

SEXUAL DIMORPHISM IN NEWBORN SOUTHERN SEA LIONS

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ABSTRACT

Male southern sea lion, *Otaria byronia*, pups born at Península Valdés, Argentina, were significantly heavier (13.7 ± 1.6 kg, $n = 37$ vs. 12.3 ± 1.4 kg, $n = 38$) and longer (0.82 ± 0.04 m, $n = 29$ vs. 0.79 ± 0.03 m, $n = 29$) than females. The rate of mass and length gain during the first month of life did not differ between the sexes (males: 0.21 kg/d, 0.003 m/d; females: 0.20 kg/d, 0.004 m/d). Sex differences in pup body size were not reflected in female nursing behavior, attendance patterns, and duration of feeding trips. These results suggest that southern sea lion mothers invest more energy in sons than in daughters during gestation, a difference consistent with the importance of large body size to the reproductive success of males in a polygynous species.

Key words: southern sea lion, *Otaria byronia*, sexual dimorphism, Península Valdés, body mass, growth rate, maternal behavior.

All otariids are polygynous (Bartholomew 1970) and in polygynous mammals large adult size is likely to benefit males more than females (Clutton-Brock *et al.* 1981, 1982). Among sea lions and fur seals, success in male-male competition for mates partially depends on strength, resistance, and fighting ability between contenders (Bartholomew and Hoel 1953, Campagna and Le Boeuf 1988). Thus, sexual selection in these species will favor large, more competitive individuals that monopolize reproduction (Bartholomew 1970, Alexander *et al.* 1979).

¹ The order of the first two authors was determined randomly.

Sexual size dimorphism of adults is striking among the otariids, with males being at least three times the mass of adult females (Bartholomew 1970, Alexander *et al.* 1979, King 1983). Under these circumstances, if the amount of parental investment partially affects adult body size, sex allocation theory predicts that mothers should invest extra resources in sons, even at an equal primary sex ratio (Maynard Smith 1980). A male-biased investment is not predicted by traditional sex-ratio theory when the primary sex ratio of the population is 1:1 (Fisher 1930). Congruent with Maynard Smith's (1980) theory, maternal investment in fur seals and sea lions is usually male biased during early gestation (York 1987), at birth (Ling and Walker 1977, Payne 1979, Costa and Gentry 1986, Trillmich 1986, Ono *et al.* 1987), and at weaning (Rand 1956, Doidge *et al.* 1984, Trillmich 1986) despite a 1:1 sex ratio at birth found in virtually all populations studied (Bonner 1968, Trillmich 1986, Kerley 1987, Roux 1987, Vaz-Ferreira and Ponce de León 1987).

The southern sea lion, *Otaria byronia*, is one of the largest and most dimorphic of the otariids. Adult males are up to five times heavier than females (Hamilton 1934, 1939). Differences in size between males and females have been documented also among juveniles (Hamilton 1934, 1939), but the question of sexual dimorphism has not been investigated in pups. The sex ratio at birth in one population of Patagonia was shown to be close to unity in a sample of 503 pups (Lewis and Ximenez 1983, Crespo 1988).

In this paper, we compare body mass and standard length at birth, and growth rate and maternal behavior during the first weeks after birth of male and female southern sea lion pups born at Península Valdés, Argentina. Following Maynard Smith (1980), we predict that male newborns should be heavier and longer than females and should grow faster. If mothers of sons do incur higher energetic costs than those with daughters, we also predict that female nursing, attendance, and foraging behavior would differ in accordance to the sex of the offspring.

METHODS

This study was conducted during two consecutive breeding seasons (January to mid-February, 1989 and 1990) at Faro of Punta Norte rookery, Península Valdés, Argentina (*see* Fig. 1 in Campagna 1985). Detailed information on the area, colony, breeding cycle, and reproductive behavior of the species is given in Campagna (1985), and Campagna and Le Boeuf (1988).

Mass, length, and growth of pups—We measured body mass and standard length of 77 pups, 44 in 1989 (24 males, 20 females), and 33 in 1990 (15 males, 18 females). Maternal investment during gestation was estimated by weighing and measuring pups within 12 h after birth. For these studies we weighed 75 newborns (37 males, 38 females), and measured 58 newborns (29 males, 29 females).

Body mass was obtained by capturing pups with a noose pole (Gentry and Holt 1982) and placing them in a canvas or nylon bag. A spring balance, with

a capacity of 50 kg (± 0.25 kg), was attached to eyelets on the bag. The pup was lifted by hand. Pups were selected before birth by marking their pregnant mothers as they arrived at the breeding area. Sex was determined when pups were weighed. Captured pups were tagged with plastic tags on the rear end of the front flipper and bleach-marked to facilitate identification for recapture. The entire operation took about 15 min, after which pups were released close to their mothers. Mothers readily accepted and nursed marked pups, all of which survived to the end of the study.

Mass gain during the first 33–45 d of the nursing period was estimated by weighing 61 pups (32 males, 29 females) at about weekly intervals, and measuring 47 of them (24 males, 23 females) to the closest centimeter. We collected 218 weights and 158 standard lengths. Each pup was handled a mean of 3.1 ± 1.0 times ($n = 61$). As body mass, standard length, and growth rate for male and female pups did not differ between years ($P > 0.05$), we combined the data for each sex.

To study pup growth, we conducted a linear regression analysis including all records available for every animal that gained mass and length. Following Kovaks and Lavigne (1986), we tested the effect of violating the assumption of lack of independence within the growth data for a linear regression analysis by selecting, at random, one value per animal and comparing the regression lines obtained in this way with one that included all data available. We found no significant difference ($P > 0.05$) in the slopes and intercepts of the compared regression lines for mass (kg) on pup age (days) in males (ANCOVA, $F = 0.04$, 0.02 , $n = 114$) and females ($F = 0.60$, 0.28 , $n = 110$), and for standard length (m) on pup age in males ($F = 0.11$, 0.42 , $n = 116$) and females ($F = 1.34$, 0.11 , $n = 110$). Likewise, a regression line of male and female mass as a function of length, including all data for male and female pups weighed and measured during the same capture, did not differ from one fitted by randomly selecting one value for each animal (ANCOVA for log-transformed data: slope, $F = 0.12$, $df = 1$, 216 ; intercept, $F = 0.74$, $df = 1$, 217 , $P > 0.05$).

Comparisons between the sexes for growth rate were conducted without controlling for differences in initial mass because mass at birth did not correlate with individual rate of mass gain (Pearson's product-moment correlation: males, $r = -0.09$, $n = 24$; females, $r = 0.17$, $n = 25$, $P > 0.05$). Similar results were obtained for length (males, $r = 0.08$, $n = 14$; females, $r = 0.05$, $n = 15$, $P > 0.05$).

We did not pursue our growth study further than the end of the breeding season because female pups begin to migrate out of the area (Lewis and Ximenez 1983).

Maternal behavior—Southern sea lion females give birth about three days after arrival, copulate six days later, and go to sea to feed about eight days after parturition. Thereafter, females alternate periods on land nursing their pups with periods feeding at sea (Campagna and Le Boeuf 1988).

We marked 77 pregnant females (44 in 1989, 33 in 1990) with paint pellets on the day they arrived at the rookery (Campagna and Le Boeuf 1988). Identification cards and serial records were kept of the daily presence and key

activities of marked females such as date of parturition, departure on a feeding trip, duration of feeding trips, and time on land after feeding.

The first five feeding trips were combined because their duration was similar (ANOVA mothers with sons: $F = 0.42$, $df = 4$, 114; with daughters: $F = 0.86$, $df = 4$, 116). Likewise, we combined the attendance periods after the first five feeding trips (ANOVA mothers with sons: $F = 1.06$, $df = 4$, 96; with daughters: $F = 0.53$, $df = 4$, 95, $P > 0.05$).

The durations of suckling sessions and on-teat periods during suckling sessions were determined by focal animal samples (FAS; Altmann 1974). Sampling started opportunistically, when a marked female began nursing her pup, and ended when nursing was over. Suckling sessions consisted of both on-teat periods and short breaks of less than 30 sec between them (Oftedal *et al.* 1987). We recorded 39 complete suckling sessions (20 h) of marked female-pup pairs (10 pups of each sex). Pups suckled only from their mothers.

Comparisons between pups of suckling behavior by sex was done without correcting for pup age or differences in duration of suckling sessions because: (1) pup age was not correlated with the proportion of on-teat time during suckling sessions at this early period of lactation (Spearman rank correlation corrected for ties, $r_{ho} = 0.20$, $n = 32$, $P > 0.05$), and (2) the proportion of on-teat time was not correlated with the length of a suckling session (Spearman rank correlation corrected for ties, $r_{ho} = -0.25$, $n = 27$, $P > 0.05$). The length of suckling sessions was correlated with pup age (Spearman rank correlation corrected for ties, $r_{ho} = 0.58$, $n = 27$, $P < 0.01$) but, in our sample, the mean age of male pups (9.2 d) was similar to that of females (8.7 d, $t = 0.21$, $df = 29$, $P > 0.05$).

Scan samples (Altmann 1974) were used to estimate the proportion of time that mothers devoted to resting, nursing, and interacting with offspring (*i.e.*, nuzzling, vocalizing). The activity of up to ten marked mothers was recorded every five minutes during 3–6 one-hour periods per day randomly distributed throughout daylight hours. A total of 9,946 records were collected during both years (6,654 in 1989, 3,292 in 1990). As time budgets did not differ between years, the data were combined (Yates' corrected Chi square, nursing = 3.21, resting = 1.92, $P > 0.05$). Interactions with offspring were recorded only in 1989.

Standard parametric tests were carried out using procedures described in Sokal and Rohlf (1981) and Snedecor and Cochran (1980) and by means of statistical programs (STATISTIX, N. H. Analytical Software and BIOM, Applied Biostatistics, Inc. 1986) after testing for normal distribution (Wilk-Shapiro test) and homoscedasticity (Bartlett's test). Non-parametric statistical tests were used when the data did not conform to the assumptions of parametric statistics even after data transformations.

RESULTS

Body mass and standard length at birth—Newborn males were 10% heavier and 4% longer than females (Table 1).

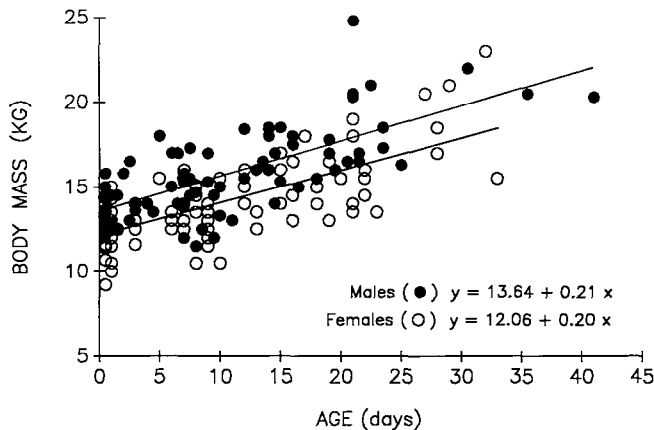


Figure 1. Regression of mass on pup's age for the first 33–45 d of life. Slopes are significantly different from zero for males (ANOVA $F = 73.52$, $df = 1, 27$, $P < 0.001$, $r^2 = 0.52$, $n = 85$) and females (ANOVA $F = 56.55$, $df = 1, 26$, $P < 0.001$, $r^2 = 0.70$, $n = 87$), but not from each other (ANCOVA $F = 0.03$, $df = 1, 161$, $P > 0.05$). Intercepts are significantly different from each other (ANCOVA $F = 41.59$, $df = 1, 162$, $P < 0.001$).

Growth rates—Males and female pups grew, in mass and length, at a similar rate during the first month and a half of life (Fig. 1, 2).

Body mass increased about 2.5 times faster than length (log mass = $2.41 \log \text{length} + 1.34$; the slope is statistically significant, $F = 323.72$, $df = 1, 91$, $P < 0.001$, $n = 137$, $r^2 = 0.71$; both sexes combined).

Seven of 31 male pups and four of 29 female pups lost mass during the first month after birth. The sexes did not differ in the proportion of pups that loss mass (Yates' corrected Chi-square = 0.30, $P > 0.05$).

Female behavior—The sex of the offspring did not affect the duration of the (1) interval between parturition and first feeding trip, (2) first five foraging trips, and (3) intervals on land after each foraging trip (Table 2).

The sex of the offspring (males *vs.* females) did not affect the percentage of time mothers devoted to nursing (12.2 *vs.* 11.0%; $n = 9,946$ scans), interacting with their pup (2.5 *vs.* 2.4%; $n = 6,654$), and resting (64.8 *vs.* 64.2%; $n = 9,946$) (Yates' corrected Chi-squares = 3.21, 0.001 and 0.92, respectively; $P > 0.05$).

Table 1. Mean (± 1 SD) body mass (kg) and standard length (m) of newborn sea lions. Differences are statistically significant for mass ($t = 4.07$, $P < 0.001$) and length ($t = 3.49$, $P < 0.001$).

	Body mass	Standard length
Males	13.7 ± 1.6 (37)	0.82 ± 0.04 (29)
Females	12.3 ± 1.4 (38)	0.79 ± 0.03 (29)

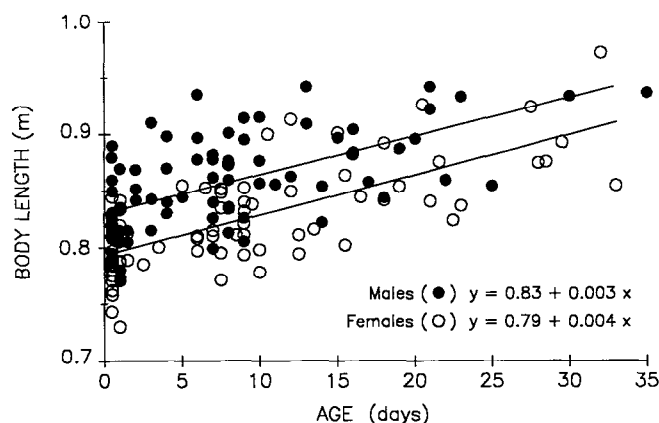


Figure 2. Regression of length on pup's age for the first month of life. Slopes are significantly different from zero for males (ANOVA $F = 39.44$, $df = 1, 26$, $P < 0.001$, $r^2 = 0.38$, $n = 82$) and for females (ANOVA $F = 77.10$, $df = 1, 23$, $P < 0.001$, $r^2 = 0.47$, $n = 74$) but not from each other (ANCOVA $F = 0.04$, $df = 1, 152$, $P > 0.05$). Intercepts are significantly different from each other (ANCOVA $F = 44.04$, $df = 1, 153$, $P < 0.001$).

The length of suckling sessions and on-teat time during suckling sessions were variable (range = 3–100 and 2–61 min, respectively) and similar for male and female pups (Mann-Whitney U-test, $U = 218, 207$, respectively; $n = 17-19$; $P > 0.05$). Male pups tended to spend more time on-teat during a suckling session ($59.8\% \pm 18.3\%$, $n = 21$) than females ($50.9\% \pm 18.2\%$, $n = 18$) but the difference was not statistically significant (Mann-Whitney U-test, $U = 250$; $n = 18-21$; $P > 0.05$).

DISCUSSION

Southern sea lions born at Península Valdés are sexually dimorphic in mass and length at birth. This result is consistent with reports on juveniles of the same species in other populations (Hamilton 1934), and on newborns of other

Table 2. Mean (± 1 SD) duration in days between birth and first feeding trip, mean duration of feeding trips (first five), and interval on land after feeding trips as a function of pup sex. (): sample size. []: number of females studied. Differences for each variable were not significant (after logarithmic transformation of the data due to heteroscedasticity; $t = 1.82, 1.19$ and 0.71 , respectively; $P > 0.05$).

	Interval birth–1 trip	Feeding trips	Attendance on land
Male pups	7.7 ± 1.1 (47) [47]	2.8 ± 1.1 (119) [51]	2.1 ± 1.0 (101) [44]
Females pups	7.3 ± 1.3 (35) [35]	3.0 ± 1.2 (121) [44]	2.0 ± 0.8 (100) [42]

otariids (Rand 1956, Ling and Walker 1977, Payne 1979, Doidge *et al.* 1984, Costa and Gentry 1986, Trillmich 1986, Croxall and Gentry 1987, Ono *et al.* 1987, Costa *et al.* 1988). The degree of sexual dimorphism of southern sea lion neonates is similar to that of fur seal neonates, in which males are 9–18% heavier than females (Trillmich 1986, Croxall and Gentry 1987). Assuming no sex difference in energy expenditure by fetuses, sexual dimorphism in size of newborn pups suggests that southern sea lion females invest more in sons than in daughters during gestation.

Contrary to other otariids, in which males increase in mass faster than females (Payne 1979, Doidge *et al.* 1984, Trillmich 1986), in the southern sea lion the sexes grow at the same rate during early lactation. However, because size dimorphism present at birth persists, sons may continue to be more costly than daughters to their mothers during lactation. This assumes that metabolic rates are similar for male and female pups. In a small sample of northern fur seal pups, males had a significantly lower metabolic rate than females (Costa and Gentry 1986) but this was not shown for other otariids.

We do not know if differences in size found at birth in the southern sea lions at Península Valdés persist until weaning, but there is evidence suggesting that this may be true. Six-month old male southern sea lion pups at the Falkland (Malvinas) Islands are longer than females, the difference in length remains in eighteen-month old individuals, and it is even more marked in older juveniles (Hamilton 1934). Moreover, data for other otariids show that sexual dimorphism at birth persists at weaning (*e.g.*, Doidge *et al.* 1984, Trillmich 1986).

As in the otariids, in some of the most polygynous and sexually dimorphic phocids, male pups tend to be heavier than females at birth, at weaning, or both, but we cannot yet conclude that females invest more in sons. In the largest of the pinnipeds, the southern elephant seal, *Mirounga leonina*, male pups born at South Georgia Island are heavier than females at birth (McCann *et al.* 1989). The mass difference persists at weaning but it is not statistically significant, probably due to a small sample size (McCann *et al.* 1989). In a sample of the same species at Península Valdés, male pups are not heavier than females at birth or at weaning. In the northern elephant seal, *M. angustirostris*, males are heavier than females at weaning (Le Boeuf *et al.* 1989), but mothers invest equally in sons and daughters when investment is measured in terms of the mother's future reproductive success (Le Boeuf *et al.* 1989), and energetics of lactation (Kretzmann 1990). Male gray seal pups are larger at birth, gain mass at a faster rate, and are weaned at a heavier mass than females (Boyd and Campbell 1971, Kovacs and Lavigne 1986, Anderson and Fedak 1987).

In the southern sea lion, size dimorphism of pups early in lactation is not reflected in differences in female nursing behavior, length of foraging trips, or periods on land attending the pup after feeding. Similar findings have been reported in the Steller sea lion, *Eumetopias jubatus* (Higgins *et al.* 1988). These results suggest that behavioral data may not be a good indicator of female differential investment in the sexes early in lactation. The effect of pup sex on female behavior may be more pronounced later in life with the increasing nutritional demands of growing pups.

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