MASS CHANGES AND METABOLISM DURING THE PERINATAL FAST: A COMPARISON BETWEEN ANTARCTIC (ARCTOCEPHALUS GAZELLA) AND GALÁPAGOS FUR SEALS (ARCTOCEPHALUS GALAPAGOENSIS)[1]

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Female mass loss and metabolic rate were measured along with changes in pup mass during the perinatal period in Antarctic and Galápagos fur seals. Antarctic fur seal females lost 3.15%, or 1.231 kg per day, of their initial body mass of roughly 39 kg. Heavier females gave birth to heavier young ($r = .644$, $P < .05$; $n = 12$) and lost significantly more mass per day than did smaller females ($r = .796$, $P < .01$; $n = 12$). In contrast, Galápagos fur seal females (37.4 kg) lost half as much mass per day (1.68% day^{-1}; 0.639 kg day^{-1}). Metabolic rates, determined by the doubly labeled water method, were considerably higher in Antarctic fur seals (4.56 W kg^{-1}) than Galápagos fur seals (1.48 W kg^{-1}). We suggest that the lower metabolic rate of Galápagos fur seal females is an adaptation to reduce thermal stress on land in the warm equatorial habitat. Measurements of metabolic rate from water influx overestimated metabolism measured with the doubly labeled water method by only 3.2% in Antarctic fur seals, while seawater drinking precluded its use in Galápagos fur seals. Metabolic rates of nonlactating Antarctic fur seals were not different from those of lactating individuals. This is consistent with other studies, which indicates that the cost of lactation is primarily associated with the energy content of milk, with little or no measurable increase in metabolism owing to the cost of milk synthesis. Total body water determinations (57.2% Galápagos; 59.7% Antarctic) were used to estimate a total fat content of 26% and 22% at parturition, respectively. Because this is only about half that reported for phocid females, we suggest that the greater fat stores of phocid seals are a major factor enabling them to fast throughout lactation.

INTRODUCTION

Considerable attention has focused on the partitioning of energy during reproduction in mammals (Peaker, Vernon, and

Knight 1984) with a growing number of studies on large mammals, especially pinnipeds (Fedak and Anderson 1982; Ortiz, Le Boeuf, and Costa 1984; Stewart and Lavigne 1984; Costa et al. 1986b; Costa and Gentry 1986; Tedman and Green 1987; Oftedal, Iverson, and Boness 1987). Most of these studies are on true seals, Phocidae, and few data are available for otariids, which have a substantially different pup-rearing system. In otariids, maternal care typically consists of a relatively short perinatal period of 7 days ashore with a pup, followed by a long period of alternating onshore lactation and foraging at sea lasting from 4 mo to 3 yr (Gentry et al. 1986). In contrast, phocids are characterized by a short, intense period of lactation, during which the pup suckles while the female fasts onshore (Bonner 1984). During this interval, most, if not all, of the material transferred to the phocid pup comes from maternal body stores.

Otariids reproduce in a broad range of habitats. Northern and Antarctic fur seals

breed on cool subpolar islands, while Galápagos fur seals breed on the warm equatorial Galápagos Islands. Obviously, these species face markedly different thermal habitats. Thermal adaptations required to reduce heat loss in the cool aquatic environment, with its high thermal conductivity, become a burden in a warm terrestrial environment with intense solar radiation, such as the Galápagos (Limberger et al. 1986). Hyperthermia may be less of a problem for subpolar fur seals, since they are rarely exposed to high levels of solar radiation. Accommodation to such divergent thermal environments may result in different metabolic profiles.

In order to examine variations in maternal energetics with respect to these habitats, we used the fact that females remain with their pups and fast for the first 7 days after parturition. At this time the mother-pup bond is developed, and the pup prepares to fast onshore alone while its mother forages at sea. Before parturition, females arrive onshore with all the necessary nutrients and energy to support themselves and the pup during these first 7 days. It is during this period that maternal care in otariids most closely resembles that of phocids. Furthermore, maternal costs are difficult to quantify during the subsequent onshore intervals because females spend only a few hours to 2 days onshore with their pups. Only three studies on the reproductive energetics of otariids exist (Costa and Gentry 1986; Oftedal et al. 1987; Higgins et al., in press). The latter two examined only the energy invested as milk provided to the young. This excludes the cost of female maintenance metabolism during lactation. In order to understand further the allocation of energy during maternal care in otariids and to examine potential differences owing to thermal habitats during the perinatal interval, we measured changes in maternal and pup body mass, and we also measured female metabolism using labeled-water methodologies.

MATERIAL AND METHODS

We studied Antarctic fur seals, *Arctocephalus gazella,* at Bird Island, South Georgia, in the South Atlantic (lat. 54°00' S, long. 38°02' W) during the austral summers of 1983–1984 and 1984–1985, and Galápagos fur seals, *Arctocephalus galapagoensis,* at Cabo Hammond, Fernandina (lat. 0°28' S, long. 91°37' W), from September to October 1984. This was done by measuring water influx of four Antarctic fur seal females during 1983–1984 and using the more accurate doubly labeled water method in addition to water influx to measure fasting metabolism in four Antarctic fur seals during 1984–1985 and three Galápagos fur seal females during 1984. We initiated doubly labeled water measurements with six Antarctic fur seal females. However, two of them departed before resampling.

For comparison, the metabolic rate of nonlactating animals was determined in nine Antarctic fur seals using water influx measurements alone. This group consisted of one female who had lost her pup 20 days earlier, one subadult female and seven subadult males. Animals were treated as below except that during the fasting measurements they were maintained singly in outside holding pens approximately 3 × 4 m in size.

METABOLIC MEASUREMENTS

Metabolism during the onshore perinatal fast (CO_2 production) and water turnover were measured using the doubly labeled water method (Lifson and McClintock 1966; Nagy 1980; Nagy and Costa 1980; Schoeller and van Santen 1982). Lactating females that had recently given birth (within 24 h) and were suckling their pups were captured weighed and restrained as described by Gentry and Holt (1982). The females' blood was then sampled for determination of isotope background-specific activity. Antarctic fur seals were then injected with 15 ml of ^{18}O water at a 15% enrichment and 3 ml of 0.85 mCi ml^{-1} tritiated water (HTO) in sterile saline. Galápagos fur seals were injected with 1.5 ml 95% ^{18}O-labeled water/10 kg body mass and 0.75 ml 97.3% deuterium oxide (D_2O)/10 kg. Blood samples (10–20 ml) were taken from either the interdigital vein or femoral sinus. Antarctic fur seals were weighed to within 50 g on a platform balance. Galápagos fur seals were weighed on spring balances to the nearest 250 g for females and 100 g for pups. After injection, the females and their pups were held in a pen or a cage

to allow for isotope equilibration. After 3 h an additional 10–20 ml of blood was collected. Females were then returned with their pups to the site of capture. The presence of the females was assured by at least three visual surveys of the rookery each day. In addition, the presence of Galápagos fur seals was determined via a radio check every 2 h. Radio transmitters were glued (with 10-min epoxy) to the mothers' backs before initial release. Females were recaptured 2.5–6 days later, and a blood sample and body weight were taken, followed by a final total body water (TBW) determination made by reinjection of 1 ml of 0.1 mCi ml^{-1} HTO or, in the case of Galápagos fur seals, 1 ml of 97.3% D_2O with a blood sample 3 h later. Pups were also reweighed at this time.

We determined TBW by the initial dilution of labeled water. There was a 1% variation in TBW determinations whether HTO, D_2O, or ^{18}O were used. Estimates of metabolic rate were derived from the water influx measurements only for 13 Antarctic fur seals during 1983–1984. In a fasting nondrinking animal, water influx is only derived from water produced from metabolism (Nagy 1975). The validity of this assumption was tested by comparing the metabolic rates derived from water influx with those derived from CO_2 production, measured with Antarctic fur seals in 1984–1985 and with the three Galápagos fur seals. CO_2 production and water influx were calculated assuming an exponentially changing body water pool (Nagy 1980; Nagy and Costa 1980). It was assumed that fat was the sole metabolic substrate during this fast. Protein oxidation contributes no more than 2.2% ± 0.5% of the total metabolic energy in fasting elephant seal pups (Pernia, Hill, and Ortiz 1980). Using the same methodology, during an equivalent perinatal fast in northern fur seals, *Callorhinus ursinus,* protein catabolism was found to contribute less than 3% to the total oxidative energy metabolism (Costa, unpublished data). Assuming an RQ of 0.71, a constant of 27.4 J ml^{-1} was derived to convert CO_2 production to energy consumption (Schmidt-Nielsen 1964, 1979). Heat production and metabolic water production were interconverted using a factor of 0.0272 ml H_2O kJ^{-1} (Schmidt-Nielsen 1964, 1979).

Tritium-specific activity was determined by scintillation spectrometry of triplicate aliquots of 200 µl of pure water in 10 ml of Betaphase cocktail (Westchem, San Diego) vacuum distilled from the serum samples. The specific activity of ^{18}O- and deuterium-labeled water was determined by mass ratio spectrometry (Global Geochemistry, Canoga Park, Calif., and Laboratory for Isotope Physics, Rijksuniversiteit te Groningen, Netherlands) of pure water distilled from plasma samples. Deuterium values determined by the former laboratory were consistently too low (as determined from known concentration standards) and were corrected to correspond to the values from the Groningen laboratory.

RESULTS

WEIGHT CHANGES DURING THE PERINATAL FAST

Antarctic fur seal females stayed ashore for about 7 days after parturition (Doidge, McCann, and Croxal 1986). During this time they lost a mean of 3.15% ± 0.11% SE, or 1.231 ± 0.055 kg per day, of their initial body mass of 39.4 ± 1.94 kg (table 1). Heavier females gave birth to heavier young (least squares linear regression r = .644, $P < .05$; $n = 12$) and lost significantly more mass per day than did smaller females ($r = .796$, $P < .01$; $n = 12$). A mother's initial body mass did not correlate significantly with her pup's subsequent weight gain during the perinatal attendance period ($r = .596$, $P > .1$; $n = 8$). The correlation between a female's mass loss and her pup's weight gain, however, approached significance ($r = .695$, $.1 > P > .05$; $n = 8$). The pups' mass gains during the perinatal period were independent of their body masses at birth ($r = .05$, NS; $n = 8$).

The length of the perinatal fast of Galápagos fur seal females (Trillmich 1986) is similar to that of Antarctic fur seal females, and initial female mass was approximately the same as for the Antarctic fur seal (table 2). However, Galápagos fur seal females lost only about half as much mass per day as did Antarctic fur seals, which may have resulted from the lower metabolism of Galápagos fur seal females (tables 3, 4). Pup growth rates for the pups whose mothers were weighed were also about half as much,

TABLE 1

MASS CHANGE OF ANTARCTIC FUR SEAL FEMALES DURING THE PERINATAL FAST, THEIR PUP BIRTH MASS, AND THE MASS CHANGE OF SOME PUPS

Animal No.	Initial Mass (kg)	Mass Change (kg/day)	Mass Change (%/day)	Pup Initial Mass (kg)	Pup Mass Change (g/day)	Pup Mass Change (%/day)	Pup Gain/ Fem Gain	Time Interval (days)	Pup Sex
446	26.70	1.058	3.96	3.80	. . .	. . .	. . .	2.551	F
239[a]	33.15	1.154	3.48	4.80	65	1.35	5.61	4.638	F
458	34.00	.997	2.93	4.10	93	2.27	9.32	5.920	F
438	36.10	1.255	3.48	5.70	131	2.19	10.45	5.100	M
464	38.25	1.199	3.13	4.95	. . .	. . .	. . .	4.213	M
428	39.40	1.200	3.05	5.30	. . .	. . .	. . .	6.000	F
442	40.05	1.010	2.52	5.20	. . .	. . .	. . .	5.000	F
233[a]	40.30	1.126	2.79	5.85	79	1.58	7.03	5.949	F
261[a]	42.50	1.353	3.18	4.55	165	4.38	12.17	4.766	F
241[a]	44.45	1.439	3.24	5.35	119	2.22	8.27	4.622	M
259[a]	44.63	1.329	2.98	5.55	104	1.88	7.84	4.801	F
462	53.30	1.654	3.10	5.45	149	2.73	8.99	5.715	F
Mean . . .	39.40	1.231	3.15	5.05	113	2.33	8.71	4.940	
SE	1.94	.055	.11	.29	12	.33	.72	.278	

NOTE.—The efficiency of pup mass gain is given as the ratio of pup mass gain to female mass loss in percent. Time interval gives the duration of the experiment.

[a] Data collected during 1984–85.

although the growth rates of 15 other Galápagos fur seal pups during the perinatal period were about the same as those for Antarctic fur seals (mean and SD: 101.6 ± 45.7 g day^{-1}; $n = 15$). Again, pup growth rate during the perinatal period showed no correlation with pup initial mass ($r = 0.25$, NS; $n = 15$).

METABOLISM

Metabolic rates, determined by doubly labeled water, were considerably higher in Antarctic fur seals (4.56 W kg^{-1}) than in Galápagos fur seals (1.48 W kg^{-1}). However, total water influx of Galápagos fur seals was almost double the rate of Antarctic

fur seals (tables 3, 4). This higher water influx was assumed to represent drinking. In fasting territorial Galápagos fur seal males, seawater drinking was regularly observed. In contrast, in Antarctic fur seal females, the close correspondence between metabolic rate estimated from water influx and that determined by the doubly labeled water method (3.2% mean difference; table 3) indicates that there was little or no exogenous water influx. It is possible that some animals, for example, female 259, consumed a small amount of water. The difference in metabolic power would require the consumption of 83 ml of water per day. In most cases free water was not available to Ant-

TABLE 2

MASS CHANGE OF GALÁPAGOS FUR SEAL FEMALES AND THEIR PUPS DURING THE PERINATAL FAST

Animal No.	Initial Mass (kg)	Mass Change (kg/day)	Mass Change (%/day)	Pup Initial Mass (kg)	Pup Mass Change (g/day)	Pup Mass Change (%/day)	Pup Gain/ Fem Gain	Time Interval (days)	Pup Sex
2-84	33.2	.527	1.59	3.6	51.6	1.4	9.8	4.84	F
3-84	37.9	.698	1.84	3.5	115.1	3.3	16.5	5.87	M
8-84	41.1	.661	1.61	3.3	20.6	.6	3.1	4.84	F
Mean . . .	37.4	.629	1.68	3.5	62.4	1.8	9.8	5.18	

NOTE.—Efficiency of pup mass gain as in table 1.

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TABLE 3

TOTAL BODY WATER (TBW), CO_2 PRODUCTION, WATER INFLUX, AND ESTIMATED METABOLIC RATE
FOR FASTING LACTATING ANTARCTIC FUR SEALS

| | | METABOLIC RATE | | | WATER | | |
ANIMAL NO.	INITIAL TBW (%)	CO_2 (ml·g^{-1} h^{-1})	Power (W/kg)	MWP (ml·kg^{-1} day^{-1})	INFLUX (ml·kg^{-1} day^{-1})	METABOLIC RATE[a] (W/kg)	ERROR (%)
239[b].......	62.4	.659	5.02	11.8	10.4	4.44	−11.4
241[b].......	61.2	.527	4.01	9.4	10.0	4.26	6.2
259[b].......	61.1	.585	4.45	10.5	12.5	5.32	19.5
261[b].......	55.4	.624	4.75	11.2	11.0	4.68	−1.4
446	58.7	. . .	. . .	. . .	13.3	5.66	. . .
458	59.6	. . .	. . .	. . .	11.4	4.85	. . .
462	59.5	. . .	. . .	. . .	10.2	4.34	. . .
464	59.9	. . .	. . .	. . .	14.4	6.13	. . .
Mean....	59.7	.599	4.56	10.7	11.7	4.96	3.2
SE	.7	.020	.22	.5	.6	.23	6.5

NOTE.—MWP is the metabolic water production derived from doubly labeled water estimates of metabolic rate. The difference between the metabolic power measured with the doubly labeled water method and that estimated by water influx is given as the error.
[a] Metabolic rate was derived from water influx data using a constant of 0.0272 ml H_2O kJ^{-1}.
[b] Data collected during 1984–1985 field season.

arctic fur seal females. Despite differences in water influx, TBW determinations were similar between the two species (57.2% Galápagos; 59.7% Antarctic; tables 3, 4). TBW of nonlactating Antarctic fur seals was higher (62.7%, table 5). Metabolic rates determined from water influx in nonlactating individuals were correlated with body mass ($r = .737$, $P < .05$; $n = 9$) and were indistinguishable from metabolic rates of lactating individuals similarly determined (fig. 1).

DISCUSSION

COMPARISON OF METHODS OF
METABOLIC MEASUREMENT

Other investigators have found that water influx significantly overestimates metabolism in penguins (Nagy, Siegfried, and Wilson 1984; Costa, Dann, and Disher 1986a) and in quail (Goldstein and Nagy 1985). The most significant potential error relevant to the present study is a possible overestimate of metabolic water production from

TABLE 4

TOTAL BODY WATER (TBW), CO_2 PRODUCTION, WATER INFLUX, AND ESTIMATED METABOLIC RATE
FOR FASTING, LACTATING GALÁPAGOS FUR SEAL FEMALES

| | | METABOLIC RATE | | | | |
ANIMAL NO.	INITIAL TBW (%)	CO_2 (ml·g^{-1} h^{-1})	Power (W/kg)	METABOLIC WATER (ml·kg^{-1} day^{-1})	TOTAL WATER INFLUX (ml·kg^{-1} day^{-1})	DRINKING (ml·kg^{-1} day^{-1})
2-84.......	58.8	.327	2.49	5.85	22.0	16.2
3-84.......	59.8	.143	1.09	2.56	19.1	16.5
8-84.......	52.9	.115	.88	2.06	24.4	22.3
Mean....	57.2	.195	1.48	3.49	21.8	18.3

NOTE.—Metabolic water production was calculated from metabolic rate determined by doubly labeled water using a conversion factor of 0.0272 ml H_2O kJ^{-1}. The amount of water consumed by drinking was determined as the difference between metabolic water and total water influx.

TABLE 5

INITIAL BODY MASS, DAILY MASS CHANGE, TOTAL BODY WATER (TBW), WATER INFLUX, AND ESTIMATED
METABOLIC RATE FOR FASTING, NONLACTATING SUBADULT MALE (SAM), SUBADULT FEMALE (SAF),
AND ADULT FEMALE (AF) ANTARCTIC FUR SEALS

Animal No.	Initial Mass (kg)	Mass Change (%/day)	Initial TBW (%)	Water Influx $(ml \cdot kg^{-1} day^{-1})$	Metabolic Rate (W/kg)	Time Interval (days)
AF 472	29.1	3.22	63.8	24.4	10.39	4.702
SAM 882....	19.6	1.78	66.8	16.4	7.00	4.878
SAM 80.....	30.7	2.23	64.7	14.9	6.34	4.750
SAM 494....	38.4	1.80	64.2	11.7	4.96	5.583
SAM 84.....	32.1	2.11	59.1	11.7	4.99	4.797
SAM 88.....	29.7	2.64	64.0	20.6	8.76	4.902
SAM 94.....	15.1	2.66	59.9	14.5	6.18	4.851
SAM 496....	27.8	2.03	63.9	19.9	8.47	5.581
SAF 86	16.7	2.87	57.8	16.2	6.89	4.802
Mean	26.6	2.37	62.7	16.7	7.11	4.983
SE	2.6	.17	1.0	1.4	.58	.115

NOTE.—Metabolism was calculated from water production using a conversion factor of 0.0272 ml H_2O kJ^{-1}.

seawater ingestion and/or exchange of un-labeled, inspired water vapor for labeled water in the animal. Seawater ingestion has already been discussed and precludes use of water-influx data to measure metabolic rate in fasting Galápagos fur seals. Potential errors resulting from the exchange of in-spired water vapor may be small in dry en-vironments but could become substantial in moist or humid habitats (Lifson and McClintock 1966; Nagy and Costa 1980). The data in table 3 indicate a mean error

of 3.2% in the measurement of metabolic rate in Antarctic fur seals. How does this error compare with the theoretical error? Assuming an oxygen extraction from air typical for marine mammals of 8% (Ridg-way 1972), we estimate that Antarctic fur seals inhaled ca. 10,000 liter air day^{-1}, and Galápagos fur seals 3,100 liters air day^{-1}. Assuming a mean temperature of 25 C for the Galápagos and 4 C at Bird Island, and a relative humidity of 80%, the absolute water content of the air would be 18.5 mg
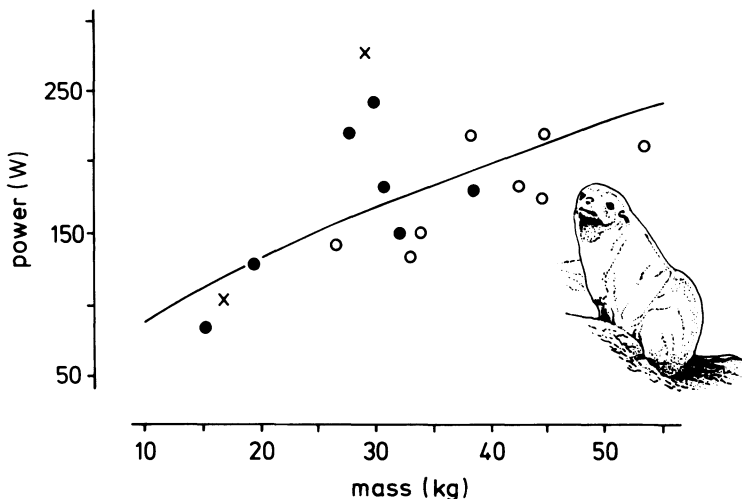

FIG. 1.—Metabolic power (W) as a function of body mass (kg) in Antarctic fur seals. Symbols O, X, and ● indicate lactating females, nonlactating females, and subadult males, respectively. Data are best fitted by an exponential curve of the form Power (W) = 22.88 · M (kg)$^{0.585}$ (r = .665, P < .01, n = 17).

H_2O liter^{-1} for the Galápagos and 5.11 mg H_2O liter^{-1} air at Bird Island. Therefore, a typical Galápagos fur seal would inhale 57 ml H_2O day^{-1} (3,100 liter · 18.5 mg H_2O l^{-1}) and an Antarctic fur seal 51 ml H_2O day^{-1} (10,000 liter · 5.11 mg H_2O liter^{-1}). This amount of respiratory water exchange would overestimate total water influx by 7% (1.5 ml H_2O kg^{-1} day^{-1}) in Galápagos fur seals and by as much as 12.4% (1.45 ml H_2O day^{-1} kg^{-1}) in Antarctic fur seals. However, this estimate does not include physical fractionation of isotopes, which tends to underestimate water influx and thus may counteract the error caused by respiratory vapor exchange (Nagy and Costa 1980; Costa et al. 1986*b*).

COMPARISONS OF METABOLISM AND MASS CHANGE

The most interesting observation from this study is the striking difference in mass loss and energy metabolism between the two fur seal species. Female Antarctic fur seals (3.15% body mass day^{-1}) lost mass at a significantly higher rate than Galápagos fur seal females (1.68% body mass day^{-1}) (Mann-Whitney U test, $U = 0$, $P < .02$), but quite similar to the 3.69% body mass day^{-1} reported for northern fur seals (table 6). There was no significant difference, however, in the observed rate of pup mass gain between the three species (table 6).

Similar rates of pup mass gain imply that the energy expended in milk production is nearly equivalent. This suggests that differences in female mass loss are related to variations in maintenance metabolism and not to milk production. Such a hypothesis is supported by the marked difference in metabolic rates of the three species (table 6). The metabolic rate of Antarctic fur seals (doubly labeled water measurements) was 3.4 times predicted basal, whereas that of Galápagos fur seals was only 1.1 times the predicted basal (Kleiber 1975; Lavigne et al. 1986). Even considering the limited data for Galápagos fur seals, the difference is significant (Mann-Whitney U-test, $U = 0$, $P < .02$).

A lower metabolic rate in Galápagos fur seal females implies a lower "metabolic overhead" while onshore. This reduced overhead should allow proportionately more energy to be channeled into milk production and pup growth (Fedak and Anderson 1982). However, the three species have similar pup growth rates. Apparently, extra energy and material is available in Galápagos fur seals, but it is not utilized for milk production and pup growth. The female may retain this energy as a buffer against the unpredictable nature of the equatorial environment (Gentry et al. 1986). Alternatively, there may be an upper limit to the amount of milk pups of this age can consume. Costa and Gentry (1986) found that milk intake was significantly lower during the perinatal period than during later suckling intervals in northern fur seals. It would be interesting to know if a similar pattern occurs in Galápagos fur seals.

TABLE 6

MASS LOSS, WATER INFLUX, MAINTENANCE METABOLISM OF FEMALE FUR SEALS (FS), THE MASS GAIN OF PUPS, AND THE RELATIVE AMOUNT OF MASS GAINED BY PUPS TO MASS LOST BY THEIR MOTHERS

	Female Mass Loss (%/day)	Water Influx (ml · kg^{-1} day^{-1})	Maintenance Metabolism (W/kg)	Pup Gain (%/day)	Pup Gain/Fem Gain
Northern FS[a]	3.69 (.16)[b]	11.4 (.6)	4.85[c] (.31)	2.93 (.25)	13.60 (.92)
Antarctic FS	3.15 (.11)	11.7 (.6)	4.96 (.23)	2.33 (.33)	8.71 (.72)
Galápagos FS	1.68	21.8	1.48	1.80	9.80

NOTE.—Data on northern fur seals from Costa and Gentry (1986).

[a] The higher growth rate and transfer efficiency of northern fur seals may reflect differences in experimental protocols. Perinatal studies with northern fur seals were carried out in penned enclosures, which virtually precluded disturbance from other animals, whereas studies with Antarctic fur seals were carried out on the rookery where considerable disturbance from male territorial displays and female-female interactions occur.

[b] Values in parentheses are ±1 SE.

[c] Metabolic rate was determined from water influx using the same method as for the Antarctic fur seal.

Fasting metabolism in fur seals correlates with differences in their physical environment. The only other subpolar fur seal, the northern fur seal, has a fasting metabolic rate almost identical to that of the Antarctic fur seal (table 6). In contrast, the "tropical" or "equatorial" Galápagos fur seal consumes energy at a considerably lower rate. Thermal differences between habitats, as well as the low population density and the consequent low rate of disturbance in Galápagos fur seal colonies, may explain this pattern.

During the summer months, air temperatures vary between −1 and 8.5 C on Bird Island (Richards and Tickell 1968) and between 6 and 13 C on the Pribilof Islands (Costa, personal observation), whereas temperatures on the Galápagos vary from a low of 20 C at night to a daytime high of 30 C (Limberger et al. 1986). More important, there are significant differences in the incident solar radiation and wind velocity. In the subpolar regions the sun is visible for only about 10% of the daytime because of fog and overcast skies. Average wind velocity at Bird Island was 5.3 m sec^{-1} (Richards and Tickell 1968).

In marked contrast are the Galápagos, where solar radiation is considerable (1,000 W m^{-2} at midday), average wind speed is only 1.2 m sec^{-1}, and the surface of exposed black lava rocks reaches 50 C. Even in the shade, rocks often reach 33 C (Limberger et al. 1986). In response to this heat load, Galápagos fur seal females become extremely quiescent. Typically, females with pups spend 92% of the day resting (during which time their pups suckle), 2% grooming and interacting with other fur seals, and 2% in the water (Trillmich, unpublished data). Often the only females left onshore are those with young pups, other individuals having long since retreated to the water to cool off. Even with the low metabolic rate, hyperthermia is not entirely avoided. During the morning, body temperature (T_b) rises steeply until the female goes into the water. This rise in T_b occurs even though the female is inactive. After the first short stay in the water she allows her T_b to fall below the nighttime level, and, thus, average daytime T_b is lower than nighttime T_b (Limberger, unpublished data). It is likely that Galápagos fur seal females behaviorally maintain their metabolism near basal. In this way, females can delay hyperthermia, thereby increasing the amount of time spent with the pup onshore.

Even with this lowered metabolic rate, they must still get wet in or near the water to cool off. Presumably, females drink during short visits to the water. Antarctic or northern fur seals, unlike Galápagos fur seals, rarely move from the birth site until it is time to depart for their first postpartum foraging trip. Consistent with these data, Gentry (1981) observed that seawater drinking was more frequent in fur seals and sea lions that inhabited warm climates. He further speculated that "Seawater ingestion is probably linked to or enhanced by evaporative loss of body water during heat stress." From the data in tables 2 and 4, seawater ingestion appears quite substantial in Galápagos fur seals, representing an average of 663 ml day^{-1}. Reports of seawater drinking in other marine mammals are mixed. Significant seawater ingestion was not observed by Depocas, Hart, and Fisher (1971) in fasted or fed harbor seals, by Ortiz, Costa, and LeBoeuf (1978) in fasting weaned elephant seal pups, or in captive northern fur seals and California sea lions (Costa 1984; Costa and Gentry 1986). However, Costa (1982) reported considerable ingestion of seawater by captive fed sea otters.

METABOLIC COST OF LACTATION

Comparison of metabolic rates between lactating and nonlactating Antarctic fur seals indicates that the cost of lactation is primarily associated with the energy contained in the milk and not the "heat increment of synthesis." Similar conclusions have been reached for northern elephant seals and northern fur seals where it was suggested that most of the cost of synthesis had already been expended while the female was at sea (Costa et al. 1986b; Costa and Gentry 1986). It is likely that blubber lipids do not require further chemical modification to produce milk. This is supported by the extreme similarity in the composition of milk and blubber lipids in northern elephant seals (Riedman and Ortiz 1979). Although the variance in our data precludes measurement of minor increases in maintenance metabolism during lactation,

even sophisticated laboratory measurements with cotton rats, *Sigmodon hispidus* (Randolph et al. 1977; Mattingley and McClure 1982), and laboratory mice, *Mus musculus* (Studier 1979) have failed to measure an increase in maintenance metabolism during lactation.

FASTING ABILITIES OF OTARIIDS AND PHOCIDS

An important component of maternal effort is the female's "metabolic overhead" (Fedak and Anderson 1982), which is composed of all metabolic costs exclusive of milk production. Reductions in metabolic overhead increase the proportion of the female's energy resources that can go into milk and, therefore, pup growth. The relatively high maintenance metabolism of northern and Antarctic fur seals suggests that they have a higher metabolic overhead than the Galápagos fur seal. Whether this is due to variations in thermal habitat alone is unclear. Metabolic data for the northern elephant seal (2.4 × BMR, Costa et al. 1986*b*) fall within the range observed for fur seals. Additional data on fasting metabolism of pinnipeds breeding under different thermal regimes are required before we can clarify whether these variations in metabolic rate reflect the extremes of habitats occupied by these fur seals.

As stated earlier, phocids and otariids have distinct reproductive patterns. Otariids fast only during the perinatal interval and subsequently forage between suckling bouts onshore, whereas phocid mothers fast during lactation and provision their young entirely from body stores. What factors limit the perinatal fast in otariids, or what is different in phocids that allows them to concentrate their investment into such a short interval? One mechanism would be for phocids to have a lower metabolic overhead that allows greater conversion of maternal body stores into milk. However, the limited data on maintenance metabolism indicate that phocids fall within the range observed for otariids. A more plausible explanation is that phocid females arrive on shore with significantly larger energy stores than do otariid females. Estimates of the lean body mass and adipose tissue can be derived from body mass and TBW measurements (Pace and Rathbun 1945; Ortiz et al. 1978; Costa et al. 1986*b*). From the data on TBW in table 3 and 4, assuming a water content for lean tissue of 73% and using the water content of Antarctic fur seal blubber reported earlier, we estimate that, upon parturition, Antarctic and Galápagos fur seals are composed of 22% and 26% fat, respectively. These values are not significantly different. In contrast, at or near parturition, northern elephant seals are composed of 39% fat (Costa et al. 1986*b*), gray seal females of 40% fat (Fedak and Anderson 1982), and harp seals of 47% fat (Stewart and Lavigne 1982). Being larger than a typical fur seal (fur seals, 40 kg; gray seals, 170 kg; harp seals, 120 kg; elephant seals, 500 kg) and bringing, relative to their body size, almost twice as much blubber ashore, female phocids thus can fast and provision their pups longer than otariid mothers. This may be one of the major adaptations enabling phocid mothers to stay ashore continuously for the entire period of lactation.

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