INVESTMENT IN SONS AND DAUGHTERS BY SOUTHERN ELEPHANT SEALS, *MIROUNGA LEONINA*, AT MARION ISLAND

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ABSTRACT

The southern elephant seal, *Mirounga leonina*, exhibits extreme sexual dimorphism and polygyny and is thought to be an ideal subject to test maternal investment theory. Predictions concerning differential investment in offspring by sex were tested on *M. leonina* breeding at Marion Island over three austral summers. Large females produced more male pups, while small females produced more female pups, providing tentative support for the Trivers and Willard (1973) hypothesis. Maternal size had a greater influence on growth rate and weaning mass than on the sex of offspring. Differential reproductive costs to adult females were not evident in terms of future fecundity or survival. In keeping with other studies on this species, we could not demonstrate any differential investment in the two sexes. We suggest that before discounting maternal investment theories, further studies need to be undertaken to determine the benefits, if any, of size at weaning on long-term survival and reproductive success.

Key words: *Mirounga leonina*, southern elephant seals, Marion Island, maternal investment, reproduction, weaning mass, birth mass, growth rate.

Since the refinement of maternal investment theory in the 1970s (Trivers and Willard 1973, Maynard-Smith 1980) there have been a plethora of studies on pinnipeds (for review see Trillmich 1996). Where variance in reproductive success (RS) is greater in offspring of one sex, and that variance is influenced by the level of maternal investment received (Trivers 1972), parents should invest more in the sex with the higher variance in RS (Trivers and Willard 1973, Maynard-Smith 1980). Two fundamental mechanisms are available to

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allow mothers to bias their allocation of resources. Trivers and Willard (1973) proposed that mothers in good body condition, which have more resources to allocate to their offspring, may bias the sex ratio towards males, the more "valuable" sex. The other mechanism is for mothers to allocate more resources postnatally to the most "valuable" offspring (Reiter *et al.* 1978, Maynard-Smith 1980).

Pinnipeds were thought to be ideal subjects to investigate investment theory (Trillmich 1996). Many pinnipeds, and southern elephant seals in particular, are highly polygynous, sexually dimorphic with males larger than females, and variance in RS probably differing greatly between the sexes. Few southern elephant seal males succeed in mating females but those that do, secure most of the matings (LeBoeuf and Laws 1994, Wilkinson and Van Aarde 1999); females provide all the parental care and rear at most one pup each year of their reproductive lives (LeBoeuf and Laws 1994).

Southern elephant seal pups are weaned at around 22 d (LeBoeuf and Laws 1994) after being fed entirely on milk produced from the mother's stored energy reserves (Fedak *et al.* 1996). Given the known high energy costs of lactation in this species (Fedak *et al.* 1996, Hindell and Slip 1997), and that it is a substantial component of the overall costs of reproduction (Bonner 1984, Oftedal 1984), differences between male and female offspring may reflect different levels of maternal expenditure (Goldsworthy 1995, Lunn and Arnould 1997).

Several studies conducted on southern elephant seals at other sites suggest that there is no differential investment in offspring (McCann *et al.* 1989; Campagna *et al.* 1992; Arnbom *et al.* 1993, 1997; Galimberti and Boitani 1999). However, none of these studies have considered the reproductive costs to females, in terms of future survival and fecundity, of producing male or female offspring. Trillmich (1996) noted that maternal investment can truly be considered only when benefits to offspring are related to a cost in fitness (not only in energetic terms) to the mother. The present study documents maternal investment at the Marion Island population of southern elephant seals. We provide data on costs of reproduction to cows in terms of future fecundity, and survival in relation to sex of offspring produced in a given year.

METHODS

The study was conducted at Trypot Beach, Marion Island (46°54'S, 37°45'E) during the austral summers of 1986, 1987, and 1988. The study beach contained a single harem, which varied in size from 35 females in 1987 to 57 in 1986. Observations were carried out throughout the 14–15 h of daylight of the three breeding seasons from the day the first cow arrived (early September) until the last cow departed the rookery (mid-November). All females hauling out on this beach during these breeding seasons were marked with bleach to facilitate individual identification, and tagged with Allflex "medium duplex" tags (Allflex New Zealand Ltd, Palmerston North, New Zealand) on their hind flippers to allow longer term identification. Pups were

given bleach marks similar to their mothers, and tagged in each hind flipper with Dal 008 Jumbotags (Dalton Supplies Ltd, Henley-on-Thames, UK).

For all females hauling out at the study site, dates of arrival and parturition were recorded. Within one day of parturition females were divided subjectively into those that were "obviously large" and those that were "obviously small" by two observers acting independently (see Campagna et al. 1992). Only females placed in the same category by both observers were included. Data for females of "intermediate size" were excluded from analyses dependent on the size of the mother, as it was not possible to accurately identify intermediate size animals. Relative maternal size was known for the mothers of 60 pups, and only data for these animals were used to examine the relationship between maternal size and other variables. In cases where comparisons did not include maternal size, data for all pups in the study were used.

Gestation lengths for females present at the study colony during consecutive breeding seasons were calculated as the intervals between the dates of birth and the first observed copulation for that individual in the previous year. Females not seen breeding in consecutive breeding seasons were assumed to have failed to pup if seen during subsequent molt or breeding periods, or to have died if never seen again.

All pups were sexed and weighed to the nearest half kilogram within 18 h of birth and again within 24 h of weaning. Growth rates were calculated by subtracting the weight at birth from the weight at weaning and dividing by the duration of lactation in days.

During the 1987 breeding season the colony was scanned daily for 14–15 hr at 5-min intervals and each pup was recorded as not sucking, sucking their filial mother, sucking another female, visible but activity undetermined, or not visible during the scan. The duration of sucking bouts was not estimated using focal animal sampling, however, pups seen sucking during two consecutive scans were assumed to have sucked during the interim period. The percentage of scans in which pups were seen sucking was taken as representative of the time spent sucking during that day (sucking intensity). To calculate the total time spent sucking during the period of parental care (sucking time), the mean daily value for sucking intensity of an individual was multiplied by the duration of lactation.

All statistical procedures follow Zar (1984) and Sokal and Rohlf (1981). Comparisons of means were made using ANOVA and ANCOVA. Ratios and proportions were compared using Chi-squared values, and Fisher's Exact test for small sample sizes. Relationships between variables were compared using correlations and least-squares regression analysis, and levels of significance show the probability of a non-zero slope. All mean values are followed by one standard deviation ($\pm$ SD) of the mean.

RESULTS

Prenatal Energy Investment

Gestation length for females producing male pups was not significantly different from those producing female pups (Table 1). During the three years

Table 1. Comparison of parameters pertaining to male and female southern elephant seal pups at Trypot Beach, Marion Island in 1986, 1987, and 1988.

	Year	Females			Males			t
		Mean	SD	n	Mean	SD	n	
Gestation length (d)		346	4.7	9	345.2	3.1	9	ns
Birth date[a]	1986	29.8	11.3	27	32.0	8.1	29	ns
	1987	27.9	10.8	18	26.6	10.0	17	ns
	1988	28.5	5.7	17	28.3	9.7	29	ns
Overall mean		28.9	9.8	62	29.3	9.3	75	ns
Birth mass (kg)	1986	34.0	5.2	27	39.7	5.5	29	***
	1987	33.7	6.1	18	40.8	4.9	17	***
	1988	34.6	6.1	17	40.6	5.7	29	**
Overall mean		34.1	5.6	62	40.3	5.4	75	***
range		22.0–47.5			25.0–50.0			
Lactation (d)	1986	21.0	1.4	26	21.3	1.8	25	ns
	1987	21.4	1.5	15	21.3	1.8	16	ns
	1988	22.3	2.9	16	21.2	1.9	26	ns
Overall mean		21.4	2.0	57	21.2	1.8	67	ns
range		17–29			17–25			
Sucking time (d)	1987	2.8	1.1	16	3.5	1.4	16	ns
Weaning mass (kg)	1986	96.3	21.4	23	108.8	20.7	24	*
	1987	97.6	13.7	15	112.2	13.1	16	**
	1988	99.6	15.2	16	118.1	18.3	26	**
Overall mean		97.6	17.5	54	113.3	18.4	66	***
range		48.0–139.0			65.0–152.0			
Pup growth rate (kg/d)	1986	3.0	0.9	23	3.2	0.8	24	ns
	1987	3.1	0.4	15	3.4	0.5	16	ns
	1988	3.0	0.7	16	3.6	0.7	26	*

Table 1. Continued.

	Females			Males			
Year	Mean	SD	n	Mean	SD	n	t
Overall mean	3.0	0.7	54	3.4	0.7	66	**
range	1.4–4.6			1.5–5.0			
Mass gain of pup (kg)							
1986	62.9	18.6	23	68.0	18.1	24	ns
1987	65.6	9.5	15	71.0	11.2	16	ns
1988	66.1	14.5	16	76.8	15.5	26	*
Overall mean	64.6	15.1	54	72.2	15.9	66	**
range	25.0–97.0			34.0–105.5			

ᵃ Day 1 is 9 September
* $P < 0.05$, ** $P < 0.1$, *** $P < 0.001$, ns: not significant at $P = 0.05$.

Table 2. Analysis of southern elephant seal birth mass in relation to sex, year, and maternal size. (SS: sum of squares).

	df	SS	F	P	Explained variation (%)
Year	2	42.6	1.0	0.36	1.9
Sex	1	232.4	11.4	0.001	10.5
Maternal size	1	863.1	42.5	<0.001	39.1
Year × sex	2	4.1	0.1	0.90	0.2
Year × maternal size	2	15.7	0.4	0.68	0.7
Sex × maternal size	1	27.1	1.3	0.25	1.2
Year × sex × maternal size	2	47.4	1.2	0.32	2.1
Error	48	975.6	—	—	44.2
Total	59	2,208.0			

of the study 75 male and 62 female pups were born on Trypot beach, giving a sex ratio of 1.21:1, which did not differ significantly from unity ($\chi^2 = 1.24$, $P = 0.227$, df = 1). Large females produced significantly more male ($n = 21$) than female ($n = 9$) pups, while small females showed exactly the opposite trend ($\chi^2 = 9.6$, $P = 0.002$, df = 1), with 9 male and 21 female pups.

Birth mass did not differ significantly between years for males ($F_{[2,72]} = 0.28$, $P = 0.762$) or females ($F_{[2,59]} = 0.11$, $P = 0.897$). Male pups were significantly heavier than females in all three years (Table 1). When data for all three seasons were combined, birth mass for males was significantly ($t = 6.54$, $P = <0.001$, df = 135) greater than for females.

Relative maternal size was known for the mothers of 43.4% (60) of the 137 pups born and allowed the examination of the relationship between birth mass and sex on size of neonate, after controlling for the effects of maternal size. Pups in this subsample did not differ in birth mass from those in the complete data set of 137 pups; however, males (41.3 ± 6.0 kg, $n = 30$) were significantly ($t = 5.1$, $P = <0.001$, df = 58) heavier than females (33.1 ± 6.4 kg, $n = 30$) which was consistent with the full data set. The sex difference in birth mass persisted when variation in maternal size was accounted for ($F_{[1,48]} = 11.4$, $P = 0.001$) (Table 2). There was also a strong relationship between maternal size and mass at birth ($F_{[1,48]} = 42.5$, $P = <0.001$) after removing the influence of year and sex. There were no significant interaction terms. Fifty-six percent of the variation in birth mass was accounted for by the independent variables, with maternal size accounting for 39% of the variation and sex of pup 10%.

Post-Natal Energy Investment

Mass at weaning did not differ significantly between years (Table 1) for males ($F_{[2,63]} = 1.69$, $P = 0.192$) or females ($F_{[2,51]} = 0.17$, $P = 0.845$).

When data for all three seasons were combined, mass at weaning for males was significantly ($t = 4.74$, $P = <0.001$, df $= 118$) greater than for females. Birth and weaning weight were significantly correlated in both males ($r = 0.584$, $n = 66$, $P = <0.001$) and females ($r = 0.647$, $n = 54$, $P = <0.001$). A 3-way ANCOVA, using birth mass as a covariate, showed no significant relationship between weaning mass and year ($F_{[2,43]} = 0.62$, $P = 0.540$), sex ($F_{[1,43]} = 0.05$, $P = 0.823$), or cow size ($F_{[1,43]} = 1.58$, $P = 0.215$).

Daily growth rate of pups during the lactation period was higher ($t = 2.84$, $P = 0.005$, df $= 118$; Table 1) in males than females. The growth rate of pups to weaning was positively and significantly correlated to their weight at birth in both males ($r = 0.316$, $n = 66$, $P = 0.01$) and females ($r = 0.340$, $n = 54$, $P = 0.012$). When the effects of cow size and year were incorporated into a 3-way ANCOVA (using mass at birth as the covariate), year ($F_{[2,43]} = 0.03$, $P = 0.973$), sex of pup ($F_{[1,43]} = 0.99$, $P = 0.326$), and maternal size ($F_{[1,43]} = 0.53$, $P = 0.471$) had no significant effect on growth rate.

Length of lactation did not differ between male and female pups (Table 1). Mean mass gain by pups during lactation was significantly ($t = 2.60$, $P = 0.009$, df $= 118$) higher among male pups (72.2 ± 15.9 kg) than female pups (64.6 ± 15.1 kg) (Table 1). A 3-way ANCOVA (with mass at birth as covariate) showed no significant relationship between mass gained during lactation and year ($F_{[2,43]} = 0.59$, $P = 0.569$), sex ($F_{[1,43]} = 0.02$, $P = 0.878$), or maternal size ($F_{[1,43]} = 1.44$, $P = 0.237$).

Levels of investment in terms of time spent sucking did not differ between male and female pups (Table 1). A 2-way ANCOVA (with age at weaning as covariate) showed no significant relationship between sucking time and sex ($F_{[1,50]} = 1.05$, $P = 0.301$) or cowsize ($F_{[1,50]} = 0.002$, $P = 0.979$).

Influence of Prior Investment on Offspring Sex Ratio

The sex of the pup produced in one year had no demonstrable influence ($\chi^2 = 0.02$, $P = 0.882$, df $= 1$) on the sex of the pup produced in the following year in the 39 cases recorded during the study. Nine of 20 females producing male pups one year produced males the following season, while 10 of 19 females producing female pups in one season produced females during the next season.

Among four small females for which these data were available, three produced female pups in both years, while one produced a male followed by a female. For nine large females, three produced males in both years, four produced males followed by females and the remaining two produced males after females. There was no influence of sex of offspring on the sex of subsequent offspring for large females (Fisher's Exact Test: $P = 0.444$).

Effect of Previous Investment on Maternal Survival and Fecundity

Of the 46 females giving birth to male pups in 1986 and 1987, 63.0% (29) were observed in following seasons, whereas 57.8% (26) of 45 females

producing female pups were seen. These figures indicate that sex of offspring has no discernible influence on short-term maternal survival ($\chi^2 = 0.26$, $P = 0.608$, df $= 1$). For small females, 53.3% (8) of 15 producing female pups were seen in the following seasons, while 75% (3) of four that produced male pups were seen. Among large females 75% (9) of 12 producing male pups were seen in following seasons, while 57.1% (4) of seven producing female pups were seen. Sex of offspring had no discernible influence on short-term maternal survival for either large (Fisher's Exact Test: $P = 0.612$), or small (Fisher's Exact Test: $P = 0.603$) females.

Fecundity was unaffected by sex of offspring produced the previous season: 90% (27) of 30 females that produced male pups gave birth in the following season, whereas 88% (22) of 25 that produced female pups gave birth in the following season (Fisher's Exact Test: $P = 0.573$). The same relationship held for both large (Fisher's Exact Test: $P = 1.000$) and small (Fisher's Exact Test: $P = 0.994$) females. Seventy-five percent (9) of 12 large females producing female pups gave birth in the following season, while 77.8% (7) of nine producing males gave birth. Among small females, 75% (6) of eight producing female pups gave birth the next year, while 66.7% (2) of three producing males did.

DISCUSSION

Offspring Sex Ratio and Prenatal Energy Investment

The present study shows that female southern elephant seals at Marion Island skew the sex of their offspring according to body size (see Trivers and Willard 1973), but do not expend energy differentially on sons and daughters postnatally. Small *M. leonina* females at Marion Island produced significantly more female than male pups, while larger females showed the opposite trend. The finding for small cows is similar to that for South Georgia where Arnbom *et al.* (1994) showed that females needed to reach a threshold *postpartum* mass of 380 kg before they produced any male pups. However, the male-skewed sex ratio in large cows in the present study was not observed at South Georgia, where larger females produced equal numbers of male and female pups (Arnbom *et al.* 1994). Our findings support the hypothesis of Trivers and Willard (1973) that females in good condition (those of large size) should modify the sex ratio of offspring as a function of the parental ability to invest. However, given the findings in the larger data set of Arnbom *et al.* (1994) in which only the smallest of females followed Trivers and Willard's (1973) model, and the larger females produced an even sex ratio, our findings may possibly be an artifact of low sample size, or a result of the categorical classification of maternal size, rather than the mass continuum used in other studies.

The observed differences in birth masses between male and female pups did not result from differences in the length of gestation. This is in contrast to the situation in red deer, *Cervus elaphus,* where higher male birth weights were associated with a longer gestation period (Clutton-Brock *et al.* 1982). The

implication in the red deer study is that since the fetus grows faster at the end of gestation, the longer period *in utero* results in a higher birth weight. Consequently, sex differences in birth weight in *M. leonina* appear to result from either differential provision of maternal resources, or differences in the abilities of fetuses of each sex to utilize these nutrients. Males were on average 6.2 kg heavier than females at birth, a difference of 18%. The higher birth masses for male pups are in accordance with studies of *M. leonina* at South Georgia (Arnbom *et al.* 1997), King George Island (Burton *et al.* 1997), Macquarie Island (McMahon *et al.* 1997), and Iles Kerguelen (Guinet 1991), while at Peninsula Valdes (Campagna *et al.* 1992) and at Iles Crozet (Guinet 1991) there were no differences in birth mass.

Birth mass in both sexes was significantly related to maternal size, as seen in other *M. leonina* populations (Arnbom *et al.* 1993), gray seals, *Halichoerus grypus* (Pomeroy *et al.* 1999), and harbor seals, *Phoca vitulina* (Bowen *et al.* 1994), although sex-specific differences in birth mass persisted when the effects of maternal size had been controlled for. Relative differences in male and female birth masses decreased among larger mothers to approximately 9%, half that seen among small mothers. Arnbom *et al.* (1994) found similar differences at South Georgia where, with increasing maternal *postpartum* mass, male pups were born between 9.5% and 16.7% heavier than female pups. The lack of difference between the sexes at both Peninsula Valdes and Iles Crozet may be explained by the small sample sizes in combination with the sample being drawn from pups of larger females where proportional differences in birth mass are lower.

Increased mass at birth of male pups has been used by several authors to indicate increased pre-natal maternal expenditure in pinnipeds (Kovacs and Lavigne 1986, Boyd and McCann 1989, Goldsworthy 1995), based on the assumption that these differences in size at birth reflect a greater demand for resources by the male fetus (Trillmich 1996). However, in Antarctic fur seals (*Arctocephalus gazella*) studies have shown that male and female pups have different body compositions (Arnould *et al.* 1996). While male *A. gazella* pups are generally heavier at birth (Boyd and McCann 1989, Lunn *et al.* 1993), they have proportionally lower lipid reserves indicating that prenatal maternal expenditure, in terms of gross energy, is similar for each sex (Arnould *et al.* 1996). If a similar situation is found in *M. leonina* then the observed differences in birth mass between sexes would not be indicative of differential energy investment.

Post-Natal Energy Investment

Postnatal maternal energy investment in *M. leonina* is limited to milk transfer from mother to offspring. Numerous studies have cited increased sucking time of males as evidence of increased maternal energy expenditure (Reiter *et al.* 1978, Clutton-Brock *et al.* 1982, Trillmich 1986, Campagna *et al.* 1992, Smiseth and Lorentsen 1995, Lea and Hindell 1997), assuming that increased sucking implied increased milk intake (Clutton-Brock *et al.* 1982). However,

the lack of a relationship between observed sucking time and weight gain in pups during the present study suggests that sucking time is a poor measure of energy delivery. This may be due to the rate of milk energy transfer varying between individuals because of individual differences in sucking behavior or milk energy content (Mellish *et al.* 1999). Individual differences in metabolism also may result in differences in growth efficiency, and thus may mask the relationship between sucking behavior and growth (Mendl and Paul 1989). Since pups were recorded as sucking when they were in contact with the nipple and "active" sucking was not the criterion used in the study, any propensity for a pup to rest "on the nipple" would bias results. In view of the above, the use of sucking time as an index of energy investment is too simplistic in its approach and should be avoided. However, this type of data may be valuable in providing information on the mechanisms of differential maternal energy expenditure in, for example, studies where a male-bias in growth rate is associated with a male-bias in sucking time, and so should not be ignored completely.

On first inspection, weaning mass, growth rate (kg/d), and mass increase between birth and weaning are all greater for males than females, while there was no difference in the lactation period. These disparities have been used in other pinniped studies to infer differential postnatal energy investment (Kovacs and Lavigne 1986, Anderson and Fedak 1987, Goldsworthy 1995) in support of maternal investment theories. Further analysis of all three variables show that all are related to mass at birth, and indeed when birth mass is used as a covariate, weaning mass, growth rates, and mass gained between birth and weaning are not related to sex of pup, year, or maternal size.

The lack of a relationship between maternal size and weaning mass in the current study is probably a consequence of the form of analysis used. As mentioned above, there is a strong relationship between birth and weaning mass, and birth mass and maternal size. If the data are examined without using birth mass as a covariate (Table 3), then weaning mass ($F_{[1,44]} = 22.10$, $P = <0.001$), growth rate ($F_{[1,44]} = 6.30$, $P = 0.016$), and mass increase ($F_{[1,44]} = 11.62$, $P = 0.001$) are all strongly related to maternal size. Maternal size has been shown in many recent studies of *M. leonina* to be the most important factor determining mass at weaning (Campagna *et al.* 1992; Arnbom *et al.* 1993, 1997; Galimberti and Boitani 1999), and in *H. grypus* (Pomeroy *et al.* 1999). In the present study birth mass appears to be the most important contributing variable to differences in measured *postpartum* parameters. However, this may be a consequence of the categorical nature of the maternal size variable used, compared to the continuous variable used in most studies.

Mass at weaning at Marion Island, while not significantly different to that at Heard Island, is significantly lower than at Macquarie Island, South Georgia, and King George Island (Burton *et al.* 1997). Our study shows that weaning mass is strongly influenced by birth mass, which in turn is a factor of female size. It could therefore be assumed that females at Marion Island are smaller than their counterparts at Macquarie Island and Atlantic Ocean sites, as was

Table 3. Analysis of southern elephant seal weaning mass in relation to sex, year, and maternal size (SS: sum of squares).

	df	SS	F	P	Explained variation (%)
Year	2	484.5	0.8	0.44	2.2
Sex	1	952.5	3.3	0.08	4.4
Maternal size	1	6,422.1	22.1	<0.001	29.4
Year × sex	2	670.9	1.2	0.32	3.1
Year × maternal size	2	343.1	0.6	0.56	1.6
Sex × maternal size	1	152.5	0.5	0.47	0.7
Year × sex × maternal size	2	23.5	0.0	0.96	0.1
Error	44	12,786.2	—	—	58.6
Total	55	21,835.2			

suggested by Burton *et al.* (1997). Unfortunately, the lack of data on body masses of adult females in the present study prevent confirmation of size differences between Marion Island and other populations.

Maternal Investment

Several studies have shown reproductive related costs in pinnipeds both in terms of lowered fecundity (Huber 1987, Testa 1987, Arnbom *et al.* 1994, Boyd *et al.* 1995), and subsequent survival (Reiter and LeBoeuf 1991, Sydeman and Nur 1994, Boyd *et al.* 1995). Arnbom *et al.* (1994) and Fedak *et al.* (1996) suggested that reproduction is more costly for small females, who invest a higher proportion of their body mass into their offspring than do larger females. Small females exhibited lower survival rates, and those with a *postpartum* mass of less than 380 kg failed to produce male pups. In the present study data suggest that there was no differential mortality, or lowered fecundity rates, of females bearing male or female pups, or any differential costs that could be attributed to maternal size. It should, however, be noted that, given the sample sizes in our study and the small effect sizes, the statistical power to correctly reject the null hypothesis of no differential investment at the 5% level, ranged from only 0.06 to 0.12. Therefore, failure to reject the null hypothesis should not be taken as strong evidence for no effect. In common with many other studies of maternal investment, the statistical power of analyses are limited by the logistical constraints on sample size.

Influence of Energy Investment on Offspring Reproductive Success and Survival

This is not the first study of a pinniped to show a lack of differential postnatal energy investment in an order thought by many to be ideal for this type of work (McCann *et al.* 1989, Bowen *et al.* 1992, Campagna *et al.* 1992,

Kretzmann *et al.* 1993, Deutsch *et al.* 1994, Trillmich 1996, Lunn and Arnould 1997). McCann *et al.* (1989) observed equal investment in *M. leonina* at South Georgia and suggested that it may occur because there was no benefit in terms of long-term survival/reproductive success to increased energy expenditure in male pups. Lunn and Arnould (1997) also put forward this theory for *A. gazella,* noting that after weaning, males experienced a 3–4-yr "growth spurt," almost certainly dependent on available food resources rather than maternal energy expenditure, and which produced the observed sexual dimorphism in this species. Such a growth spurt would violate the assumptions of the Trivers and Willard (1973) hypothesis.

The limited data available on survival in relation to weaning mass are equivocal. LeBoeuf *et al.* (1994) found survival of *M. angustirostris* to age 1 yr was independent of mass at weaning, and Wilkinson and Bester (1990) showed that in *M. leonina* at Marion Island, weaning mass had no influence on survival over the first postweaning foraging trip. In contrast, McMahon *et al.* (2000) and Arnbom *et al.* (1993) both found a significant relationship between weaning mass and survival to age 1 yr in *M. leonina* at Macquarie Island and South Georgia, respectively.

Data on the relationship between mass at weaning and survival to maturity, and reproductive success of offspring are lacking for pinnipeds and, notwithstanding the issue of juvenile growth spurts as described above, it is not yet possible to determine the benefits, if any, of a larger than average size at weaning.

In conclusion, the present study, while providing evidence that female southern elephant seals skew the sex of their offspring according to their ability to invest, does not show any differential postnatal energy investment between the sexes at Marion Island, nor differential costs associated with raising male and female pups. The lack of differential investment, and costs associated with it, seen in this study weaken the finding on skewed sex ratio, since without an increased cost in raising male offspring, there is no selective advantage for females in good condition to produce them. The lack of differential investment in the present study is similar to that found for *M. leonina* at South Georgia (McCann *et al.* 1989; Arnbom *et al.* 1993, 1997), Patagonia (Campagna *et al.* 1992), and the Falkland Islands (Galimberti and Boitani 1999). We are, however, in agreement with the view that, before discounting maternal investment theories, studies need to be undertaken to determine the benefits, if any, of size at weaning on long-term survival and reproductive success (Fedak *et al.* 1996, Trillmich 1996).

Island. We thank Dr. Claudio Campagna and an anonymous referee for valuable comments on an earlier version of the manuscript.

LITERATURE CITED

ANDERSON, S. S., AND M. A. FEDAK. 1987. Grey seal, *Halichoerus grypus*, energetics: Females invest more in male offspring. Journal of Zoology, London 211:667–679.

ARNBOM, T., M. A. FEDAK, I. L. BOYD AND B. J. MCCONNELL. 1993. Variation in weaning mass of pups in relation to maternal mass, postweaning fast duration, and weaned pup behaviour in southern elephant seals (*Mirounga leonina*) at South Georgia. Canadian Journal of Zoology 71:1772–1781.

ARNBOM, T., M. A. FEDAK AND P. ROTHERY. 1994. Offspring sex ratio in relation to female size in southern elephant seals, *Mirounga leonina*. Behavioural Ecology and Sociobiology 35:373–378.

ARNBOM, T., M. A. FEDAK AND I. L. BOYD. 1997. Factors affecting maternal expenditure in southern elephant seals during lactation. Ecology 78:471–483.

ARNOULD, J. P. Y., I. L. BOYD AND D. G. SOCHA. 1996. Milk consumption and growth efficiency in Antarctic fur seal (*Arctocephalus gazella*) pups. Canadian Journal of Zoology 74:254–266.

BONNER, W. N. 1984. Lactation strategies in pinnipeds: problems for a marine mammalian group. Symposium of the Zoological Society of London 51:253–272.

BOWEN, W. D., W. T. STOBO AND S. J. SMITH. 1992. Mass changes of grey seal *Halichoerus grypus* pups on Sable Island: Differential investment reconsidered. Journal of Zoology, London 227:607–622.

BOWEN, W. D., O. T. OFTEDAL, D. J. BONESS AND S. J. IVERSON. 1994. The effect of maternal age and other factors on birth mass in the harbour seal. Canadian Journal of Zoology 72:8–14.

BOYD, I. L., AND T. S. MCCANN. 1989. Pre-natal investment in reproduction by female Antarctic fur seals. Behavioral Ecology and Sociobiology 24:377–385.

BOYD, I. L., J. P. CROXALL, N. J. LUNN AND K. REID. 1995. Population demography of Antarctic fur seals: The costs of reproduction and implications for life-histories. Journal of Animal Ecology 64:505–518.

BURTON, H. R., T. ARNBOM., I. L. BOYD, M. N. BESTER, D. VERGANI AND I. S. WILKINSON. 1997. Significant differences in weaning mass of southern elephant seals from five Sub-antarctic islands in relation to population declines. Pages 335–338 *in* B. Battaglia, J. Valencia and D. W. H. Walton, eds. Antarctic communities: Species, structure and survival. Cambridge, Cambridge University Press.

CAMPAGNA, C., B. J. LEBOEUF, M. LEWIS AND C. BISIOLI. 1992. Equal investment in male and female offspring in southern elephant seals. Journal of Zoology, London 226:551–561.

CLUTTON-BROCK, T. H., F. E. GUINNESS AND S. D. ALBON. 1982. Red deer: The behavior and ecology of two sexes. University of Chicago Press, Chicago, IL.

DEUTSCH, C. J., D. E. CROCKER, D. P. COSTA AND B. J. LEBOEUF. 1994. Sex- and age-related variation in reproductive effort of northern elephant seals. Pages 169–210 *in* B. J. LeBoeuf and R. M. Laws, eds. Elephant seals: Population ecology, behavior and physiology. University of California Press, Berkeley, CA.

FEDAK, M. A., T. ARNBOM AND I. L. BOYD. 1996. The relation between the size of southern elephant seal mothers, the growth of their pups, and the use of maternal energy, fat and protein during lactation. Physiological Zoology 69:887–911.

GALIMBERTI, F., AND L. BOITANI. 1999. Demography and breeding biology of a small, localized population of southern elephant seals (*Mirounga leonina*). Marine Mammal Science 15:159–178.

GOLDSWORTHY, S. D. 1995. Differential expenditure of maternal resources in Antarctic

fur seals, *Arctocephalus gazella,* at Heard Island, southern Indian Ocean. Behavioural Ecology 6:218–228.

GUINET, C. 1991. Growth from birth to weaning in the southern elephant seal (*Mirounga leonina*). Journal of Mammalogy 72:617–620.

HINDELL, M. A., AND D. J. SLIP. 1997. The importance of being fat: Maternal expenditure in the southern elephant seal *Mirounga leonina.* Pages 72–77 *in* M. Hindell and C. Kemper, eds. Marine mammal research in the southern hemisphere. Volume 1. Status, ecology and medecine. Surrey Beatty & Sons, Chipping Norton.

HUBER, H. R. 1987. Natality and weaning success in relation to age of first reproduction in northern elephant seals. Canadian Journal of Zoology 65:1311–1316.

KOVACS, K. M., AND D. M. LAVIGNE. 1986. Growth of grey seal (*Halichoerus grypus*) neonates: differential maternal investment in the sexes. Canadian Journal of Zoology 64:1937–1943.

KRETZMANN, M. B., D. P. COSTA AND B. J. LEBOEUF. 1993. Maternal energy investment in elephant seal pups: Evidence for sexual equality? American Naturalist 141: 466–480.

LEBOEUF, B. J., AND R. M. LAWS. 1994. Elephant seals: An introduction to the genus. Pages 1–26 *in* B. J. LeBoeuf and R. M. Laws, eds. Elephant seals: Population ecology, behavior and physiology. University of California Press, Berkeley, CA.

LEBOEUF, B. J., P. MORRIS AND J. REITER. 1994. Juvenile survivorship of northern elephant seals. Pages 121–136 *in* B. J. LeBoeuf and R. M. Laws, eds. Elephant seals: Population ecology, behavior and physiology. University of California Press, Berkeley, CA.

LEA, M. A., AND M. A. HINDELL. 1997. Pup growth and maternal care in New Zealand fur seals, *Arctocephalus forsteri,* at Maatsuyker Island, Tasmania. Wildlife Research 24:307–318.

LUNN, N. J., AND J. P. Y. ARNOULD. 1997. Maternal investment in Antarctic fur seals: Evidence for equality in the sexes. Behavioral Ecology and Sociobiology 40:351–362.

LUNN, N. J., I. L. BOYD, T. BARTON AND J. P. CROXALL. 1993. Factors affecting the growth rate and mass at weaning of Antarctic fur seals at bird Island, South Georgia. Journal of Mammalogy 74:908–919.

MAYNARD-SMITH, J. 1980. A new theory of sexual investment. Behavioral Ecology and Sociobiology 7:247–251.

MCCANN, T. S., M. A. FEDAK AND J. HARWOOD. 1989. Parental investment in southern elephant seals, *Mirounga leonina.* Behavioral Ecology and Sociobiology 25:81–87.

MCMAHON, C. R., J. VAN DEN HOFF, H. R. BURTON AND P. D. DAVIS. 1997. Evidence for precocious development in female pups of the southern elephant seal *Mirounga leonina* at Macquarie Island. Pages 92–96 *in* M. Hindell and C. Kemper, eds. Marine mammal research in the southern hemisphere. Volume 1. Status, ecology and medecine. Surrey Beatty & Sons, Chipping Norton.

MCMAHON, C. R., H. R. BURTON AND M. N. BESTER 2000. Weaning mass and the future survival of juvenile southern elephant seals, *Mirounga leonina,* at Macquarie Island. Antarctic Science 12:149–153.

MELLISH, J. E., S. J. IVERSON AND W. D. BOWEN. 1999. Variation in milk production and lactation performance in grey seals and consequences for pup growth and weaning characteristics. Physiological and Biochemical Zoology 72:677–690.

MENDL, M., AND E. S. PAUL. 1989. Observations of nursing and sucking behavior as an indicator of milk transfer and parental investment. Animal Behavior 37:513–514.

OFTEDAL, O. T. 1984. Milk composition, milk yield and energy output at peak lactation: a comparative review. Symposium of the Zoological Society of London 51: 33–85.

POMEROY, P. P., M. A. FEDAK, P. ROTHERY AND S. ANDERSON. 1999. Consequences of

maternal size for reproductive expenditure and pupping success of grey seals at North Rona, Scotland. Journal of Animal Ecology 68:235–253.

REITER, J., AND B. J. LeBOEUF. 1991. Life history consequences of variation in age at primiparity in northern elephant seals. Behavioral Ecology and Sociobiology 28: 153–160.

REITER, J., N. L. STINSON AND B. J. LeBOEUF. 1978. Northern elephant seal development: The transition from weaning to nutritional independence. Behavioral Ecology and Sociobiology 3:337–367.

SMISETH, P. T., AND S. H. LORENTSEN. 1995. Evidence of equal maternal investment in the sexes in the polygynous and sexually dimorphic grey seal (*Halichoerus grypus*). Behavioral Ecology and Sociobiology 36:145–150.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. W. H. Freeman & Co., New York, NY.

SYDEMAN, W. J., AND N. NUR. 1994. Life history strategies of female northern elephant seals. Pages 137–153 *in* B. J. LeBoeuf and R. M. Laws, eds. Elephant seals: Population ecology, behavior and physiology. University of California Press, Berkeley, CA.

TESTA, J. W. 1987. Long-term reproductive patterns and sighting bias in Weddell seals (*Leptonychotes weddelli*). Canadian Journal of Zoology 65:1091–1099.

TRILLMICH, F. 1986. Maternal investment and sex allocation in the Galapagos fur seal, *Arctocephalus galapagoensis.* Behavioral Ecology and Sociobiology 19:157–164.

TRILLMICH, F. 1996. Parental investment in pinnipeds. Advances in the Study of Behavior 25:533–577.

TRIVERS, R. L. 1972. Parental investment and sexual selection. Pages 135–179 *in* B. Campbell, ed. Sexual selection and the descent of man. Aldine publication Corporation, Chicago, IL.

TRIVERS, R. L., AND D. E. WILLARD. 1973. Natural selection of parental ability to vary sex ratios of offspring. Science 179:90–92.

WILKINSON, I. S., AND M. N. BESTER. 1990. Duration of post-weaning fast and local dispersion in the southern elephant seal, *Mirounga leonina,* at Marion Island. Journal of Zoology, London 222:591–600.

WILKINSON, I. S., AND R. J. VAN AARDE. 1999. Marion Island elephant seals: The paucity of males hypothesis tested. Canadian Journal of Zoology 77:1547–1554.

ZAR, J. H. 1984. Biostatistical analysis. Second edition. Prentice-Hall, Englewood Cliffs, NJ.