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Mass transfer from mothers to pups and mass recovery by mothers during the post-breeding foraging period in southern elephant seals (*Mirounga leonina*) at King George Island

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Abstract Mass transfer from mother to pup during the lactation period, and mass recovery for the same females during the foraging period were measured in the southern elephant seal at King George Island, Antarctica. During the 19.2 ± 0.9-day lactation period measured (which represented 87% of the entire nursing), females lost a mean mass of 10.56 ± 1.76 kg/day (n = 27), while their pups gained a mean mass of 5.27 ± 1.1 kg/day. There was a correlation between daily body weight gain in pups and daily weight loss by their mothers. Pup weaning mass was positively related to maternal post-partum mass. Serial samples showed that weight losses by females and gains by their pups were not linear over lactation, but showed lower values at the beginning and at the end of lactation. During the 60.5 ± 6.2-day foraging phase between the end of lactation and molt, females gained 2.21 ± 0.65 kg/day (n = 12), or 54% of the mass lost during nursing. Growth rates reported here are higher than those reported in other breeding sites. However, the ratio of body mass loss by females to gain by their pups was similar, suggesting that higher growth rates and greater weaning mass at South Shetland are due to a higher mean weight of females on arrival at this breeding site. The foraging period was shorter and the mass gained greater than those measured at South Georgia; this could be related to relatively shorter distances to foraging areas.

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Introduction

Southern elephant seals have a circumpolar distribution in the Southern Ocean. The breeding sites are placed in sub-Antarctic islands, with the only continental breeding site at Península Valdés, Argentina. At the South Shetland Islands, pregnant females start to haul out from the end of September to November. They give birth approximately 1 week after arrival and nurse their pups for about 23 days. During the suckling period pups increase their birth weight by 3–4 times . As with most phocid pinnipeds, female southern elephant seals experience high demands on body reserves during this period, not only when mothers fast but also when they suckle their pups (McCann et al. 1989). After breeding, females spend about 70 days at sea, after which time they come back ashore to molt (Boyd et al. 1993).

Growth rates of southern elephant seal pups have been reported at several sub-Antarctic islands (e.g. Laws 1953; Little et al. 1987; Guinet 1991; Hindell et al. 1994) but size and weight loss by their mothers recorded only at South Georgia (McCann et al. 1989; Fedak et al. 1994). Additionally, weight gains by females between lactation and molt were reported by Boyd et al. (1993).

The mass of pups at weaning at the South Shetland Islands, is higher than at any other site.

The aims of the present study were to test the possibility that inter-island growth rate differences might be due to differences in maternal mass at parturition, and to measure weight gain during the foraging phase between the end of lactation and molt for this population.

Materials and methods

The study was carried out at Stranger Point, King George Island (62°14′S, 58°40′W), during the 1994/1995 and 1995/1996 austral spring and summer. This breeding population is located at the southernmost distribution range for this species. Approximately 500 pups are born at Stranger Point each season along about 6 km of coast. On the day of parturition, 27 female southern elephant seals were randomly selected and immobilized with ketamine hydrochloride using an intramuscular dose of 2.61–5.61 mg/kg body weight. When the animals were manageable, the females were weighed in a net stretcher suspended from a load cell (Challenger AZM, 1000 ± 0.5 kg) attached to an aluminium tripod. After weighing, standard length and girth were measured and females were hot-iron branded (Ingham 1967). After finishing the procedure for the females, their pups were weighed and marked with paint and flipper tags. Three days before the expected weaning date (Carrick et al. 1962; McCann 1982), the 27 mother-pup pairs were recaptured, immobilized, weighed and measured as before. An additional weighing was carried out for all pups on or within 1 day of weaning.

To compare the daily weight loss by females and gain by their pups at different stages during the suckling period, sequential weights were carried out on 7 of the 27 mother-pup pairs. These pairs were weighed on the parturition day, on the 4th, 14th and 19th day of lactation and, whenever possible, on the 21st day. For comparison, we defined four different periods: 1st (0–4 days); 2nd (4–14 days); 3rd (14–19 days); 4th (19–21 days).

After the end of the breeding season, daily checks were made for the presence of marked seals at Stranger Point. Twelve of the 27 females from the lactation period study returned to Stranger Point to molt between the end of December and February. These animals were immobilized and the procedure for weighing was repeated.

The experimental period for this group, i.e., the days between the first and last procedures during the lactation period ($\overline{X} = 19.3 \pm 0.8, n = 12$), was shorter than their entire lactation period ($\overline{X} = 22.7 \pm 1.9, n = 12$). Since the weight loss of females is not linear over lactation but shows lower values at the beginning and at the end of lactation (see results), we estimated the additional weight loss from the last weighing to the end of lactation (A) as follows:

$$A(kg) = (Fw * 0.0103\,kg/kg * day) * D + (Pw * 0.0083\,kg/kg * day) * D + G$$

where Fw = last weight of females (kg); 0.0103 = mass-specific mass loss rate (kg/kg * day), estimated from 5 females during molt; D = days of lactation after the last weighing; Pw = weight of pups (kg) measured during the last procedure for a mother-pup pair during lactation; 0.0083 = mass-specific mass loss rate (kg/kg * day), estimated from 20 pups during fast, and G = mass gains by the pup since the last procedure for a mother-pup pair until they were weaned.

Mass-specific mass loss rate (kg/kg * day) during the fast was calculated by dividing daily mass loss by the mean mass of the females or pups. Mean mass was calculated from the arithmetic mean measured over a period of at least 20 days during molt for females, or 30 days after weaning for pups.

All percentage data were arcsine-transformed before being subjected to analysis of variance (ANOVA).

Values are given as means ± SD except where otherwise indicated.

Results

Breeding

Twenty-seven mother-pup pairs were weighed when mothers gave birth. The initial weight of females ranged from 379.5 to 847.5 kg ($\overline{X} = 642.6 \pm 121.8$ kg, $n = 27$). The period between the first and second weighings (19.2 ± 0.9 days) was shorter than the females' lactation period ($\overline{X} = 22.1 \pm 2.3$ days). During the experimental period, females lost a mean mass of 10.56 ± 1.76 kg/day, ($n = 27$). The rate of mass loss of females was positively correlated with initial body weight (Fig. 1).

The mean mass of newborn pups was 47.6 ± 6.4 kg ($n = 27$), and during the experimental period pups gained 5.27 ± 1.1 kg/day. Data on birth and weaning weight for pups whose mothers were recaptured during molting are shown in the appendix. The mean rate of weight gain by pups was significantly correlated with a mean rate of weight loss by their mothers (Fig. 2). The slope of this relationship (0.54) is the mass transfer efficiency, i.e. kilogram of pup mass gained per kilogram of maternal mass lost.

Pup weight at weaning ranged from 111.5 to 206 kg with a mean of 154.1 ± 27.6 kg. Pups gained a mean mass of 106.5 ± 24 kg during the entire lactation period. The weaning mass was positively correlated with the initial post-partum mass ($F_{(1,25)} = 38.6, P < 0.001, r^2 = 0.59$).

The mean rate of mass loss by mothers sampled sequentially (expressed as percentage of initial body mass) and the mean growth rates of their pups (expressed as percentage of the last weighing during the experimental period) were significantly different among the periods considered (ANOVA, $F = 9.18$, $P < 0.001$ for females; ANOVA, $F = 10.77$, $P < 0.001$ for pups). The percentage of mass loss by females or gain by their pups in the 1st period was significantly lower than in the 2nd and 3rd periods (Table 1, Fig. 3).

The maximum total mass loss of any female was 273.5 kg over 20 days, which was a mean mass loss of 13.68 kg/day. However, the maximum mass loss rate was recorded in the 2nd period (15.5 kg/day) in a female weighed sequentially, whose total weight loss was 256 kg over 19 days.

Finally, the minimum mass loss of any female was 139.5 kg over 20 days, which represented a mean mass loss of 6.98 kg/day. The lowest values were registered in

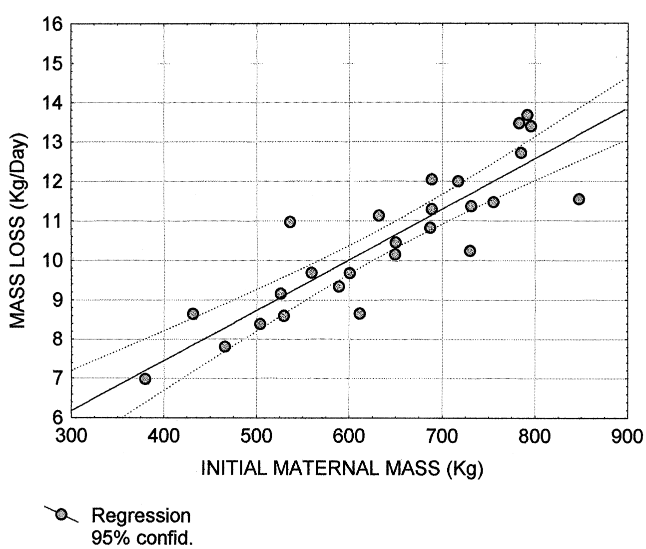

Fig. 1 Relationship between post-partum mass of mother (Mp) and daily mass loss (Dm): Dm = 2.48 + 0.013 * Mp, $F_{(1,25)} = 85$, $P < 0.001$, $r^2 = 0.77$

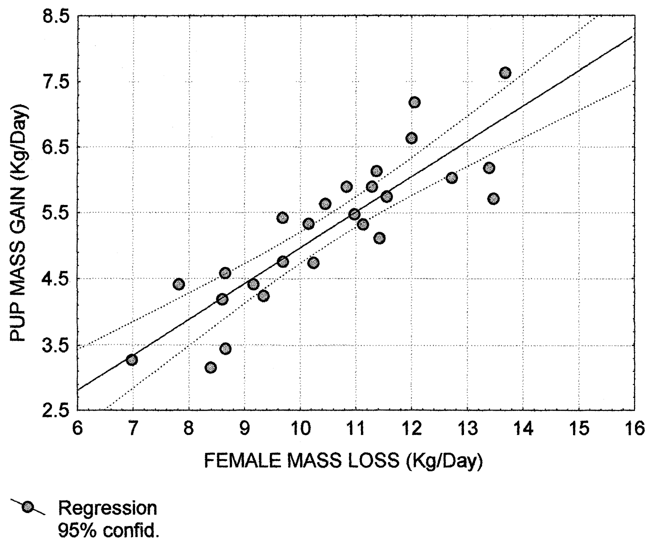

Fig. 2 Relationship between rate of mass loss by females (Rf) and rate of mass gain by their pups (Rp): Rp = −0.47 + 0.54 ∗ Rf, $F_{(1,25)} = 75.4, P < 0.001, r^2 = 0.74$

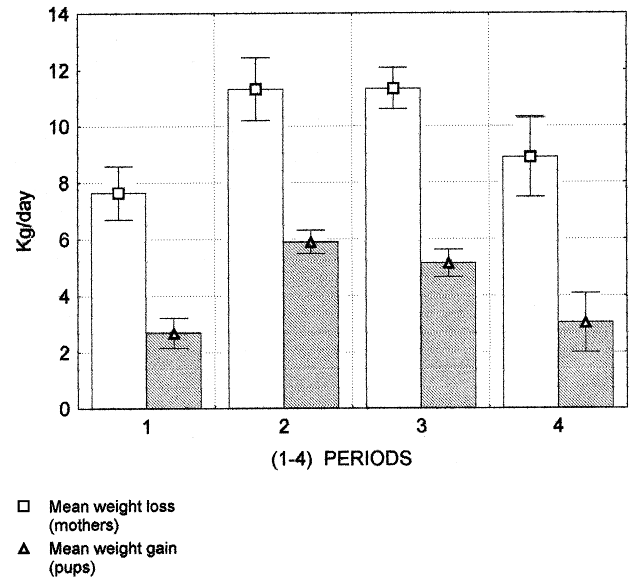

Fig. 3 Mass loss by females and weight gain by their pups in couples weighed sequentially. Values represent mean ± standard error for four periods during lactation: 1st (0–4 days); 2nd (4–14 days); 3rd (14–19 days); 4th (19–21 days)

the same female (which was weighed sequentially) in the 1st (4.88 kg/day) and 4th (4.75 kg/day) periods.

Foraging period

Females spent a mean time of 60.5 ± 6.2 days at sea between the end of lactation and molt (Table 2). There was a positive correlation between the departure date at the end of lactation and the date of return to molt ($F_{1,10} = 11.8, P < 0.05, r^2 = 0.49$). The daily mass gain for individuals during this period was 2.21 ± 0.65 kg/day (n = 12), which represented a mean mass gain of 132 ± 35.6 kg during this period. The recovery of mass during the foraging period represented a mean of 54.5% of the weight lost during lactation.

There was no significant correlation between the rate of mass gained or the total mass gained and the time spent at sea, or with the mass of females at the end of lactation.

Table 1 Mean mass loss rate by females (expressed as percentage of initial body mass) and mean pup growth rates (expressed as percentage of last weighing during experimental period) at different periods during lactation: 1st (0–4 days); 2nd (4–14 days); 3rd (14–19 days); 4th (19–21 days)

Period	(n)	Females		Pups	
		Mean	SD	Mean	SD
1st	7	1.2^{a}	0.23	1.8^{a}	0.7
2nd	7	1.8^{b}	0.19	4.1^{b}	0.5
3rd	7	1.8^{b}	0.29	3.6^{b}	0.9
4th	4	1.6^{ab}	0.35	2.1^{ab}	1.4

[ab]Means not sharing a common superscript $^{(a,b)}$ are significantly different at $P < 0.05$, Tukey test

Discussion

Phocid seals have a characteristic lactation pattern, which involves the production of an energetically rich milk, a relatively short suckling period and spatial and temporal separation of pupping and nursing activities from foraging (Bonner 1984; Oftedal et al. 1987). This pattern determines a depletion of an important proportion of the females' reserves after lactation. During the 19.2 days of the experimental period, southern elephant seals at King George Island lost a mean total mass of 202 ± 34 kg (n = 27) or about 32% of their body mass. The estimated mass losses over the entire lactation period, using the equation, would be 35% of their body mass at the beginning of lactation. Northern elephant seals lose 42% of their mass during the 26.5 days of the lactation period (Costa et al. 1986). A longer lactation period in northern elephant seals than in the southern species would produce a relatively higher maintenance cost. However, the observed differences can also be related to a proportionately greater nutrient transfer, since fat reserves of pups at weaning are higher in northern elephant seals (50% of weaning mass, Ortiz et al. 1978; Kretzman et al. 1993) than in southern elephant seals (37–41% of weaning mass, Bryden 1969; Hindell et al. 1994; Carlini et al. 1995).

The mean rate of mass loss by females was highly variable, the lowest being 6.98 kg/day and the highest 13.68 kg/day, and it was related to female mass at parturition (Fig. 1).

The relation between maternal mass at parturition and the weaning mass observed in this study had been previously shown at other breeding sites (McCann et al. 1989; Campagna et al. 1992; Arnbom et al. 1993). Fe-

Table 2 Mass loss of adult female southern elephant seals during lactation and mass gained during foraging period between the end of lactation and the beginning of molt

Seal	Mass at start of lactation	Mass at end of lactation	Days of lactation	Δ Mass (kg)	Time spent at sea (days)	Mass gain at sea (kg)	Mass gain kg/day
848	631.5	398	22	233.5	58	98	1.69
61	847.5	584.5	24	263	59	95.5	1.62
67	649.5	389	26	259.5	67	125	1.86
64	535.5	327	19	208.5	71	168.5	2.37
53	600	390	23	210	54	174	3.22
98	717	439.5	24	277.5	60	204	3.4
42	688.5	428.5	23	259	65	108	1.67
92	731	495	22	236	64	109	1.7
3	688.5	410.5	25	278	52	136.5	2.63
74	795.5	522.5	21	273	60	153.5	2.56
70	730	502	23	228	51	120	2.35
36	529	348.5	21	180.5	65	94	1.45
Mean	678.6	436.2	22.7	242.3	60.5	132.2	2.21
SD	95.9	75.8	1.9	31.4	6.2	35.6	0.65

male elephant seals remain with their pups throughout lactation. All the energy required to suckle the pup is contained in the maternal body reserves. Hindell et al. (1994) suggested that the growth rate can be related to maternal condition rather than simple mass. Although this can be so, it seems that heavier mothers would have at least more absolute reserves, especially if the enormous difference in the mass of females at parturition (379.5–847.5 kg) is considered. Additionally, it is suggested that larger animals are able to use proportionally more of their adipose tissue for milk production than smaller ones (Costa 1991). According to this, larger females would have more available reserves than smaller females to invest in their pups, as was showed by McCann et al. (1989), Campagna et al. (1992) and Arnbom et al. (1993). A differential rate of growth by the pup seems to be achieved mainly by the different rate of milk ingestion, but it may also be partly due to the production of fatter milk, since important differences in fat content have been observed at the same stages of lactation in different females of southern elephant seals (Carlini et al. 1994; Hindell et al. 1994).

During the experimental period, females lost mass at a mean rate of 10.56 ± 1.76 kg/day (n = 27), while their pups gained 5.27 ± 1.1 kg/day (n = 27). The values reported here are significantly higher than those reported by McCann et al. (1989) at South Georgia [7.8 ± 1.2 kg/day (n = 15), t-test $P < 0.001$, and 3.7 ± 0.8 kg/day (n = 15), t-test $P < 0.001$] respectively. Although the mean mass of females after parturition was different at both breeding sites (506 ± 110 kg, n = 15 and 643 ± 122 kg, n = 27 for South Georgia and our study respectively), the ratio of body mass gain by pups to mass loss by their mothers was similar in both populations. Moreover, the mean daily mass changes expressed as percentage of initial body mass (1.5% for South Georgia and 1.6% for this study) were also similar, suggesting no differences in transfer efficiency at both breeding sites. Therefore, the higher mean growth rate and weaning mass for pups at South Shetland could be explained by differences in the initial body mass of their mothers.

Although the reproductive pattern adopted by these animals allows them to feed far away from the breeding site and utilize a dispersed prey resource, and to disperse the lactation costs over 10 months (Costa et al. 1986; Costa 1991), the mass and body composition at the beginning of lactation will be related to their feeding success during the non-breeding period in a determined foraging area. Hindell et al. (1994), comparing pup growth rates at different breeding sites, did not find geographic trends among them, since the lowest and the highest growth rates were from islands in the southern Indian Ocean, while the two populations from the southern Atlantic had growth rates significantly different from each other. Additionally, we found the highest growth rate reported at South Shetland. However, Burton et al. (1994) suggested that lower pup mass at weaning observed in populations in the Indian Ocean, in comparison with those in the Atlantic Ocean, could be related to the population declines observed in the Indian Ocean.

After weaning, southern elephant seal pups fast over a mean period of 45 days before departing to sea (Arnbom et al. 1993). Weaning mass may be an important factor determining survival, since we observed that pups spent, on average, 54% of their energy reserves during fasting (A.R. Carlini, H.O. Panarello, M.E.I. Mórquez, G.E. Soave and G.A. Daneri, unpublished data). Arnbom et al. (1993) suggested that large pups at weaning may have an advantage over small ones because they will have proportionately greater energy reserves when going to sea, and also the benefit of a longer post-weaning fast during which they may learn social, diving and swimming behavior.

Females spent on average 60.5 days between the end of lactation and molt (Table 2). The mean value is significantly lower than that reported by Boyd et al. (1993) at South Georgia (72 ± 0.9 days, n = 8, t-test $P < 0.001$). To calculate mass gain during this period, we must estimate the mass of mothers when they leave the beach after lactation. Since we suggested that mass loss rate by females at the end of lactation was lower than that observed between the 4th and 19th days of lactation, a simple extrapolation of the mean rate of weight loss during the experimental period (approximately 1st to 19th days) may result in an overestimation of weight loss during lactation, and therefore an overestimation of weight gained during the foraging period. For the 12 females recovered when they arrived to start molt, the experimental period measured was 19.3 $\pm$ 0.8 days (range 19–21) and the entire suckling period was 22.7 $\pm$ 1.9 days. For these females we estimated mass loss by the equation for a mean of 3.4 $\pm$ 2.2 days (range 0–7), which represented a mean of 29 $\pm$ 21 kg. If the mean mass loss rate between 1 and 19 days had been used, total mass loss in this period would have been estimated to be 38 $\pm$ 24 kg, or about 1.3 times our estimate for the last part of lactation.

The mean rate of mass gain by females while at sea (Table 2) is significantly higher than that observed by Boyd et al. (1993) (1.5 $\pm$ 0.45 kg/day (n = 8), t-test $P < 0.02$) at South Georgia. Females in our study gained a total mean mass of 132 kg, which is 23% higher than that at South Georgia (107.7 kg). However, these values represent a similar percentage of their mass when females leave the beach at the end of lactation (30.3 and 29.8% respectively). Although feeding success can be related to the size of a female, the weight gained in our samples was widely variable (94–204 kg) and independent from mass at the end of lactation (Table 2). Although foraging areas used between lactation and molt are not known for this breeding group, McConnell et al. (1992) reported that three post-breeding females tracked from South Georgia traveled in a direct way to areas of the Antarctic Polar Front continental shelf margin, which is highly productive (Ainley and De Master 1990). Foraging in the same areas by the breeding population at South Shetland Islands would require less time and energy and might explain, at least partially, the differences in mass gain and the time spent at sea.

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Appendix Weight at birth and at weaning for pups whose mothers returned to land for molt

Mother number	Pup number	Birth mass (kg)	Weaning mass (kg)
848	842	46.5	152.5
61	95	49	164
67	65	52	177
64	56	47.5	151.5
53	68	43	150
98	97	46.5	189
42	41	53	195
92	47	45	161.5
3	91	52	189
74	93	53	175
70	52	57	156.5
36	35	40	128

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