reflection of the fact that lactation duration did not vary significantly with pupping date. In Antarctic fur

seals, the timing of weaning was more synchronous than the timing of pupping (Doidge and Croxall 1989). This however, was not the case for harbour seals, as evidenced by the similar standard deviations of pupping date and weaning date.

Weaning mass of harbour seal pups was positively correlated with parturition mass, but not with maternal age. The lack of an age effect on weaning mass appears to contradict my predictions of improvements in maternal physiology or behaviour with age would lead to improved pup traits. Path analyses (see below) however, suggest that age affects intermediary pup traits that ultimately affect weaning mass.

In harbour seals, relative weaning mass was slightly greater in small than large females (30.3% versus 28.8%). This may indicate a greater dependence on supplemental energy by small females.. Contrary to my prediction of that maternal investment would increase with age, relative weaning mass did not differ by age class. It is important to note, however, that this measure of maternal energy investment is not entirely appropriate for species that forage during lactation, since it does not take into account energy intake or differences in activity.

It has been suggested that rate of pup mass gain may be a better measure of maternal investment in pinnipeds than relative weaning mass (Costa 1991). In harbour seals, maternal effects on the rate of mass gain followed the same patterns as relative weaning mass. Rate of mass gain was significantly greater for pups of large females, but did not vary by maternal age class (Table 5.1). Because of variable activity levels of pups, even rate of mass gain is not a satisfactory measure of maternal energy investment in harbour seals. The only way to obtain a true measure of maternal energy investment

throughout lactation would be through dedicated studies on energetics (e.g., Costa 1991; Bowen et al. in prep.). Using the two best measures available to me in this study, I must conclude that maternal energy investment does not appear to increase with age, contrary to my prediction. Maternal energy investment does, however, appear to increase with initial maternal mass, supporting the hypothesis that small size is a limiting factor within harbour seals.

Path analysis of maternal effects

Most results discussed to this point have dealt with relationships between two variables at a time. This is a common practice in many biological studies, particularly of pinnipeds, and is therefore useful for making interspecific comparisons. However, to obtain an overall picture of how variables interact, multivariate analyses are much more appropriate. I formulated two path models, one linking traits at birth to weaning, and the other from birth to mid lactation . The models are clearly simplistic, and do not contain all measured variables. This was partially due to limitations of sample size. Some variables were also excluded to avoid using correlated variables that measured very much the same thing, such as pup mass gain and rate of mass gain.

The parameter estimates in the path diagrams presented here must be considered tentative since sample size is just above the lowest allowable limit of 5 cases per path (Petraitis et al. 1996). It is also noteworthy that growth rate had a high amount of unexplained variation (88%), thus there are clearly variables not included in the diagram that affect growth. Such variables may include pup sex (a categorical variable unsuited to path analysis) and, perhaps quite importantly, maternal foraging. I will however assume

the relative ranks of the path coefficients that were included in the diagram are correct.

As predicted, both maternal age and parturition mass played significant roles in determining pup traits from birth through to weaning. Their effects on birth mass were similar. They differed however, in their effects on pup traits during lactation. Parturition mass affected pup growth rate and weaning mass more strongly than did age. As shown in the path diagram, the effect of parturition mass on weaning mass begins at birth, with heavier pups being born to larger females, and continues through lactation by its positive effect on growth rate and lactation duration.

Age had a stronger, and negative, effect on lactation duration, suggesting that as a females ages, she takes less time to raise a pup to weaning. As indicated in the path diagram, part of this is due to the positive effect of age on parturition mass and thus on growth rate, as well as its positive effect on birth mass. There was, however, an additional direct negative link between age and lactation, that explained variation in lactation duration unaccounted for by parturition mass or birth mass. This may reflect behavioural or physiological differences in younger females that increase lactation time. For example, as seen in the analyses of pup mass gain, pups of young females continued to gain mass at the same intermediate rates of mass gain in late lactation as in mid lactation, whereas growth rates decreased in pups of older maternal age classes. Lactation lasted 2 days longer for young females than old females on average. This “catch-up phase” in late lactation led to similar overall growth rates for all age classes and, in fact, similar weaning masses. It also explains the lack of a significant path between age and growth rate, even though there is evidence for differential effects of age on growth rate

earlier in lactation.

There was good agreement between most raw correlation coefficients of the data used in the path model (Table 5.4a) and the effect strengths suggested by the path diagram (Table 5.4b). Two values however differed considerably. Lactation duration was not significantly correlated with parturition mass ($r = -0.01$), but the effect strength of parturition mass on lactation duration was 0.12. In bivariate correlation, the positive effect of parturition mass on lactation duration was masked by its positive correlation with pup growth rate and birth mass, and their negative effects on lactation duration. Similarly, the bivariate correlation coefficient between lactation duration and weaning mass was only 0.15, as compared with the effect strength of 0.59. Again the strong positive effect of lactation duration on weaning mass was masked by the positive effects of pup growth rate and birth mass on weaning mass, and their negative effects on lactation duration. In path analysis, the standardized partial regression coefficients represent the expected change in a dependent variable, with other variables held statistically invariant (Dobson and Michener 1995). This makes path analysis suitable for finding relationships that might not show up using simple bivariate correlations.

In the weaning model it was not possible to include maternal mass loss as a variable, since the sample size of maternal mass loss at weaning ($n = 28$) would have invalidated the model (Petraitis et al. 1996). Including maternal mass loss to 15 dpp in the mid lactation model showed that parturition mass has a strong effect on maternal loss rate, which in turn affects pup growth rate. Some of the strongest effects in the mid lactation model were those of maternal age on pup mass and on growth rate. This result

was very different from the weaning model, in which age had no direct path to growth rate, and had only weak effects on weaning mass and growth rate. This reflects the slower early growth and mass gain of pups and young females. That these age effects were weak in the weaning model, but not the mid lactation model, reflects the “catch-up phase” of pups of young females in late lactation suggested earlier.

These models illustrate the effectiveness of path modelling to study causal mechanisms in multivariable systems. The main conclusions to be drawn from these models are that both maternal age and mass affect pup traits throughout birth, lactation, and weaning, and that relationships between traits can change over the course of lactation.

Equal investment during lactation

On average, male pups weighed significantly more (1.7 kg) than female pups at weaning. This result contrasts with earlier studies of harbour seals on Sable Island. Muelbert and Bowen (1993) did not find a significant difference in weaning mass by pup sex. In a reanalysis of their original data ($n = 52$), means of weaning mass were similar to those found here, with males 1.5 kg heavier than females. The apparent disagreement between these two studies is undoubtedly due to the greater sample size and thus greater power in this study.

After controlling statistically for birth mass, 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, rather than differential maternal energy investment during lactation, based on pup sex. This is supported by the lack of sex-related differences in other traits during lactation such as lactation duration, mass gain,

rate of mass gain, and index of mass transfer (Table 5.6). Therefore, the hypothesis that females will invest more in offspring during lactation *because they are male* (Trivers and Willard 1973; Maynard Smith 1980) is not supported by data on harbour seals. Similar results and conclusions were found for California sea lions, *Zalophus californianus* (Ono and Boness 1996).

Regardless of the proximal cause, mass at birth weaning of males were greater in harbour seals, as were relative birth mass and relative weaning mass. This implies greater overall energy investment in male pups, but does this translate into a greater reproductive cost (*sensu* Trivers 1972) of raising a male pup? It is not possible to resolve this question for harbour seals using this data set, as it does not include data on subsequent survival or fecundity of females. In other mammals, greater mass of males at birth or weaning does not necessarily lead to increased maternal reproductive costs. For example, although male bison, *Bison bison*, were heavier at birth, subsequent 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 had no significant effect on a female's reproductive performance the following year, or on her subsequent survival (LeBouef et al. 1989).

In species in which sons cost significantly more to rear than daughters, sex ratio theory predicts a female-biased sex ratio at the end of parental investment (Fisher 1930; Leigh 1970). In harbour seals, sex ratio at weaning did not differ from parity overall, or by maternal age class or mass class. In a much larger sample of more than 11,000 northern elephant seals, sex ratio at weaning also did not differ from parity (Le Boeuf et

al. 1989). Similar results were found in southern elephant seals (Campagna et al. 1992). These data suggest that additional energetic costs of raising male pups may not be biologically significant among phocid seals (Le Boeuf et al. 1989).

Summary

The strategy of maternal care in harbour seals strategy influences life-history traits of females and pups throughout lactation. Interspecific comparisons of these traits support predictions that maternal effects of parturition mass and maternal mass loss on offspring traits are weaker in harbour seals than in fasting phocids, and stronger than in otariids.

Compared with other phocids, harbour seal pups are unusually large at birth relative to maternal mass, but this relative difference disappears by weaning. This supports hypotheses that relatively large mass at birth is an adaptation for entry into the cold marine environment shortly after birth.

This study supports behavioural and physiological work that suggests small harbour seal females begin to forage sooner after parturition. In addition, measures of maternal energy investment—although not ideal for harbour seals—suggest that investment is greater on average for larger females. Thus, maternal body mass can affect maternal behaviour during lactation, and limit relative maternal investment.

Maternal age and parturition mass affected pup traits during lactation, but their relative influence varied over the course of lactation. During late lactation, pups of young females were able to “catch-up” with other pups, eliminating differences in weaning mass and growth rate that were apparent at mid lactation . Studies in which measurements are

taken only in mid lactation, as a substitute for measurements at weaning, may lead to misleading conclusions about effects of maternal age or mass.

At weaning, there were no ultimate effects of maternal age class on weaning mass or rate of mass gain of pups, after controlling for maternal mass. The lack of an ultimate age effect appeared contrary to predictions based on age-related maternal improvements and on trade-offs between growth and reproduction. Path analysis showed, however, that age acted on weaning mass through intermediary traits. The effects of parturition mass on weaning mass and rate of mass gain were stronger than those of maternal age, and maternal mass class significantly affected weaning mass, mass gain, rate of mass gain, and relative weaning mass. Thus, in harbour seals, maternal mass—an indicator of maternal condition—affects offspring during lactation more than does maternal age.

Male harbour seal pups weighed more at weaning than female pups. This resulted from differences in birth mass, rather than differential maternal energy investment during lactation. Sex ratio at weaning did not differ from unity. Several other studies suggest that additional costs of raising male pups are not biologically significant in phocid seals. In harbour seals, it is not known whether greater mass of males at weaning has biological significance, since the relationship between weaning mass and adult mass is not known.

Appendix 5.1. Calculation of the effect strength of variables in the weaning path model (Figure 5.8b; $n = 51$). The effect strength of one variable on another is the sum of the direct path (if any) and the products of any compound paths (Klem 1995).

Effect strength of log age:

on log parturition mass = **0.40**

on log birth mass = $0.27 + (0.40 \times 0.46) = \mathbf{0.45}$

on lactation duration = $-0.36 + (0.40 \times 0.29) + (0.40 \times 0.34 \times -0.45) = \mathbf{-0.31}$

on growth rate = $0.40 \times 0.34 = \mathbf{0.14}$

on weaning mass = $(-0.36 \times 0.59) + (0.27 \times 0.45) + (0.40 \times 0.46 \times 0.45) + (0.40 \times 0.29 \times 0.59) + (0.40 \times 0.34 \times -0.45 \times 0.59) + (0.40 \times 0.34 \times 0.87) = \mathbf{0.14}$

Effect strength of log parturition mass:

on log birth mass = **0.46**

on lactation duration = $0.29 + (0.34 \times -0.45) = \mathbf{0.12}$

on growth rate = **0.34**

on weaning mass = $(0.46 \times 0.45) + (0.29 \times 0.59) + (0.34 \times -0.45 \times 0.59) + (0.34 \times 0.87) = 0.207 + 0.171 - 0.090 + 0.296 = \mathbf{0.58}$

Effect strength of log birth mass:

on weaning mass = **0.45**

Effect strength of growth rate:

on lactation duration = **-0.45**

on weaning mass = $0.87 + (-0.45 \times 0.59) = \mathbf{0.60}$

Effect strength of lactation duration:

on weaning mass = **0.59**

Appendix 5.2. Calculation of the effect strength of variables in the mid lactation path model (Figure 5.9b; $n = 69$). The effect strength of one variable on another is the sum of the direct path (if any) and the products of any compound paths (Klem 1995).

Effect strength of log age:

on log parturition mass = **0.44**

on log birth mass = $0.39 + (0.44 \times 0.26) = \mathbf{0.50}$

on rate of maternal mass loss = $0.44 \times 0.61 = \mathbf{0.27}$

on mid lactation growth rate = $0.45 + (0.44 \times 0.61 \times 0.27) = \mathbf{0.52}$

on day-15 pup mass = $(0.39 \times 0.42) + (0.45 \times 0.68) + (0.44 \times 0.26 \times 0.42) + (0.44 \times 0.61 \times 0.27 \times 0.68) = \mathbf{0.57}$

Effect strength of log parturition mass:

on log birth mass = **0.26**

on rate of maternal mass loss = **0.61**

on mid lactation growth rate = $0.61 \times 0.27 = \mathbf{0.16}$

on day-15 pup mass = $(0.26 \times 0.42) + (0.61 \times 0.27 \times 0.68) = \mathbf{0.22}$

Effect strength of log birth mass:

on day-15 pup mass = **0.42**

Effect strength of maternal rate of mass loss:

on mid lactation growth rate = **0.27**

on day-15 pup mass = $(0.27 \times 0.68) = \mathbf{0.18}$

Effect strength of mid lactation growth rate:

on day-15 pup mass = **0.68**

CHAPTER 6

GENERAL CONCLUSIONS

Offspring phenotype can be affected by maternal features in ways that are not directly related to genotype. For example, maternal age and maternal condition change over the lifetime of a female, and can directly influence life-history traits of offspring. Often, however, effects of maternal age and body size are studied independently of one another. I studied selected life-history traits of harbour seal females and pups throughout the period of maternal investment, over a wide range of maternal age and mass, to examine the relative influence of maternal effects.

Maternal effects from birth through weaning

The main maternal effects I examined were maternal age, parturition mass, and pupping date. Over a 10- year period on Sable Island, pupping date of harbour seals increased, and maternal age structure changed. Despite these changes, there was no significant interannual variation in pup traits from birth through weaning. The lack of interannual variation in birth mass and weaning mass may reflect strong selective pressure on these traits. The lack of interannual variation in pup traits also suggests that female harbour seals are capable of buffering their young from environmental variation.

Pupping date was not a significant maternal effect on any pup traits that I measured. Contrary to studies on other mammals in which birth date was related to offspring survival, there was no tendency for older or larger harbour seals to give birth

early in the pupping season. I hypothesized that selective forces acting on pupping date on Sable Island affect females similarly, regardless of maternal age or mass.

Maternal age and mass were significant maternal effects on pup traits at birth, but their influence changed with age. Path analysis was well suited to exploring the causal relationships of maternal effects. At birth, effects of age were stronger than those of parturition mass. In fact, parturition mass had no significant effect on birth mass, but simply covaried with age. Age effects were significant among young females, but not among intermediate-aged females or older females. Limited evidence suggested that in young females, age itself was not as important a determinant of offspring birth mass as was reproductive experience. Experience could lead to behavioural improvements, such as increased foraging ability during pregnancy, or physiological improvements, such as improved intrauterine transfer of nutrients to the fetus. Such effects of reproductive experience on birth mass may apply to mammals in general.

In mid lactation, maternal age and parturition mass affected rate of pup mass gain and lactation duration, such that pups of young and small females weighed less and gained mass at lower rates. During late lactation pups of young females were able to “catch-up” with other pups in terms of body mass and overall growth rate, by maintaining similar rates of pup growth while those of older females declined.

At weaning, there were no direct effects of maternal age class on weaning mass or rate of mass gain, after controlling for maternal mass. The lack of a direct age effect appeared contrary to predictions based on age-related maternal improvements, and on trade-offs between growth and reproduction. Path analysis showed, however, that age

acted on weaning mass through intermediary traits. The effects of parturition mass on weaning mass and rate of mass gain were stronger than those of maternal age, and maternal mass class significantly affected weaning mass, mass gain, rate of mass gain, and relative weaning mass. Thus, in harbour seals, maternal mass—an indicator of maternal condition—had a stronger effect on pup traits during lactation than did maternal age.

The relative importance of the maternal effects of age and parturition mass varied over the stages of maternal care in harbour seals. During gestation, maternal age had a significant effect on pup birth mass, while parturition mass did not. In mid lactation, both maternal age and parturition mass affected pup growth rate and mass, but the effects of age were stronger. And at weaning, parturition mass had stronger effects on growth rate and weaning mass than did maternal age. This study illustrates the importance of collecting data on both maternal parameters.

Maternal effects in relation to strategies of maternal care

The strategy of maternal care in harbour seals strategy influences life-history traits of females and pups throughout lactation. Interspecific comparisons of these traits support predictions that maternal effects of parturition mass and maternal mass loss on offspring traits are weaker in harbour seals than in fasting phocids, and stronger than in otariids.

This study supported behavioural and physiological work that suggests small harbour seal females begin to forage earlier. In addition, measures of maternal energy investment—although not ideal for harbour seals—suggested that investment was lower

average among small females. Thus maternal body mass of species that forage during lactation can affect maternal behaviour, and limit maternal investment.

Differential maternal investment?

Sexual-selection theory predicts that in polygynous species in which males are larger than females, mothers in good condition should invest more in male offspring. One way this can be accomplished is for older or larger females to vary the sex ratio towards males at birth. In harbour seals, sex ratio at birth did not vary with maternal age or parturition mass. This was in agreement with most evidence on phocid and otariid seals.

Differential investment theory predicts that female harbour seals will invest more energy in male pups than female pups during the period of maternal care. There was evidence for differential energy investment during gestation, as male newborns weighed more on average than females. Weaning mass was also greater for male pups, but this resulted from differences in birth mass, rather than differential maternal energy investment during lactation. In harbour seals, it is uncertain whether greater male mass at birth and weaning is biologically significant, as the relationship between pup mass and adult mass is unknown.

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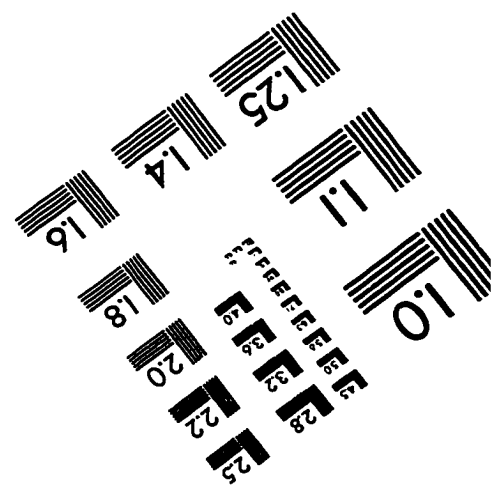
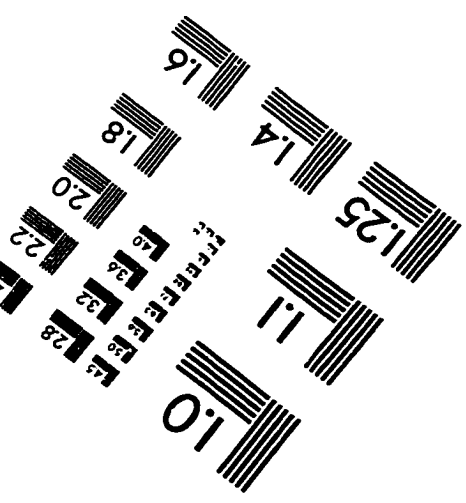
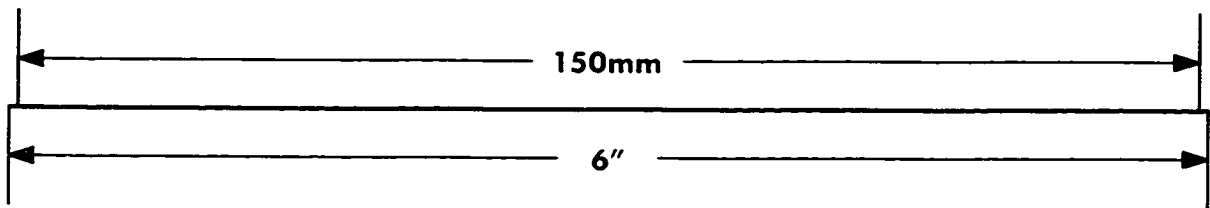
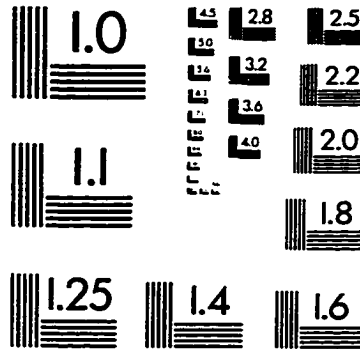
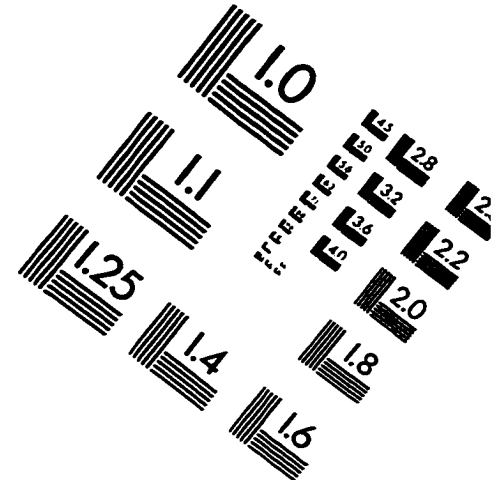
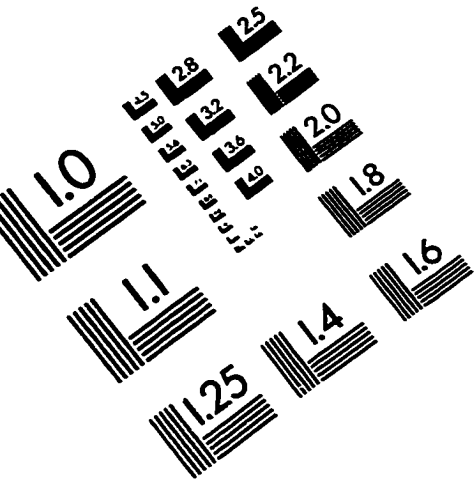
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IMAGE EVALUATION TEST TARGET (QA-3)



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