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## FORAGING ENERGETICS OF ANTARCTIC FUR SEALS IN RELATION TO CHANGES IN PREY AVAILABILITY<sup>1</sup>

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**Abstract.** This research examines the energy budget of breeding female Antarctic fur seals, both when food was plentiful and when it was scarce. The energy expenditure and change in body mass of lactating female Antarctic fur seals, *Arctocephalus gazella*, foraging at sea was measured in two years using doubly labeled water at South Georgia Island. There was no difference between years in mass gain, water influx, mass-specific field metabolic rate (FMR), or absolute FMR. Mean at-sea FMR over both years was  $9.52 \pm 0.55$  W/kg ( $n = 22$ ), a value that is 6.7 times the predicted basal rate but only 1.9 times the FMR measured onshore. Comparable results have been reported for similar-sized northern fur seals.

Krill, the nearly exclusive prey of breeding females, were very scarce in 1984 at South Georgia. Fur seal foraging trips were twice as long in 1984 as in 1985 and total mass-specific energy expended by females during these trips was significantly greater. In addition, females were significantly lighter at parturition in 1984, and both pup mortality and the proportion of pups that died from starvation were double the 1985 values.

Female condition at parturition and average foraging-trip duration (i.e., offspring-provisioning rate) appear to reflect prey availability. The similarity between years in mass increase suggests that females do not return to feed their pups until they replenish their own reserves. Antarctic fur seal females may have a limited ability to increase the relative time spent foraging because even in normal years only 5% of their time at sea is spent resting. This contrasts with northern fur seals, *Callorhinus ursinus*, which typically spend 17% of their time at sea inactive. Apparently these northern seals can increase their foraging effort by increasing the proportion of time spent foraging. This would account for the observed between-year difference in at-sea FMR of *C. ursinus* while foraging-trip duration remained fairly constant.

**Key words:** annual variation; *Arctocephalus gazella*; doubly labeled water; ecological energetics; energy budget; feeding rate; field metabolic rate; food consumption; foraging efficiency; prey (krill) availability; South Georgia Island; sub-Antarctic; water flux.

### INTRODUCTION

There have been few field studies of mammalian reproductive energetics, chiefly because this requires knowledge of several linked components, such as cost of travel to and from feeding sites, food consumption, and cost of lactation, none of which is simple to measure. Recently a number of studies have focused on phocid seals (Pinnipedia: Phocidae). These animals offer a fairly simple and tractable system to study. In most species females fast while ashore throughout lactation so that the energy transferred can be readily estimated and the metabolic costs of mother and pup measured simultaneously (Fedak and Anderson 1982, Stewart and Lavigne 1984, Costa et al. 1986, Anderson and Fedak 1987).

However, to date estimates of reproductive ener-

getics take no account of the cost to the female of the acquisition of energy stores that are used to feed the pup. In fur seals (Pinnipedia: Otariidae), females rearing offspring alternate periods of suckling ashore with foraging trips to sea. This behavior permits estimation of the energy costs of foraging as well as those associated with milk transfer to the pup. There has only been one such study to date, that of northern fur seals (*Callorhinus ursinus*) (Costa and Gentry 1986). In the present paper we investigate the energy budget of breeding female Antarctic fur seals (*Arctocephalus gazella*) at Bird Island, South Georgia, South Atlantic, in two seasons, one of low (austral summer 1984) and one of high (austral summer 1985) food availability. We provide empirical data on the energy costs of foraging at sea and examine how females rearing pups respond to variations in food availability.

Antarctic fur seals have been extensively studied at South Georgia and their basic breeding biology is well

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known (Bonner 1968). Female fur seals arrive ashore from mid-November until mid-December, giving birth to their single pups within 2 d of arrival. Ninety-five percent of the pups are born in a 3-wk period, with a mean pupping date of 5 December (Payne 1977). A postpartum estrus follows in about 5 d and females depart for sea to forage 0–2 d after copulating (McCann 1980, Doidge et al. 1986). Normal foraging trip duration is 4 d, alternating with shore-based pup-suckling bouts of  $\approx 2$  d (Doidge et al. 1986). The lactation period (pup rearing) lasts  $\approx 117$  d and females are onshore with their pups for 36% of this time (Doidge et al. 1986). During pup rearing, females feed almost exclusively on Antarctic krill (*Euphausia superba*) (Bonner 1968, Croxall and Pilcher 1984, Doidge and Croxall 1985).

During the 1984 season the distribution and abundance of Antarctic krill at South Georgia, and the subsequent effect on top predators (and especially Antarctic fur seals), was the most anomalous in the 10 yr for which detailed data are available (Croxall et al. 1988, Priddle et al. 1988). Starting during the 1983 austral winter, oceanographic anomalies in the Scotia Sea were associated with significantly reduced krill biomass (Heywood et al. 1985). These conditions persisted into the 1984 summer, especially in the northern Scotia Sea around South Georgia (Priddle et al. 1988). The reduced abundance of krill (and presumably also its availability to predators) and the apparent absence of swarms was associated with very poor reproductive performance of krill-eating penguins, albatrosses, and fur seals. There were significant decreases for some or all species in offspring provisioning, growth rates, and survival (Croxall et al. 1988). By the 1985 summer krill were once again abundant around South Georgia, and the production and survival of offspring of krill-eating seabirds and seals was typical of average values for 1975–1986.

#### MATERIALS AND METHODS

Lactating female Antarctic fur seals breeding on Bird Island, South Georgia (54°00' S, 38°02' W), were studied during the austral summers of 1984 (1983–1984) and 1985 (1984–1985). At-sea metabolism ( $\text{CO}_2$  production) and water turnover were measured using the doubly labeled water method (Lifson and McClintock 1966, Nagy 1980, Nagy and Costa 1980, Costa 1987) with 8 females during 1984 and 15 during 1985.

Females that had been suckling their pups and were about to depart on their second or fourth trip to sea in 1984 or their second trip to sea in 1985 were captured using a rope noose attached to a 3-m pole. The fur seals were quite tame, allowing us to approach within 1 to 2 m. Once captured, animals were restrained using a specially constructed board, described in detail by Gentry and Holt (1982). Once restrained, the females ceased to struggle, and in many instances upon release walked away, re-located their pups, and lay down with-

in 10 m of the release site. In order to control for intra-annual differences, measurements were made during the second trip to sea in both years. In 1984 we had planned to make replicate measurements on the same females during their fourth trip to sea. Unfortunately the pups of three of these females died due to starvation. This allowed replicate measurements on only three females and so measurements were made on three additional females that were foraging during their fourth trip to sea. If we had been able to anticipate the severity of the 1984 season we would have adopted a different experimental design. Given the severity of the 1984 season, data collection for the 1985 field season was designed to concentrate on interannual differences as measured during the second trip to sea, because there was a larger data base for this period in 1984.

Once the females were restrained, blood samples (10–20 mL) were taken (either via the interdigital vein or the pelvic plexus) for determination of isotope background specific activity; this was followed by an intraperitoneal injection of 3–5 g of 95% oxygen-18 water and 37 MBq tritiated water in 3 mL of sterile saline. Body mass was measured with a platform balance accurate to 50 g. While each female was restrained, her standard length (tip of nose to tip of tail) (ASM 1967) was measured. After injection the females and their pups were placed in holding pens. Three hours later an additional 10–20 mL blood sample was collected. By waiting 3 h we were assured that complete isotope equilibration had occurred because it is typically complete within 90 min in this species (Costa 1987). To allow for precise determination of departure and arrival times and to aid in recovery, a 150-g radio transmitter (148–149 MHz; Advanced Telemetry Systems, Bethel, Minnesota) was glued to each female's back using a fast-setting epoxy resin (Devcon "5 Minute Epoxy"). Females and their pups were then returned to the site of capture. The arrival and departure of females was monitored with a Telonics Inc. (Mesa, Arizona) TR-2 scanning telemetry receiver interfaced to an Esterline-Angus strip-chart recorder, as well as by daily visual surveys of the rookery. Females were recaptured on average 2.5 h (range: 0.5–11.5 h) after returning from a foraging trip which lasted 3–18 d. On recapture, body mass was recorded and a blood sample taken. This was followed by a final total body water (TBW) measurement determined by injection of 1 mL of 18.5 MBq/mL tritiated water (HTO) with another blood sample 3 h later. In all cases TBW was determined by the initial dilution of HTO (Nagy and Costa 1980). TBWs calculated by oxygen-18 dilution were within 0.5–3% of those determined by HTO. In some cases females had been previously captured for determination of parturition body mass, sampling of milk, or tagging. In these cases additional blood samples were collected to record intra-individual variation in the natural abundance of oxygen-18 ( $n = 6$ ).

FMR (field metabolic rate) data collected over the

entire measurement interval included variable amounts of onshore FMR. Data were normalized to estimate FMR while at sea by correcting for the portion of time spent onshore. Time onshore was calculated as the difference between the measurement interval and the departure and arrival of the animal from a foraging trip. Onshore  $FMR_M$  (mass-specific FMR) was assumed to be 4.96 W/kg, the rate reported for Antarctic fur seal females during the onshore perinatal period (Costa and Trillmich 1988). At-sea FMR was then calculated for each female by solving the following relationship for "At-sea FMR":

$$\text{Measured FMR} = \frac{[(\text{Onshore FMR}) \cdot (\% \text{ Time Onshore})] + [(\text{At-sea FMR}) \cdot (\% \text{ Time at Sea})]}{100}$$

The effect of metabolic measurements on female behavior was examined by monitoring the behavior of a second group of females. Within 5 d of parturition these females were captured, weighed, equipped with a radio transmitter, flipper-tagged, and bleach-marked. These females were then released and left undisturbed for the remainder of the field season. Attachment of transmitters during the perinatal period insured that females remained with their pups for at least 3 d prior to their first trip to sea and that at least 10 d and one at-sea cycle had elapsed prior to measurement of the duration of the second trip to sea. Comparisons were made of at-sea and onshore attendance patterns of these females and those used in metabolic measurements over the second and, in 1984, the fourth foraging trips.

Variation in female condition, during both the breeding season and between seasons, was examined by comparing female mass within 1 d of parturition to subsequent measurements taken during the season. In 1984, 15 females were studied (8 with female pups, 7 with male pups); 2–4 mass determinations per individual were made from 0 to 52 d postpartum. The 1985 sample was 24 females (14 with female pups, 10 with male pups) and records covered 0–91 d postpartum. The sample included some of the same females used in the energy study.

The specific activity of tritium was determined by scintillation spectrometry of triplicate aliquots of 200  $\mu\text{L}$  of pure water (vacuum distilled from the serum samples) in 10 mL of Betaphase scintillation cocktail (Westchem, San Diego, California). The specific activity of oxygen-18 water was determined by mass-ratio spectrometry (Global Geochemistry, Canoga Park, California) of pure water distilled from plasma samples.  $\text{CO}_2$  production and water influx were calculated using Eq. 3 presented in Nagy (1980) and Eqs. 5 and 6 in Nagy and Costa (1980) assuming an exponentially changing body-water pool. A constant of 25.2 J/mL was used to convert  $\text{CO}_2$  production to energy consumption (Costa 1987), calculated from the composition of the average Antarctic fur seal diet, which during normal seasons consists exclusively of mature

Antarctic krill in the ratio of 79% female to 21% male (Croxall and Pilcher 1984). This diet has a mean composition of 5.51% fat, 10.6% protein, 0.7% carbohydrate, and 76.8% water (plus chitin and ash) and an energy content of 5.507 kJ/g wet mass (Clarke 1980).

Data are given as means  $\pm 1$  SE. Unless otherwise stated, differences between means were tested using the Mann-Whitney  $U$  test and correlations using least squares linear regression analysis.

## RESULTS

### *Interannual differences*

*Female body mass and condition.*—At parturition, females in 1984 were significantly lighter (11%) than in 1985 (1984:  $35.6 \pm 1.83$  kg,  $n = 15$ ; 1985:  $40.2 \pm 1.03$  kg,  $n = 24$ ;  $U = 99$ ,  $P < .01$ ). Females used in metabolic studies were also lighter prior to their second trip to sea in 1984 ( $27.3 \pm 1.2$  kg,  $n = 6$ ) than those studied in 1985 ( $34.0 \pm 1.6$  kg,  $n = 15$ ) (Tables 1 and 2,  $U = 9$ ,  $P < .01$ ). Because females from the two years had equivalent standard lengths (1984:  $119 \pm 2.6$  cm,  $n = 6$ ; 1985:  $118 \pm 2.3$  cm,  $n = 15$ ;  $U = 43$ ,  $P > .10$ ), these data suggest that females in 1984 were in poorer condition than females in 1985.

The pattern of female mass change after parturition, however, did not appear to differ between years (Fig. 1), and there was no significant difference between seasons in females' mean percentage of postpartum body mass ( $U = 44$ ,  $n = 15, 24$ ,  $P < .01$ ). In both 1984 and 1985 females maintained body mass throughout the study period, although the inter-individual variation appeared to be greater in 1984 than in 1985.

Total body water (TBW) content may also provide an index of body condition because animals with a high fat content have a lower relative water content than lean animals (Pace and Rathbun 1945; e.g., a fat-free fur seal would be 73% water, whereas a very fat fur seal would be 50% water). However, this apparently was not the case; there was no difference in the females' water content either between years or upon arrival or departure. We examined this relationship by comparing the slopes and intercepts of the regression equations relating TBW and female body mass both between years and between initial and final measurements (analysis of covariance). The data were pooled, yielding a highly significant regression equation for TBW (in litres) as a function of female body mass ( $M$ , in kilograms):  $\text{TBW} = 3.045 \pm 0.5697 M$  ( $r = 0.898$ ,  $P < .01$ ,  $n = 49$ ; Fig. 2). It is likely that the presence of large quantities of milk in the mammary glands precludes the use of water content as an index of adipose stores in lactating fur seals.

With only two exceptions, females gained mass during their foraging trips (Tables 1 and 2). Interestingly, the FMR of these females was almost equivalent to the mean for their respective seasons. This indicates that FMR was no different between successful and unsuccessful

TABLE 1. Measurement interval, time at sea, mass change, water influx, and mass-specific metabolic rate (FMR<sub>M</sub>) of female Antarctic fur seals over their second and fourth foraging trips during austral summer 1984 at South Georgia.

Animal	Pup sex	Measurement interval (d)	Time at sea (d)	Mass		Mass change		Water influx (ml·kg <sup>-1</sup> ·d <sup>-1</sup> )	FMR <sub>M</sub>		
				Initial (kg)	Final (kg)	Per trip (%)	Per day (%)		CO <sub>2</sub> flux (mL·g <sup>-1</sup> ·h <sup>-1</sup> )	(W/kg)	At sea* (W/kg)
Second trip to sea											
430	M	11.00	10.15	26.95	29.25	7.86	.77	152	1.49	10.55	11.02
436	F	9.91	9.82	28.85	30.10	4.15	.42	171	0.94	6.62	6.64
440	F	9.94	9.01	25.75	24.75	-4.04	-.45	137	1.20	8.50	8.87
448	M	9.09	9.03	31.90	34.70	8.07	.89	201	1.48	10.48	10.52
450	M	7.05	5.91	27.25	27.85	2.15	.36	179	1.19	8.43	9.10
474	F	7.90	6.23	23.35	24.30	3.91	.63	139	1.13	8.00	8.82
Mean		9.15	8.36	27.34	28.49	3.68	.44	163	1.24	8.76	9.16
SE		0.59	0.75	1.18	1.57	1.82	.20	10	0.09	0.62	0.63
Fourth trip to sea											
434	M	12.04	†	34.30	39.50	13.16	1.09	191	1.42	10.06	
436	F	15.92	†	28.95	33.40	13.32	0.84	151	‡	...	
440	F	9.18	8.39	25.25	29.35	13.97	1.52	214	1.02	7.22	7.44
450	M	11.19	9.70	24.30	30.65	20.72	1.85	203	‡	...	
500	?	8.96	†	28.70	30.15	4.81	0.54	189	1.46	10.34	
Mean		11.46	9.05	28.30	32.61	13.20	1.17	190	1.30	9.21	
SE		0.66		1.76	1.85	2.53	0.23	11	0.11	1.00	

\* At-sea FMR<sub>M</sub> = {measured FMR<sub>M</sub> - [(4.96 W/kg)·(% time onshore)]}/(% time at sea).

† Transmitters either were not available or had fallen off, precluding measurement of time at sea.

‡ Prolonged trip durations resulted in oxygen-18 levels too close to background to allow determination of CO<sub>2</sub> production.

cessful foragers. The average total mass gain over the trip was not different between the two seasons ( $U = 55$ ,  $n = 6$ ,  $15$ ,  $P > .10$ ). However, the rate of mass gain was 241% greater in 1985 than in 1984 (1984 mean =  $0.44 \pm 0.20$  kg,  $n = 6$ ; 1985 mean =  $1.06 \pm 0.22$  kg,  $n = 15$ ;  $t$  test,  $t = 1.749$ ,  $P < .05$ ).

*Foraging-attendance patterns.*—In 1984 foraging trips averaged 87% longer than trips in 1985 (1984

mean =  $8.4 \pm 0.8$  d,  $n = 6$ ; 1985 mean =  $4.5 \pm 0.3$  d,  $n = 15$ ;  $U = 2$ ,  $P < .01$ ; Table 3). We believe that differences in foraging pattern were not related to handling stress because there was no significant difference between experimental and control females in trip duration or time spent onshore in either 1984 ( $t$  test,  $t = 0.97$ ,  $P > .10$ ) or 1985 ( $t = 0.47$ ,  $P > .10$ ) (Table 3). Equivalent differences in 1984 and 1985 foraging trip

TABLE 2. Measurement interval, time at sea, mass change, water influx, and mass-specific metabolic rate (FMR<sub>M</sub>) of Antarctic fur seal females foraging during their second trip during the austral summer 1985 at South Georgia.

Animal	Pup sex	Measurement interval (d)	Time at sea (d)	Mass		Mass change		Water influx (mL·kg <sup>-1</sup> ·d <sup>-1</sup> )	FMR <sub>M</sub>		At sea* (W/kg)
				Initial (kg)	Final (kg)	Per trip (%)	Per day (%)		CO <sub>2</sub> flux (mL·g <sup>-1</sup> ·h <sup>-1</sup> )	(W/kg)	
229	F	4.868	3.097	30.00	29.20	-2.74	-0.88	141	1.28	9.07	11.41
243	M	3.682	3.374	45.65	46.30	1.40	0.42	170	.83	5.78	5.86
251	F	6.887	5.166	32.05	34.30	6.56	1.27	159	.92	6.53	7.05
257	F	4.560	4.421	23.10	25.35	8.88	2.01	234	1.42	10.03	10.19
265	F	4.831	4.398	32.10	32.50	1.23	0.28	171	1.40	9.92	10.40
269	F	7.101	5.285	39.40	41.15	4.25	0.80	92	0.77	5.48	5.66
271	M	3.828	3.080	39.75	41.05	3.17	1.03	138	1.15	8.15	8.92
273	F	4.962	3.519	39.55	40.00	1.13	0.32	133	1.17	8.29	9.65
275	M	5.097	4.835	27.60	30.65	9.95	2.06	193	1.11	7.90	8.06
281	M	6.701	5.713	33.40	36.90	9.49	1.66	185	1.62	11.51	12.64
287	M	4.139	3.740	35.55	37.10	4.18	1.12	181	1.58	11.19	11.86
291	M	4.297	4.199	30.70	33.50	8.36	1.99	155	1.16	8.22	8.29
299	F	6.837	5.604	29.20	32.00	8.75	1.56	194	1.23	8.71	9.54
430	M	6.750	6.642	29.50	33.65	12.33	1.86	209	1.40	9.92	10.00
434	M	6.708	4.777	42.70	43.50	1.84	0.38	119	1.96	13.88	17.49
Mean		5.417	4.523	34.02	35.81	5.25	1.06	165	1.27	8.97	9.80
SE		0.325	0.271	1.61	1.48	1.11	0.22	10	0.08	0.58	0.76

\* At-sea FMR<sub>M</sub> = {measured FMR<sub>M</sub> - [(4.96 W/kg)·(% time onshore)]}/(% time at sea).

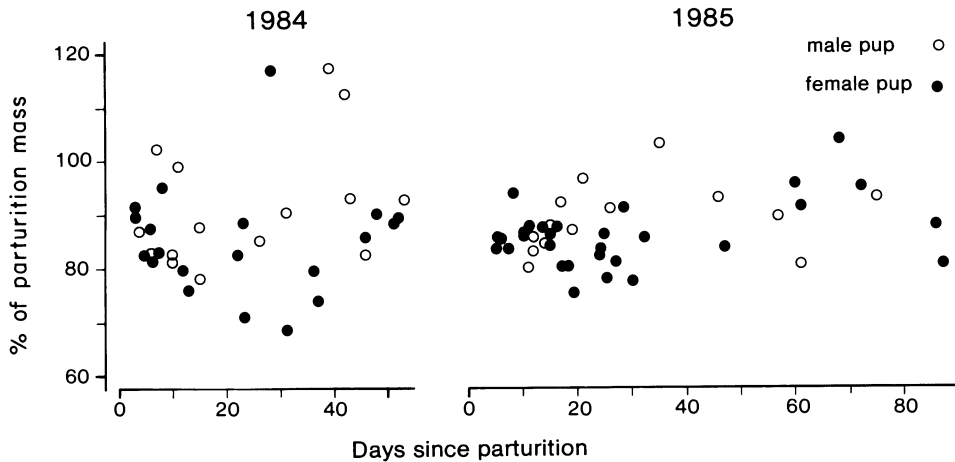


FIG. 1. Body mass (expressed as percent of maternal mass at parturition) in relation to time since parturition in female Antarctic fur seals in 1984 and 1985. There was no relationship between mean female postpartum mass and sex of pup ( $U = 44$ ,  $P > .10$ ).

durations were also reported by Croxall et al. (1988) for a larger sample of females that was monitored visually ("monitoring" group). Since these data were collected by censusing the beaches visually in the morning and evening throughout the season, comparisons should only be made between years and not between radio-telemetered and "monitored" individuals. There was no correlation between relative mass change over the second trip to sea and trip duration for both years combined ( $r = 0.17$ ,  $n = 21$ ,  $P > .10$ ; Fig. 3) and for 1984 treated separately ( $r = 0.23$ ,  $n = 6$ ,  $P > .10$ ). However, trip duration and mass change were significantly correlated for 1985 females ( $r = 0.75$ ,  $n = 15$ ,  $P < .01$ ).

**Foraging energetics.**—There were no significant differences between years in the mass-specific rate of energy utilization (i.e., field metabolic rate [ $FMR_M$ ], water influx (Tables 1 and 2), or  $FMR$  as a function of female body mass (Fig. 4). Due to the longer foraging trips in 1984 and, consequently, the relatively smaller percentage of time spent onshore, corrections of measured  $FMR_M$  to yield at-sea  $FMR_M$  were smaller in 1984 ( $4.3 \pm 1.5\%$ , range: 0.2–9.3) than in 1985 ( $7.7 \pm 1.8\%$ , range: 0.8–20.6) (Tables 1 and 2). Metabolic rate was highly significantly correlated with female body mass ( $r = 0.555$ ,  $n = 24$ ,  $P < .01$ ; Fig. 4). This relationship fit the data as well as did a correlation between  $FMR$  and body mass raised to the 0.75 power ("metabolic

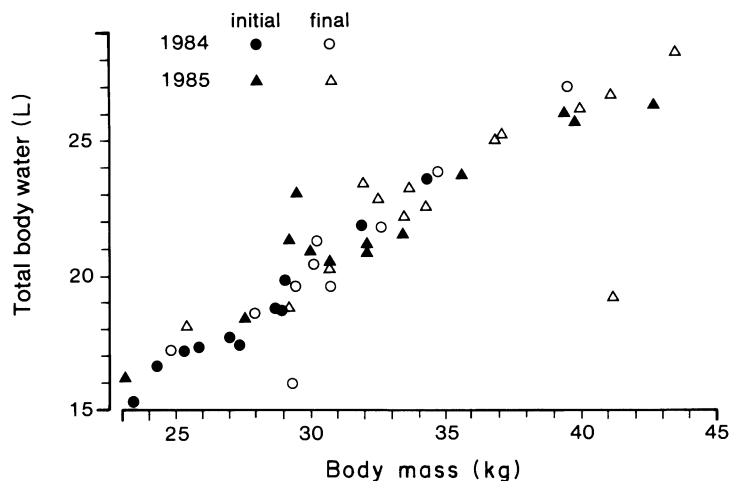


FIG. 2. Total body water content (TBW, in L) in relation to body mass ( $M$ , in kg) in female Antarctic fur seals followed a highly significant least squares linear regression ( $r = 0.898$ ,  $P < .01$ ) and can be calculated as  $TBW = 0.5697 M + 3.045$ . There was no difference between years or between determinations made at the beginning of a measurement interval (initial) or on recapture after returning from a trip to sea (final) (analysis of covariance).

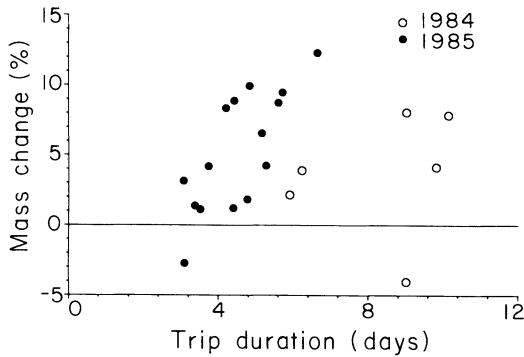


FIG. 3. Relationship between mass change during the second foraging trip to sea and the duration of this trip in female Antarctic fur seals during a poor year (1984) and a normal year (1985). Trip duration was significantly greater (mean 87%) in 1984 than in 1985 ( $U = 2$ ,  $P < .01$ ), whereas there was no relationship between percent mass gain and year ( $U = 65$ ,  $P > .10$ ).

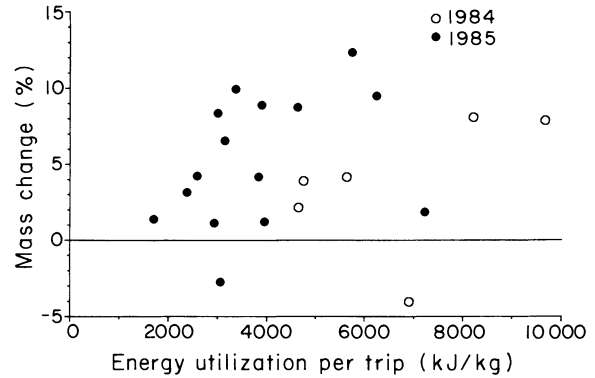


FIG. 5. Mass change over the second foraging trip to sea in relation to energy utilization during the same trip by female Antarctic fur seals in a poor year (1984) and a normal year (1985). Total energy utilization was significantly greater (mean = 71%) in 1984 than in 1985 ( $U = 10$ ,  $P < .01$ ), whereas there was no difference between years in percent mass change over a trip ( $U = 65$ ,  $P > .10$ ).

mass";  $r = 0.556$ ,  $n = 24$ ,  $P < .01$ ). Therefore metabolic comparisons between individuals of different body mass were partially normalized by use of mass-specific metabolism (W/kg). Although there was no difference in the rate of energy utilization, mass-specific energy expended over a complete foraging trip was significantly greater for females in 1984 ( $6633 \pm 821$  kJ/kg,  $n = 6$ ) than in 1985 ( $3884 \pm 393$  kJ/kg,  $n = 15$ ) ( $U = 10$ ,  $P < .01$ ; Fig. 5). This was due simply to the longer duration of foraging trips in 1984. There was no correlation between energy expenditure and relative mass gain, either between seasons or within seasons treated separately (1984:  $r = 0.438$ ,  $n = 6$ ,  $P > .05$ ; 1985:  $r = 0.343$ ,  $n = 15$ ,  $P > .05$ ; 1984 and 1985 combined:  $r = 0.140$ ,  $n = 21$ ,  $P > .10$ ) (Fig. 5).

#### Intra-annual differences

Data are available on intra-annual variations only for 1984. Females returning to shore after their fourth trip to sea showed 357% as much proportional gain ( $13.2 \pm 2.5$  % of body mass,  $n = 5$ ) as did females returning after their second trip to sea ( $3.7 \pm 1.8$  %,  $n = 6$ ) ( $U = 2$ ,  $P < .01$ ). Increased mass gain was not significantly associated with an increase in trip duration (second trip mean duration =  $9.15 \pm 0.59$  d,  $n = 6$ , fourth trip mean duration =  $11.46 \pm 1.26$  d,  $n = 5$ ,  $U = 7$ ,  $P > .1$ ) or increased FMR, but rather with an increase in the rate of proportional mass gain per trip (second trip mean =  $0.44 \pm 0.20$  %/d,  $n = 6$ , fourth trip mean =  $1.17 \pm 0.23$  %/d,  $n = 5$ ;  $U = 0$ ,  $P < .02$ ).

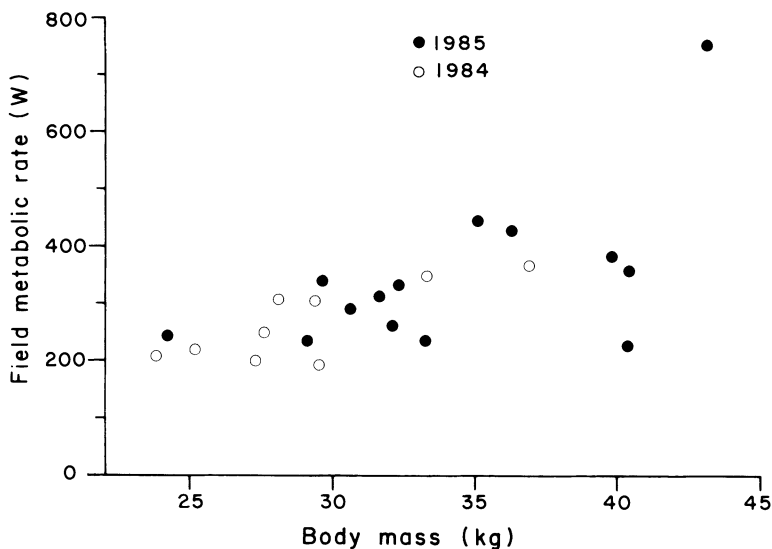


FIG. 4. Field metabolic rate (FMR, in W) in relation to body mass ( $M$ , in kg) in female Antarctic fur seals. A least-squares linear relationship yields a highly significant correlation ( $r = 0.555$ ,  $P < .01$ ) that follows  $FMR = 10.9M - 41.1$ .

However, these conclusions are tentative due to the small sample size and because the data for the fourth trip to sea include data only from females able to successfully rear their offspring beyond the second trip to sea. These successful females were able to increase body mass at rates similar to those achieved in 1985. We were unable to complete repeat measurements on females 430, 448, and 474, because their pups died of starvation.

*Differences associated with pup sex.*—There were no significant associations between pup sex and trip duration ( $U = 56$ ,  $n = 10, 11$ ;  $P > .10$ ), female FMR ( $U = 38$ ,  $n = 10, 11$ ;  $P > .10$ ), percent mass gain ( $U = 34$ ,  $n = 10, 11$ ;  $P > .10$ ), or total energy expenditure over a foraging trip ( $U = 45$ ,  $n = 10, 11$ ;  $P > .10$ ). There was no difference between the postpartum mass of females with male pups and females with female pups ( $U = 44$ ,  $n = 10, 12$ ;  $P > .10$ ) and no relationship between pup sex and female mass later in the season relative to her postpartum mass ( $U = 103$ ,  $n = 12, 23$ ;  $P > .10$ ).

## DISCUSSION

### *Foraging energetics*

*Energy costs.*—The mean at-sea FMR<sub>M</sub> of all female Antarctic fur seals foraging over both years was  $9.52 \pm 0.55$  W/kg,  $n = 22$ . This is 6.7 times the predicted mass-specific basal metabolic rate (BMR<sub>M</sub>) for a terrestrial animal of equal size and is comparable to the  $8.18 \pm 0.67$  W/kg reported for similar-sized northern fur seal females foraging in the Bering Sea (Costa and Gentry 1986). An FMR<sub>M</sub> of 6.7 times basal may suggest that foraging is quite costly, or it may indicate that predicted BMR<sub>M</sub> is falsely low. Similarly, the FMR<sub>M</sub> for foraging female northern fur seals is 6.0 times the predicted BMR<sub>M</sub> (Costa and Gentry 1986) but only 2.5 times the BMR<sub>M</sub> measured by Miller (1978). Measurements of basal metabolic rate are not available for Antarctic fur seals, and although recent arguments suggest that Kleiber's (1975) metabolic-rate-to-body-mass regression is applicable to phocids (Lavigne et al. 1986), it may underestimate the basal metabolic rate of otariids.

Interestingly, the at-sea metabolic rate of Antarctic fur seal females is only 1.9 times the rate measured during their period of fasting onshore while suckling their pups (4.96 W/kg; Costa and Trillmich 1988). This suggests either that the increased metabolic demands associated with swimming and foraging at sea are not great or that metabolic rates onshore are elevated. Comparable data for northern fur seals indicate that metabolism while at sea was 1.8 times the rate determined for individuals fasting onshore (Costa and Gentry 1986).

*Foraging efficiency.*—Previous studies have defined "foraging efficiency" as the usable (metabolizable) energy gained while foraging divided by the energy ex-

pendent while foraging (Nagy and Shoemaker 1984). If certain assumptions are made, the foraging efficiency of Antarctic fur seals can be calculated from feeding rates determined from the water influx and metabolic rate data in Tables 1 and 2. This calculation requires data on dietary composition, and the assumptions (1) that food is the only source of exogenous water, (2) that sea-water ingestion is minimal, and (3) that unlabeled exchange of HTO (tritiated water) across the respiratory or skin surface is negligible. Validation studies on pinnipeds indicate that when the composition of the diet is known there is excellent agreement between actual food intake and food intake estimated from water influx measurements [within  $\pm 1.8\%$  in northern fur seals and  $\pm 1.2\%$  in California sea lions, *Zalophus californianus* (Costa 1987)]. During normal seasons the diet of female Antarctic fur seal consists exclusively of mature Antarctic krill in the ratio (by mass) of 79% female to 21% male krill (Croxall and Pilcher 1984). This diet has an energy content of 5.507 kJ/g wet mass and is 76.8% water (Clarke 1980). Net preformed water intake can be calculated by subtracting the metabolic water production (MWP) from total water influx. MWP is calculated from metabolic rate determined by doubly labeled water using a conversion of 0.026 mL/kJ (Costa 1987). Food intake can then be estimated by dividing the rate of preformed water entry by the water content of the diet. The mean water influx for both seasons was  $169 \text{ mL} \cdot \text{kg}^{-1} \cdot \text{d}^{-1}$ . Subtracting a metabolic water production of  $20.4 \text{ mL} \cdot \text{kg}^{-1} \cdot \text{d}^{-1}$  yields a net preformed water intake of  $149 \text{ mL} \cdot \text{kg}^{-1} \cdot \text{d}^{-1}$ . Dividing by the water and energy content of the diet yields a food intake of  $194 \text{ g} \cdot \text{kg}^{-1} \cdot \text{d}^{-1}$  or  $11.5 \text{ W/kg}$ . Correcting for an assumed rate of fecal and urinary energy loss of 10% (Miller 1978) generates a net energy intake rate of  $10.34 \text{ W/kg}$ . Dividing the rate of usable energy consumed ( $10.34 \text{ W/kg}$ ) by the rate of energy expended ( $9.52 \text{ W/kg}$ ) yields a foraging efficiency of 1.09. The only other information on foraging efficiency for marine mammals is a value of 1.24 for northern fur seals feeding on fish and squid in the Bering Sea (Costa and Gentry 1986).

This suggests that the Antarctic fur seal may have a lower feeding efficiency, but comparisons should be made with caution because there are several sources of potential bias. First, if seawater is ingested, food intake and foraging efficiency would be overestimated. However, it is unlikely that seawater ingestion has occurred since the preceding calculation indicates that if anything the rate of food intake is too low. Second, and probably more important, calculation of food intake is dependent on accurate knowledge of the diet and of its water and energy content (Costa 1987). There are no quantitative data on fur seal diet during 1984, but qualitative observations of the color and content of scats indicated that it was predominantly, if not exclusively krill. However, the energy content of krill varies markedly with size, sex, and reproductive status;



TABLE 3. Duration of the second foraging trip and the subsequent visit ashore by female Antarctic fur seals in 1984 and 1985. The "control" and "experimental" categories refer to animals that had been fitted with radio transmitters (this study). The "monitoring" category refers to seals in a study by Croxall et al. (1988) that had data collected by visually monitoring females over the entire season.

Seal category	Foraging trip duration (days)		Time onshore (days)	
	1984	1985	1984	1985
Monitoring				
Mean	6.8	3.1	1.8	1.5
SE	0.8	0.1	0.1	0.1
n	180	186	180	186
Control*				
Mean	7.0	4.9	1.1	3.2
SE	1.2	1.1	0.1	0.3
n	6	7	6	7
Experimental*				
Mean	8.4	4.5	1.1	1.9
SE	0.8	0.3	0.1	0.8
n	6	15	6	2

\* Differences between experimental and control females were not significant for either 1984 ( $t$  test,  $t = 0.97$ ,  $P > .10$ ) or 1985 ( $t = 0.47$ ,  $P > .10$ ).

for example, from 3.84 kJ/g wet mass for males to 5.46 kJ/g wet mass for gravid females (Clarke 1980). If fur seals consumed primarily male or nongravid female krill during 1984 in contrast to the typical diet (21% male and 79% female krill; Croxall and Pilcher 1984) they would consume metabolizable energy at a rate of 8.3 W/kg. This is unlikely, since this would put them in negative energy balance (metabolic rate = 9.52 W/kg). Conversely, if fur seals ate only gravid female krill they would consume metabolizable energy at a rate of 11.2 W/kg. Given these data, the highest foraging efficiency ratio for these females if they had consumed exclusively gravid female krill would be 1.18, which is a value still lower than that reported for northern fur seals.

An alternative method of estimating foraging efficiency that does not require dietary information is to estimate the energy content of the mass gained over the foraging trip. In lactating females it is likely that most if not all of this mass increase is milk contained in the mammary gland. For simplicity we assume that all of this increased body mass is such milk; in this species the energy content of milk is 17.7 kJ/g (D.P. Costa, *personal observation*). Over both seasons females stored energy at a rate of 1.92 W/kg ( $9.36 \text{ g} \cdot \text{kg}^{-1} \cdot \text{d}^{-1} \times 17.7 \text{ kJ/g}$ ; Tables 1 and 2). The rate of metabolizable energy intake is 11.44 W/kg (metabolic rate of 9.52 W/kg + storage rate of 1.92 W/kg). Foraging efficiency calculated by this method as total metabolizable energy consumed divided by energy expenditure is 1.20 ( $11.44 \text{ W/kg} / 9.52 \text{ W/kg}$ ), nearly equivalent to the foraging efficiency of 1.18 calculated for females on a diet of mature gravid female krill.

Similar calculations with data on northern fur seals confirms that they have a higher foraging efficiency. In this species the net body mass gain is  $17.8 \text{ g} \cdot \text{kg}^{-1} \cdot \text{d}^{-1}$  and the milk energy content 19.9 kJ/g (Costa and Gentry 1986). Females acquired stored energy at a rate of 4.1 W/kg while expending 8.18 W/kg, which yields a foraging efficiency of 1.5, a value higher than the 1.2 calculated above for Antarctic fur seals. This supports our conclusion, based on feeding rate data, the northern fur seals feeding on fish and squid exhibit higher foraging efficiencies than Antarctic fur seals feeding on krill.

#### Foraging strategies

Fisheries and research data indicate a greatly reduced abundance of krill around South Georgia in 1984 (see Introduction). There were several obvious differences between 1984 and 1985 in the performance of female Antarctic fur seals during their foraging trips (Table 4). The postpartum mass of female Antarctic fur seals indicated that they were significantly lighter on arrival at Bird Island in 1984 than in 1985; this difference persisted at least through the first half of the lactation period. During the experimental period (and, indeed, throughout lactation) foraging trips to sea were nearly twice as long in 1984 as in 1985. On foraging trips in 1985 females gained significantly more mass per day than in 1984, but there was no overall difference in gain per trip because females in 1984 remained at sea longer. There was also no difference between years in the rate of energy expenditure while at sea, but, because of the increased duration of foraging trips, the total energy expended per foraging trip was significantly greater in 1984 (Table 4).

What do these data suggest about how female fur seals organize foraging activities in response to different levels of food availability? First, it appears that females stay at sea long enough to accomplish a substantial proportionate change in body mass. While at sea they need to replenish their reserves, replacing energy lost while fasting ashore and suckling their pups, to acquire fresh energy stores to fuel the return journey to the breeding site and, if possible, to provide sufficient food (milk) for the pup to enable it to maintain normal or maximum growth. In 1984 females apparently took so long to fulfill these requirements that foraging trips lasted twice the normal time. This resulted in 32% pup mortality, of which 68% died of starvation. Pup mortality typically ranges from 14 to 22%, of which 22 to 40% die from starvation in normal years (Croxall et al. 1988). Second, the data suggest that female fur seals did not increase their daily energy expenditures while at sea, because they were either unable, or unwilling, to work harder.

This behavior, whereby female fur seals meet their own energy needs even though this may jeopardize the survival of their offspring, is consistent with expectations for long-lived vertebrates (Stearns 1976). In such

TABLE 4. Comparison of body mass and energy expenditure associated with at-sea foraging trips in 1984 and 1985 by female Antarctic fur seals. Data are means  $\pm$  1 SE.

Parameter	1984	1985	Ratio 1984/1985	Significance
Female condition				
Standard length (cm)	118 $\pm$ 2	119 $\pm$ 3	0.99	NS
Mean initial mass (kg)	27.3 $\pm$ 1.2	34.0 $\pm$ 1.6	0.80	$P < .01$
Trip duration (days)	8.36 $\pm$ 0.75	4.52 $\pm$ 0.27	1.85	$P < .01$
Mass change during foraging				
(% body mass per day)	0.44 $\pm$ 0.20	1.06 $\pm$ 0.22	1.42	$P < .05$
(% body mass per trip)	3.68 $\pm$ 1.82	5.25 $\pm$ 1.11	0.70	NS
Energy expenditures				
FMR <sub>M</sub> (W/kg)	9.16 $\pm$ 0.63	9.80 $\pm$ 0.76	0.93	NS
Energy used per trip (kJ/kg)	6634 $\pm$ 821	3884 $\pm$ 393	1.71	$P < .01$

species the survival of progeny in any one year is always likely to be subordinate to ensuring the survival of the adult, providing it has the expectation of future reproductive events in more favorable circumstances.

How do the responses of Antarctic fur seals compare with those of northern fur seals, the only other marine mammal for which similar data exist (Table 5)? The main differences are that, in two different seasons, northern fur seal females modified FMR and kept trip duration constant, instead of keeping FMR constant and varying trip duration as did Antarctic fur seal females. Why do these two very similar-sized species, both inhabiting subpolar environments, adopt such different strategies? In particular, why did female Antarctic fur seals in 1984 not work harder (even at the cost of increased energy demand) and return to the pups on a normal attendance schedule, thereby reducing the risk of pup mortality due to starvation?

It may be that Antarctic fur seals normally operate near their metabolic maximum and have little ability to increase their foraging effort. Such a metabolic "ceiling" may be due in part to a limited ability to modify time-activity budgets while foraging. A similar metabolic ceiling has been suggested to account for the recorded metabolic rates of birds engaged in rearing young (Drent and Daan 1980, Reyer and Westerterp 1985). In support of this argument, the highest mean FMR reported for northern fur seals is quite similar to that observed for Antarctic fur seals. In normal years, Antarctic fur seal females spend 60% of their time swimming, 35% of their time diving, and only 5% resting (Kooyman et al. 1986). In contrast, northern fur seals spend 57% of the time swimming, 26% diving, and 17% resting (Gentry et al. 1986). Thus northern fur seals normally spend more than three times as long resting and must have greater scope for increasing their time spent actively foraging. If Antarctic fur seals normally operate near a metabolic maximum, then increases in their work rate may not have been possible. In addition, 1984 was the most anomalous year for Antarctic fur seals in a decade of observations, with

krill very uncommon and mainly dispersed (i.e., not in swarms); this meant that the chance of encountering swarms may not have been improved by working harder.

Another consideration in evaluating interspecific differences in rates of energy acquisition is the ability to switch and the cost of switching between different types of prey. Antarctic fur seal females normally only feed on one prey species, krill, during the breeding season, even in years of greatly reduced prey availability. Northern fur seal females, however, prey on a variety of species (Perez and Bigg 1986) that apparently require markedly different foraging patterns (Gentry et al. 1986, Loughlin et al. 1987, Costa 1988). Therefore interannual changes in FMR while at sea may to some extent reflect alterations in foraging or diving patterns that accompany changes in target prey species. Preliminary data coupling energetics with dive patterns suggest that different foraging behaviors have different metabolic costs (Costa 1988). For example, female northern fur seals make half as many dives when preying upon walleye pollock (*Theragra chalcogramma*), Pacific herring (*Clupea harengus*), and capelin (*Mallotus villosus*), which are principally demersal and deep-living (185-m mean dive depth), as they do when preying upon vertically migrating squid of the family Gona-

TABLE 5. Comparison of foraging trip duration, and mass changes and energy expenditure associated with this, by female northern and Antarctic fur seals in different years. Northern fur seal data are from Costa and Gentry (1986).

Species	Sam ple size	Year	Trip duration (days)	Mass change		Rate of energy ex- pendi- ture (W/kg)
				%/trip	%/day	
Northern fur seal	5	1981	5.94	10.5	1.76	6.57
	6	1982	6.72	12.1	1.80	9.79
Antarctic fur seal	6	1984	8.36	3.7	0.44	9.16
	15	1985	4.52	5.3	1.06	9.80

tidae (mostly *Gonatus* spp., *Berryteuthis magister*) when they are near the surface (50–60 m mean dive depth) (Loughlin et al. 1987). Furthermore, pollock, herring, and capelin have significantly greater energy yields than squid.

One unexpected result of this study of Antarctic fur seals was the considerable individual variation in FMR, even in 1985, the year of normal prey availability. We speculate that this may relate to the fact that the main prey targets of Antarctic fur seals are krill swarms. Krill are usually present in patchily distributed swarms, so the FMR of any individual fur seal would be greatly influenced by how long it took to find a swarm and the characteristics (e.g., size, density) of the swarm.

The relationship between the distribution and abundance of krill and fur seal energy expenditure and provisioning rate is obviously a complex one (see Croxall et al. 1985). It is likely to be further elucidated only by acquiring data on at-sea activity patterns, feeding (diving) locations, and energy budgets from the same individuals and then relating these to fine-scale information on krill density and distribution.

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