

SHORT NOTE

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Energy gain and loss during lactation and postweaning in southern elephant seal pups (*Mirounga leonina*) at King George Island

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Abstract Deuterium-labeled water was used to measure changes in the proximate body composition during the lactation period and after weaning in southern elephant seal pups at King George Island, South Shetland Islands, Antarctica. During the lactation period (23.0 ± 1.4 days) pups gained a mean of 4.9 ± 0.5 kg/day ($n = 7$). Of the total mass gain (112 ± 8 kg), 38% was water, 48% was fat, and 11% was protein. This represented an increase in total body gross energy of 2437 ± 145 MJ. The proportion of body mass represented by fat was less than 2% at birth, increasing to 35 ± 2% at weaning. We followed the pups during a mean period of 36 ± 3 days after weaning. During this period, pups had a mean loss of 1.21 ± 0.10 kg/day ($n = 7$) comprising 39% water, 48% fat, and 12% protein. The energy cost over this period was 952 ± 168 MJ, which represented, on average, 39% of the total energy gained during the suckling period.

adopted by this species. As with other phocids, the rapid transfer of energy is made possible by the high lipid content in milk (Bonner 1984; Costa et al. 1986; Tedman and Green 1987; Oftedal et al. 1993), which contributes to rapid post-natal growth. Pups treble their birth weight in the 23 days of the lactation period.

Female southern elephant seals have a mean fat content in milk of about 39% (Bryden 1968a). The capacity of the pups to assimilate milk with a high fat content allows them to rapidly build up a thick blubber layer, which serves as an insulating barrier against cold ambient conditions (Bryden 1968b). Moreover, pups undergo a protracted fast immediately after weaning, when they draw on their thick blubber layer as the main source of energy. Weaned pups of southern elephant seals at King George Island are heavier at weaning than at other breeding sites (Burton et al. 1997). The aim of this work was to measure the energy reserved by pups during the lactation period and to ascertain how much of this energy was utilized during fasting at King George Island, South Shetland Islands, Antarctica.

The study was conducted at Stranger Point (62°14'S, 58°40'W) from September 1994 to January 1995. Body composition was determined for seven pups (four males and three females) at three different stages: at the beginning of lactation, at weaning, and at the end of a mean period of 36 days after weaning.

Each pup was separated from its mother to a distance of 15 m within 12 h after birth, weighed (nearest 0.5 kg) and marked, and a blood sample (20–30 ml) was taken from the extradural vein. A preweighed dose (1.7–2.3 g or 0.043 ± 0.006 g/kg) of deuterium oxide (D₂O, 99.8% purity) was then administered by intramuscular injection. The dose of D₂O was weighed to the nearest 0.0001 g. The pups were left for 4 h after injection to allow the D₂O to fully equilibrate with the total water pool, and then a second blood sample was taken. Each pup was recaptured within 24 h of weaning, weighed, and a blood sample (20–30 ml) taken to ascertain residual D₂O levels. A preweighed amount of D₂O (5–6 g or 0.031 ± 0.004 g/kg) was then administered by

Southern elephant seals differ from terrestrial mammals in relation to the rate and conditions of energy transfer. High rates of energy transfer and mothers' fast during nursing are characteristic of the lactation pattern

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intramuscular injection. Weaned pups were restrained for 4 h to prevent them from going into the water during the equilibration of the isotope. After this period, a blood sample (20–30 ml) was obtained from each pup.

The last procedure was carried out after a mean period of 36 days after weaning. The weanlings were captured, weighed, and the procedure used on the day of weaning was repeated.

Blood samples were left to clot in sealed vials for 8 h, then centrifuged and the serum was drawn off by pipette and stored in airtight vials at -14°C . Subsequently the samples were frozen under liquid nitrogen and the water was obtained from serum under vacuum. D_2O concentration was measured from a subsample (5 ml) of the water obtained. This water was reduced to hydrogen with hot zinc and was measured with a gas-isotope-ratio mass spectrometer (Finningan Delta-s, McKinney-type) (Coleman et al. 1982).

Total body water (TBW) was calculated from the dilution of D_2O measured in the blood sample after a 4-h equilibration period according to the equations provided by Schoeller et al. (1980). This method overestimates water mass, because some isotope atoms become incorporated into body tissues, thereby giving an erroneously high estimate of TBW (Pinson 1952; Nagy and Costa 1980; Oftedal and Iverson 1987). Estimates of TBW were corrected using the regression equation for grey seals (Reilly and Fedak 1990).

Body composition was calculated from total mass and TBW, using equations provided by Reilly and Fedak (1990), which were derived from analyses of whole-body chemical composition of grey seals. Calculation of total body gross energy (TBGE) assumed

energy densities of 39.5 kJ/g for fat and 23.5 kJ/g for protein (Reilly and Fedak 1990).

Table 1 shows body mass at birth and increase in body mass and change in body composition during nursing. The observed increase in body mass from birth to weaning was composed of 38% water, 48% fat, and 11% protein. This represents an increase of 2437 ± 145 MJ in TBGE (values are given as means \pm SD except where otherwise indicated).

The proportion of body mass represented by fat was 1.8 ± 1.5 kg (or $2 \pm 4\%$) at birth, increasing to 56 ± 3 kg (or $34.5 \pm 2.3\%$) at weaning. The large increase in fat concentration from birth to weaning caused a corresponding dilution of other constituents, such as water (from 70 to 48%) or protein (from 24.8 to 15.5%).

The energy density of the weight gain was 21.7 ± 1.4 MJ/kg.

Table 2 shows body mass at weaning and changes in body mass and body composition during the post-weaning period. Pup mean mass at weaning was composed of 48.2% water, 34.5% fat, and 15.5% protein. Of the total mass loss, $39 \pm 8\%$ was water, $48 \pm 11\%$ was fat, and $12 \pm 3\%$ was protein. The fat content of pups decreased from $34.5 \pm 2.3\%$ at the end of lactation to $29.4 \pm 4\%$ at the end of the fasting period measured. The energy spent during the period measured was 952 ± 168 MJ, which represents 39% of the energy gained during lactation.

Previous studies have shown that pups at weaning at King George Island are heavier than at other breeding sites (Burton et al. 1997), which is probably due to the greater arrival mass of their mothers, since it has been shown that this determines most of the variation in pup

Table 1 Changes in body mass and body composition during the nursing period

Pup	Initial mass (kg)	Δ Mass (kg)	Nursing period (days)	Δ TBW (l)	Δ Protein (kg)	Δ Fat (kg)	Δ TBGE (MJ)
815	45.5	116.5	23	45.5	13.6	55.8	2522
843	45.5	114.5	24	43.8	13	56.2	2523
808	48.5	109.5	25	42.2	12.5	52.5	2370
824	57.5	105.5	24	36.4	10.3	57.5	2515
818	56.5	100	22	39.6	11.9	47.1	2139
823	46	114	21	41.5	12	57.4	2551
821	49	126.5	22	53.4	16.4	51.9	2436
Mean	49.8	112.4	23	43.2	12.8	54.1	2437
SD	5.1	8.5	1.4	5.4	1.9	3.8	145

Table 2 Changes in body mass and body composition during the period measured after weaning

Pup	Weaning mass (kg)	Mass loss (kg)	Days	Δ TBW (l)	Δ Protein (kg)	Δ Fat (kg)	Δ TBGE (MJ)
815	162	48	42	19.5	5.9	21.9	1003
843	160	42.5	39	18.5	5.8	17.6	829
808	158	38	32	17.5	5.5	14.3	695
824	163	43	35	15.9	4.6	21.9	975
818	156.6	44.5	37	13.4	3.5	27.1	1154
823	160	41.5	34	11.1	2.7	27.4	1145
821	175.5	50	35	24.1	7.7	17.3	863
Mean	162	43.9	36.3	17	5.1	21.1	952
SD	6.3	4	3.3	4.2	1.7	5	168

Table 3 Mass gain and percentage of body fat in pups of southern elephant seals at two different breeding sites.

^a From Hindell et al. (1994)

^b This study

^c A *t*-test for unequal variances (Games-Howell) was used

	Macquarie Island ^a	King George Island ^b	<i>P</i> (<i>t</i> -test)
Mass at birth (kg)	44.8 ± 4.9, <i>n</i> = 13	49.8 ± 5.1, <i>n</i> = 7	< 0.05
Rate of mass gain (kg/day)	3.5 ± 0.8, <i>n</i> = 13	4.9 ± 0.5, <i>n</i> = 7	< 0.01
Mass at weaning (kg)	114 ± 16.6, <i>n</i> = 13	162 ± 8.5, <i>n</i> = 7	< 0.001
Fat at weaning (kg)	44.3 ± 12.9, <i>n</i> = 19	55.8 ± 2.9, <i>n</i> = 7	< 0.05 ^c
% Fat at weaning	40.8 ± 12.7, <i>n</i> = 19	34.5 ± 2.3, <i>n</i> = 7	> 0.05 ^c

weaning mass (Arnbom et al. 1993). Although the body composition data reported here come from only seven pups, their average masses at birth and weaning were not significantly different from those reported in a study carried out by Burton et al. (1997) which included a greater sampling size (49.8 ± 5.1 kg, *n* = 7 vs 46.1 ± 6.9 kg, *n* = 162, *t*-test, *P* = 0.16 and 162 ± 8.5 kg, *n* = 7 vs 159.1 ± 29.8 kg, *n* = 388, *t*-test, *P* = 0.79).

The mean weight of fat at birth measured in our study for pups of southern elephant seals was 1.8 kg, and it increased to 56 kg at weaning. Early body-composition data for southern elephant seals were derived from dissection of pups of varying ages (Bryden 1969). Moreover, using dilution techniques, Hindell et al. (1994) reported data on body composition for pups of southern elephant seals at Macquarie Island. Compared with this group, mass at birth in our study was significantly greater, but the differences in mass at weaning were mainly due to the differences observed in the rate of weight gained during the suckling period (Table 3). Greater mean mass at weaning at South Shetland in relation to Macquarie Island allows larger absolute energy reserves (Table 3). However, fat reserves expressed as percentage of body mass at weaning were similar in both populations, which seems to indicate that pups in this population are larger – not fatter – than those at Macquarie. Pups of northern elephant seals show higher fat reserves at weaning which represent about 50% of body weight (Ortiz et al. 1978; Rea and Costa 1992; Kretzmann et al. 1993). The equation utilized in those studies to measure total body fat was provided by Pace and Rathbun (1945) and was later modified by Ortiz et al. (1978), and it assumes that adipose and lean tissue contain 10% and 73% water respectively (Ortiz et al. 1978; Costa et al. 1986). The use of this equation in our study would produce an increase of 3.5% in total body fat at weaning. The percentage of body fat at weaning is higher in the northern species when the same method of calculation is used (48.4 ± 2.7% vs 38 ± 2.6%). Although pups of northern elephant seals have about 4–9% of adipose tissue near birth (Rea and Costa 1992; Kretzmann et al. 1993), which is slightly higher than the values obtained at birth in our study, differences at weaning are mainly due to the differences found in the composition of the mass gained. In pups of northern elephant seals, adipose tissue represented about 65–71% of total weight gained during lactation (Rea and Costa 1992; Kretzmann et al. 1993), whereas in our study, using the same method of calculation, adipose tissue represented 55%. This could be due to differences in milk composition and to the longer lactation period in

the northern species, as was suggested by Hindell et al. (1994). The observed pattern of mass gain (Table 1) corresponds with that of other phocids, in which growth during lactation involves extensive deposition of adipose tissue, with proportionately little growth in lean tissue (Worthy and Lavigne 1983; Oftedal et al. 1987). Weight gained during lactation represented an increase of 2437 ± 145 MJ in TBGE. Pups gained an average of 106 MJ/day during lactation, which was 4.5 times the daily amount spent during fasting.

After weaning, pups group near the harem. Since at South Shetland weaning occurs in a period of intense thawing, pups were frequently observed in rills and small pools. Generally, pups begin to enter the sea 1 week after weaning, which is coincident with movements away from the place where they were born.

During the fasting period, weaned pups lost a mean mass of 1.21 ± 0.1 kg/day. The rate of weight loss in our study is higher than that at Peninsula Valdés (0.92 kg/day) and at South Georgia (0.97 kg/day) (Campagna et al. 1992; Arnbom et al. 1993). Nevertheless, considering that the rate of weight loss is related to pup mass at weaning, the differences could be explained by differences in the weight at weaning for the three populations.

The mean of weight lost during this period (Table 2) represented 39% of the energy gained during the suckling period. However, if we consider a mean fasting period of 42 days (A.R. Carlini, personal observation), instead of the 36 days measurement, the energy lost would be half of the energy reserved during lactation.

Although the relationship between weight and survival in this species is not yet clear, it is probable that greater mass, which gives the pup at least greater absolute energy reserves, could maximize their chances of survival during their early life at sea.

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