INCREASED FOOD AND ENERGY CONSUMPTION OF LACTATING NORTHERN FUR SEALS, *CALLORHINUS URSINUS*

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ABSTRACT

Data from pelagic northern fur seals, *Callorhinus ursinus*, taken during 1958-74 by the United States and Canada in the eastern Bering Sea were analyzed to determine relative feeding rates of lactating and nonlactating females. Estimates of the quantity of food and energy consumed by these seals during July-September were evaluated. The average daily feeding rate (adjusted for percentage of time feeding at sea) for lactating seals is 1.6 times that for nonlactating seals. During July-September, the total population of lactating and nonlactating females were estimated to consume 146.5×10^3 t (204.5×10^9 kcal) and 43.1×10^3 t (60.2×10^9 kcal) of food respectively. Fish accounted for 66.4% of food biomass (69.4% of total energy consumption); squid, the remainder.

The energetics of reproduction, especially during lactation, are poorly documented for free-ranging animals. The various reproductive states of domestic mammals, e.g., cattle, sheep, etc., have been extensively studied; and there has also been considerable research on rodents, e.g., mice, voles, etc., under both laboratory and field conditions. As a result of these studies it is widely accepted that most nursing females require considerably more energy than do nonnursing females of the same species, age, and size. Brody (1945) also noted that the maintenance requirements of lactating animals are elevated relative to nonlactating animals.

In some mammalian species, food intake during lactation may be up to 5 times greater than that observed in nonpregnant, nonlactating adult females, and lactating animals often convert considerable body substance to support the lactation process (Baldwin 1978). Previous studies on terrestrial mammals have specifically shown increased energy consumption by lactating females relative to nonlactating females. For example, captive deer mice, *Peromyscus maniculatus*, have a 96% to a 194% increase (Stebbins 1977); and ewes have a 116% increase (Engels and Malan 1979). The bat, *Myotis thysanodes*, which undergoes thermoregulatory physiological changes during reproductive stages, also has higher energy requirements for lactating females (Studier et al. 1973). Lactating humans are recommended to increase food consumption by at least 25% (Eagles and Randall 1980); however, some lactating humans in Guatemala meet their additional lactation energy costs by fat loss (Schutz et al. 1980).

There are few studies on the energetics and consumption of food during lactation by marine mammals. Lactation appears to drain the energy reserves of large baleen whales; the blubber of lactating females (e.g., blue, *Balaenoptera musculus*, and fin, *Balaenoptera physalus*, whales) is lean and emaciated compared with nonlactating females (Lockyer 1978, 1981a). Lockyer (1981b) estimated that adult female sperm whales, *Physeter macrocephalus*, need to increase their food intake by about 32-63% during lactation, meaning that they would need to feed 4 or 5 times daily to meet higher energy requirements. Lockyer (1981b) also estimated that minke, *Balaenoptera acutorostrata*, and fin whales increase their food intake by 75 and 86%, respectively. Spotte and Babus (1980) did not find a significantly increased mean feeding rate for one captive, pregnant bottlenosed dolphin, *Tursiops truncatus*, but standard deviations were consistently greater. In addition, during the first 3½ mo of lactation, a captive mother bottlenosed dolphin consumed 170% more food than she did while not lactating the following year (Mooney[2]). Costa and Gentry (in press) derived metabolic rates for lactating female northern fur seals from measurements of water flux and discussed the components of the

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energy budget for females and pups during the first two months of the reproductive cycle.

Although most mammals ingest more food while they are lactating than they would in a nonlactating state, many species of phocid seals fast during the lactation period (Harrison 1969). These seals (e.g., gray seal, *Halichoerus grypus*, and northern elephant seal, *Mirounga angustirostris*) do not feed from parturition to weaning of the young, and all of their energy needs during lactation must be met by metabolism of in situ energy such as fat reserves. This behavior has been well documented for the gray seal (e.g., Amoroso and Matthews 1951, 1952; Fedak and Anderson 1982) and also for the harp seal, *Phoca groenlandica*, (Lavigne et al. 1982). However, metabolism of fat reserves does not reduce the energetic costs of producing offspring; it merely shifts the time that energy must be acquired, at some energy cost for storage (Millar 1978).

The objectives of this study were to show, using both stomach content and body mass data, that lactating female fur seals ingest more food than nonlactating females in order to meet their increased energy requirements for maintenance and milk production, and to make estimates of the magnitude of this difference in food ingestion. For this study, we utilized data from postpartum and nonpregnant adult, female northern fur seals, *Callorhinus ursinus*, taken pelagically during 1958-74.

METHODS

Data on the contents of stomachs from the female northern fur seals taken pelagically (Fig. 1) in the eastern Bering Sea during 1958-74 by the United States and Canada were analyzed to determine the relation between lactation and food consumption during the summer breeding season. Only data from female fur seals (age ⩾4 yr) which had information on both body mass and stomach content mass were included. Age was determined from longitudinal half-sections of the upper canine teeth by counting the annual growth layers in the dentine, a method widely accepted by researchers during recent decades to determine the age of many species of mammals (Klevezal' and Kleinenberg 1967). Methods used during 1958-74 to determine age, reproductive status, and the different items in the stomachs were discussed by Lander (1980).

The data used in this study represented stomach contents under different stages of digestion; however, it was not possible to make comparisons between stages because no data on stages of digestion were recorded. Rates of digestion of all prey were assumed to be similar for all females during the same time interval. In our study, all postpartum females were considered lactating, and all nonpregnant (not postpartum) females were considered nonlactating.

Statistical Methods

The cumulative frequency distributions of data on mass of total stomach contents for both lactating and nonlactating females were compared using the one-tail Kolmogorov-Smirnov two-sample test (Siegel 1956).

Data from seals with empty stomachs or stomachs with only a trace of contents (i.e., <10 cc) were considered as zero mass and pooled with data from seals with food in their stomachs. Data for different ages and months were pooled to provide sufficient sample size for analysis because the normal approximation to compute confidence limits is only valid if sample sizes are adequate (Cochran 1977). In order to use parametric statistics, and yet not seriously violate basic assumptions of normality, data were transformed by the modified arcsine transformation discussed by Zar (1974):

$$X = \sqrt{M + 0.5} \quad \arcsin \quad \sqrt{(S + 0.375)/(M + 0.75)}$$

where M is the net body mass (excluding mass of stomach contents, S) and X is the transformed value. This equation was used because of its utility where a large number of the data were from stomachs containing only a trace or less.

The transformed values on the mass of total stomach contents (expressed as a percentage of net body mass) obtained from the above equation were transformed back to percentages to obtain means. We calculated an index of the relative intake of food by lactating females compared with that of nonlactating females by multiplying the ratio of their respective mean mass of stomach contents by 100. The t-test for two independent samples, with the assumption of unequal variance (Snedecor and Cochran 1980), was used on the transformed data to determine if any significant difference in total food consumption and body mass existed between females of different reproductive status.

The relative importance of individual prey in the total diet was assessed using the modified volume percentage method (Bigg and Perez 1985). Only foods with fleshy remains were used as evidence of diet in this method, and the procedure combined the traditional methods of volume and frequency of occurrence. The proportion of total fish and total squid

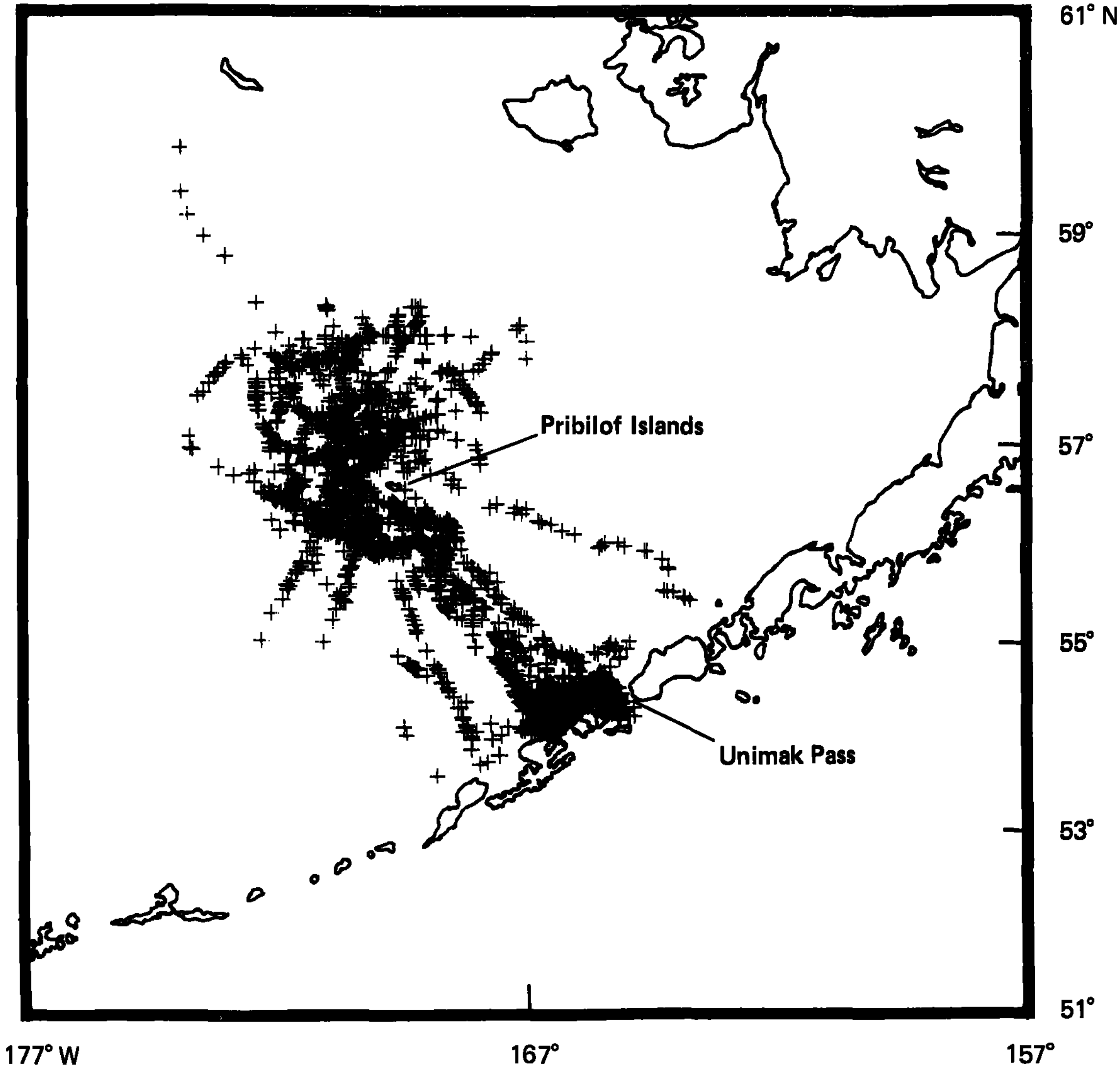

FIGURE 1.—Locations where 3,494 adult female northern fur seals (ages ≥4 yr), whose data were analyzed in this study, were taken by the United States and Canada in the eastern Bering Sea during July-September 1958-74.

in the diet was determined by frequency, while the ration of each species within only fish and squid was determined by volume. Statistical comparison of the diets of lactating and nonlactating females included 1) the Spearman rank correlation coefficient (Siegel 1956; Fritz 1974), 2) percentage similarity (Goodall 1973), and 3) 2 × 2 contingency table analysis (Zar 1974) on the number of stomachs with fish or squid.

Feeding Time at Sea

The largest breeding population of northern fur seals (currently estimated at 8.7×10^5 for a declining population; North Pacific Fur Seal Commission 1984) resides on the Pribilof Islands during the summer months. Pups first appear in late June (Bartholomew and Hoel 1953) and the mean date of pup birth based on recent data is 5 July (Gentry and Holt in press); a date median between values cited by Bartholomew and Hoel (1953) and Peterson (1968). After this time, adult females spend a number of days on shore in several visits to the islands during June-November, and the intervening days between these visits at sea foraging for food (Bartholomew and Hoel 1953; Peterson 1968). They do not feed daily.

Once arriving at the rookery, a parturient female gives birth to one pup, initiates lactation, comes into estrus, and copulates with a male, but does not feed. Gentry and Holt (in press) provided data showing that the average adult female is on shore about 1 d before and 7.4 d after parturition. Each subsequent shore visit lasts about 2.2 d (Peterson 1968; Gentry and Holt in press). The duration of the first sea trip is the shortest (4.8 d), with the duration of the subsequent sea trips increasing at a rate of an additional 1.2 d/30 d postpartum (Gentry and Holt in press).

Recent data collected on the Pribilof Islands by Gentry and Holt (in press) suggests that nonpregnant (= nonlactating) adult females arrive later (about 8 d) on the rookeries and that they may show a somewhat different behavioral pattern than pregnant females. Their first foraging trip at sea is longer (8.9 d), but each of their subsequent shore visits is of constant duration (2.5 d). From these data we derived values for total percent of time spent at sea during July-September (92 d) for the average adult female. Assuming birth of pups on 5 July, this was 69.3 and 75.9% for lactating and nonlactating females, respectively. However, it should be noted that individual females vary from these averages because the period during which adult females first arrive on the rookeries extends over 30 d (Bartholomew and Hoel 1953; Peterson 1968; Gentry and Holt in press).

Feeding Rate Calculations

Bigg et al. (1978) provided data on feeding rates for three captive adult female northern fur seals. Their data for these seals were 5,977 kcal/d (3.0 kg; 6.7% of body mass), 6,118 kcal/d (3.1 kg; 7.6% of body mass), and 5,055 kcal/d (2.5 kg; 8.5% of body mass). These captive northern fur seals were maintained with a diet of Pacific herring (2.01 kcal/g during winter), and it was necessary to consider the energetic concentration of the seal's diet in the wild with respect to the data in Bigg et al. (1978). We derived the following relationship from these data:

$$\text{Daily energy consumption (kcal/d)} = 375.47\ M^{0.75}$$

by averaging the results given for the three captive seals. We calculated average daily feeding rates using this relationship and data on seal body mass.

TABLE 1.—Body mass (minus stomach contents mass) of lactating (postpartum) and nonlactating female northern fur seals (ages ⩾4 yr pooled) taken pelagically in the eastern Bering Sea and western Alaska, 1958-74.

	Lactating		Nonlactating	
Month	n	$\bar{x}$ and 95% C.I. (kg)	n	$\bar{x}$ and 95% C.I. (kg)
June	[1]499	41.10 ± 0.54	128	29.77 ± 1.41
July	743	34.04 ± 0.42	376	31.49 ± 0.70
Aug.	1,481	35.62 ± 0.30	551	31.05 ± 0.57
Sept.	305	36.46 ± 0.34	118	30.19 ± 1.36
July-Sept.	2,529	35.26 ± 0.23	1,045	31.11 ± 0.42

[1]Pregnant (prepartum) females. Body mass does not include fetal mass.

RESULTS

Body Mass

Table 1 gives the mean values of body mass of adult female northern fur seals (age ⩾4 yr) taken during June-September in the eastern Bering Sea and western Alaska. During July-September, the average lactating female (mean 35.3 kg, median age 10 yr) had a body mass 1.13 times that of the average adult nonlactating female (mean 31.1 kg, median age 5 yr; seals age ⩾4 yr only). However, as Figure 2 shows, lactating and nonlactating females of the same age were similar in body mass. The differences shown in Table 1 are primarily due to the higher proportions of lactating females at older ages (Lander 1981).

Lactating females exhibited a significant ($P <$ 0.001) loss of 7.1 kg of body mass between June and July following parturition (Table 1). This is based

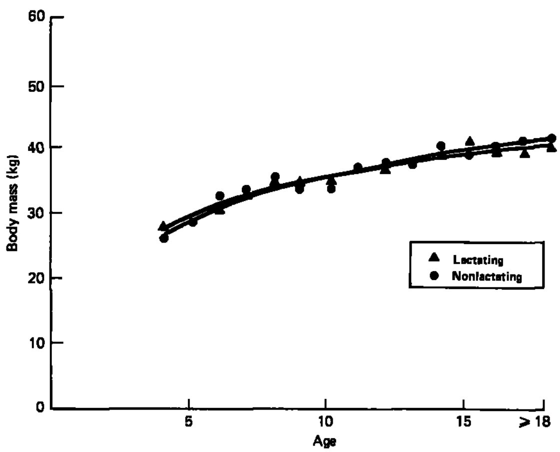

FIGURE 2.—Mean body mass (minus stomach contents mass) of lactating and nonlactating female northern fur seals by age taken pelagically in the eastern Bering Sea and western Alaska during July-September 1958-74.

on data for pregnant females, after excluding fetal mass, which we used to represent body mass of lactating females prior to parturition. Figure 3 shows that this loss in body mass occurred for all ages.

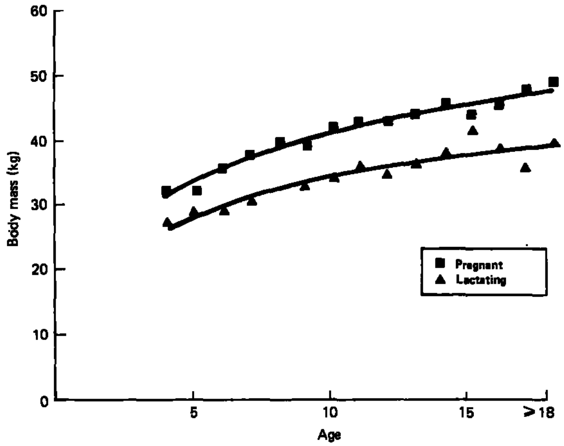

FIGURE 3.—Mean body mass (minus stomach contents and fetal mass) of pregnant (prepartum) and lactating (postpartum) female northern fur seals by age taken pelagically in the eastern Bering Sea and western Alaska during June and July respectively (1958-74).

Relative Food Intake

We found a significant difference ($P < 0.05$) in the relative magnitude of food consumption between lactating and nonlactating female northern fur seals during July-September, but not October, and Figure 4 shows the relative percentage frequency of the number of lactating and nonlactating adult females showing different masses of stomach contents during July-September (pooled data). It is apparent that a greater proportion of lactating females contained food in their stomachs. Lactating females significantly ($P < 0.001$) ingested more food because they had lower cumulative percentages of empty stomachs and stomachs with smaller quantities of food than did nonlactating females.

Table 2 presents the results of analyses between lactating and nonlactating females for the July-September period by time of collection during the day. Our calculated values of the index of relative food intake after sunrise were 162% during 0-3 h, 166% during 4-7 h, 537% during 8-11 h, and 585% during 12-15 h ($P < 0.05$). The calculated index values during 8-15 h after sunrise are excessive, presumably an artifact of food digestion in the stomach.

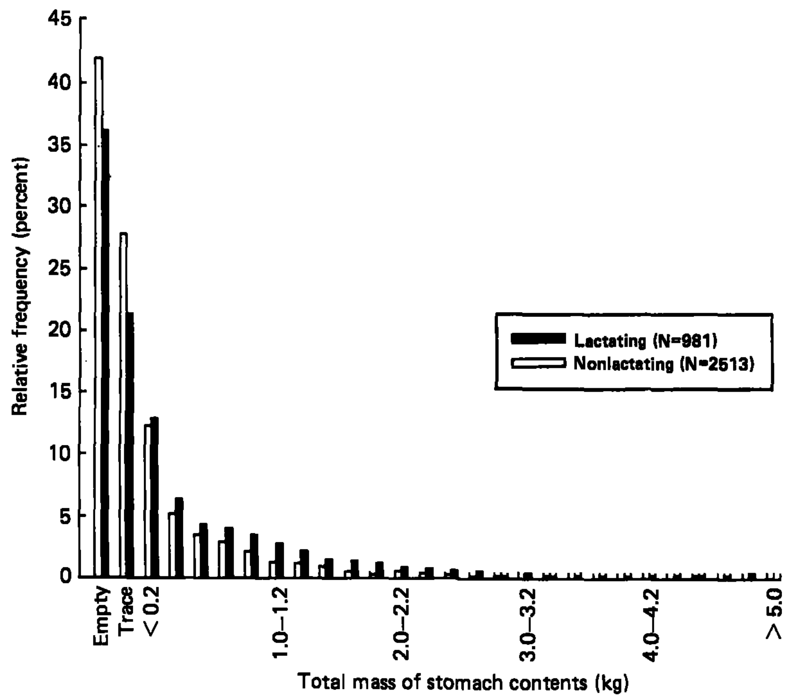

FIGURE 4.—The relative percentage frequency of lactating and nonlactating female northern fur seals (age ≥4 yr) by total mass of stomach contents during July-September.

TABLE 2.—Body mass and arcsine transformed mass of stomach contents (expressed as a percentage of body mass) for lactating (LACT) and nonlactating (NON) female northern fur seals (age ≥4 yr) by hour of collection after sunrise during July-September 1958-74. The relative consumption index (percentage expression of the ratio of the proportion of body mass which was stomach contents for lactating females relative to that for nonlactating females) is also given.

Hours after sunrise	Reproductive condition	n	Body mass (kg) $\bar{x}$ and 95% C.I.	Mass of stomach contents as percentage of body mass: Arcsine units $\bar{x}$	Arcsine units SE	Percentage units $\bar{x}$	Relative consumption index (%)	P[1]
0-3	LACT	312	35.7 ± 0.7	1,355.81	57.24	1.558	161.6	<0.05
	NON	108	31.4 ± 1.5	997.74	83.33	0.964		
4-7	LACT	1,070	35.5 ± 0.4	623.22	25.86	0.333	165.7	<0.05
	NON	381	31.1 ± 0.7	453.29	35.42	0.201		
8-11	LACT	906	35.0 ± 0.4	408.80	24.46	0.145	537.0	<0.05
	NON	365	31.4 ± 0.7	167.27	20.22	0.027		
12-15	LACT	225	34.6 ± 0.7	415.60	47.64	0.152	584.6	<0.05
	NON	127	30.5 ± 1.2	161.66	36.38	0.026		

[1]Significance levels for comparisons between the mean proportions of body mass which was stomach contents (arcsine units) for lactating and nonlactating females were determined by t tests.

To derive a single index value for relative food consumption between lactating and nonlactating females, we performed alternative calculations. In this case we did not simply pool data because that would not adequately account for digestion trends. Northern fur seals feed primarily at night or in the early morning hours (Fiscus et al. 1964; Gentry et al. in press); therefore, we considered the value at 0-3 h after sunrise (0.96; Table 2) as the relative daily quantity of stomach contents for nonlactating seals. Feeding more than once a day to satisfy only energy needs of maintenance and routine activity should be done by all fur seals, and would already be included in these results (Table 2) when the inherent relative rate of digestion is examined. However, lactating females require additional food intake for milk production, and we added an increment (0.12) to the value observed at 0-3 h after sunrise (1.56; Table 2) to calculate an adjusted index of 1.68% of body mass. This incremental value was derived first by calculating the rate of decrease between data values for partially digested stomach contents at the different hourly time intervals. We assumed the rate of digestion throughout the day was the same for lactating females as that observed for nonlactating females. Next, keeping the value for lactating females at 0-3 h after sunrise (1.56) as constant, we summed the absolute value of the differences between the expected values for remaining stomach contents and the observed values in Table 2 to obtain a value of 0.12. We then calculated a value of 174% as our index of relative food intake (i.e., the ratio of 1.68 for lactating females relative to 0.96 for nonlactating females) for a typical foraging day. However, because females do not feed every day during the breeding season (Bartholomew and Hoel 1953; Peterson 1968; Gentry and Holt in press), the average daily feeding rate (adjusted for percentage of time feeding at sea) for lactating seals is 1.6 times that for nonlactating seals during July-September, i.e, the increased cost of lactation is +59.8%.

Estimated Energy and Food Requirements

Lactating and nonlactating female northern fur seals consumed the same species of prey in relatively similar proportions within their diet, when feeding in the same general area at the same time during 1958-74. Ranks of importance of prey to the diet were significantly correlated ($P < 0.05$); the percent similarity of relative prey importance by percent modified volume was 80%; and there was no significant difference in the frequency of food stomachs containing fish or squid. Being culled from the same region and for the same season, data for all adult females were pooled.

We derived a gross energy estimate of 1.40 kcal/g as the average energetic density of northern fur seal prey during July-September based on their relative dietary importance and information in the literature on their energy content (Table 3). Using the data on seal body mass (Table 1) and increased cost of lactation (+59.8%), we calculated average daily feeding rates of 18.2% (6.42 kg) and 11.4% (3.55 kg) of total body mass, respectively, for the average lactating and nonlactating adult female. This represents daily energy consumption requirements of

TABLE 3.—Relative dietary importance, energy value and average daily consumption of prey by individual lactating and nonlactating female northern fur seals (age ≥4 yr) in the eastern Bering Sea during July-September.

Prey	Relative dietary importance (%)[1]	Energy (kcal/g)[2]	Relative energy value in diet (%)[3]	Estimated average consumption: Biomass (kg/d) Lactating	Biomass (kg/d) Nonlactating	Energy (kcal/d) Lactating	Energy (kcal/d) Nonlactating
Pacific herring	7.67	[4]2.17	11.95	0.49	0.27	1,070	590
Salmonids	1.87	[5]2.01	2.69	0.12	0.06	240	130
Capelin	14.85	[6]1.31	14.00	0.95	0.53	1,250	690
Deepsea smelt	3.30	[7]0.76	1.81	0.21	0.12	160	90
Walleye pollock	36.11	[6]1.41	36.51	2.32	1.28	3,270	1,800
Atka mackerel	1.05	[8]1.58	1.19	0.07	0.04	110	60
Pacific sand lance	0.43	[5]1.22	0.38	0.03	0.02	40	20
Flounders	1.10	[5]1.20	0.94	0.07	0.04	80	50
Subtotal (fish)	66.38	[9]1.46	69.47	4.26	2.36	6,220	3,430
Gonatid squid	33.62	[10]1.27	30.53	2.16	1.19	2,740	1,510
Total	100.0	[9]1.40	100.00	6.42	3.55	8,960	4,940

[1]Percent modified volume of stomach contents data collected during 1958-74.

[2]For some species, data were derived from results of proximate analyses on muscle tissue composition using energetic density factors of 9.50, 5.65 and 4.00 kcal/g (gross energy), respectively for fat, protein, and carbohydrate (Watt and Merrill 1963). Data for other species were based on bomb calorimetry analyses of whole specimens.

[3]Derived by multiplying columns 1 and 2, and summing to 100%.

[4]Based on proximate analysis data for Pacific herring, *Clupea harengus pallasi*, in Bigg et al. (1978).

[5]Based on proximate analysis data for salmonids (Salmonidae); Pacific sand lance, *Ammodytes hexapterus*; and flounders (Pleuronectidae) in Sidwell (1981).

[6]Based on data from heat of combustion in analyses of whole fish specimens of capelin, *Mallotus villosus*, and walleye pollock, *Theragra chalcogramma* [Miller, L. K. 1978. Energetics of the northern fur seal in relation to climate and food resources of the Bering Sea. U.S. Mar. Mammal Comm. Rep. MMC-75/08, 27 p.]

[7]Based on proximate analysis data for deepsea smelt (Bathylagidae) in Childress and Nygaard (1973).

[8]Based on proximate analysis data for Atka mackerel, *Pleurogrammus monopterygius*, in Kizevetter (1971).

[9]Average value of prey species in diet adjusted by their relative dietary importance.

[10]Perez, M. A. 1984. Unpubl. data. Northwest and Alaska Fish. Cent. Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

8,960 kcal and 4,940 kcal for the average, individual lactating and nonlactating adult female northern fur seal during July-September (Table 3). Average postpartum females not in a lactating state would have a daily energy consumption requirement of 5,430 kcal or feeding rate of 11.0% (3.89 kg) of total body mass.

Table 3 also provides estimates for each food item of the total energy and biomass consumed daily by the average individual adult female. Lactating females each consume about 6,220 kcal/d gross energy (4.3 kg/d) of fish and 2,740 kcal/d gross energy (2.2 kg/d) of squid, and each nonlactating individual consumes about 3,430 kcal/d gross energy (2.4 kg/d) of fish and 1,510 kcal/d gross energy (1.2 kg/d) of squid. Female northern fur seals are not able to feed every day, and thus estimated consumption for the average foraging day is 8,980 kcal/d gross energy (6.1 kg/d) of fish and 3,950 kcal/d gross energy (3.1 kg/d) of squid by lactating seals, and 4,530 kcal/d gross energy (3.1 kg/d) of fish and 1,990 kcal/d gross energy (1.6 kg/d) of squid by nonlactating females.

We also calculated estimates of the total energy in biomass consumed by all adult females during July-September in the eastern Bering Sea (Table 4). Because the northern fur seal population has been declining in recent years (North Pacific Fur Seal Commission 1984) we used 80% of the estimated population values given by Lander (1981): 2.61×10^5 pregnant/postpartum and 1.19×10^5 nonpregnant adult females (age ≥4 yr). We assumed all of these seals are present in the eastern Bering Sea during this period. Because 5% of the pups born on St. Paul Island, Pribilof Islands, between 1975 and 1982 died on the rookeries during July and August (Kozloff 1985), we modified our calculations to reflect the number of postpartum females which are nonlactating. We thus estimated a total of 2.48×10^5 lactating and 1.32×10^5 nonlactating adult females (age ≥4 yr). Multiplying individual estimates by these population totals, lactating females consume an estimated collective total of 204.5×10^9 kcal gross energy (146.5×10^3 t) and nonlactating females consume an estimated collective total of 60.2×10^9 kcal gross energy (43.1×10^3 t) of food. Therefore, all adult female northern fur seals consume an estimated collective biomass of 189.6×10^3 t with a gross energy value of 264.7×10^9 kcal during July-September, of which 69.4% of this energy (183.7×10^9 kcal; 125.9×10^3 t) are fish and 30.6% (81.0×10^9 kcal; 63.7×10^3 t) are squid.

TABLE 4.—Estimated energy value and consumption of fish and squid by the total population of lactating and nonlactating female northern fur seals (age ≥4 yr) during July-September (92 days).

		Lactating females			Nonlactating females		
			Total seasonal consumption by population (2.48 × 10^5)			Total seasonal consumption by population (1.32 × 10^5)[2]	
Prey	Energy (kcal/g)[1]	Individual average consumption (kg/d)[1]	Biomass (× 10^3 t)	Energy (× 10^9 kcal)	Individual average consumption (kg/d)[1]	Biomass (× 10^3 t)	Energy (× 10^9 kcal)
Fish	1.46	4.26	97.2	141.9	2.36	28.7	41.8
Squid	1.27	2.16	49.3	62.6	1.19	14.4	18.4
Total	1.40	6.42	146.5	204.5	3.55	43.1	60.2

[1]From Table 3.
[2]Includes postpartum females that fail to lactate.

DISCUSSION

The food consumption data presented in Table 2 were based on partially digested stomach contents, and thus underestimate the actual feeding rates of adult female northern fur seals. It is apparent from these data that lactating seals obtain most of their energy needs by filling their stomachs slightly more than the nonlactating seals early in the day and by eating additional food later in the day. Any female, whether lactating or not, may eat more than once during the day, as captive northern fur seals often do (Spotte 1980). Females must feed more than once during the 24-h period (on those days when they are able to feed) to meet their daily food requirements because the maximum observed stomach contents by percentage of body mass during July-September 1958-74 were 13.8 and 8.2%, respectively, for lactating and nonlactating females (Perez[8]), which are less than their predicted feeding rates. In addition, digestion does vary among individual seals and with the type and amount of prey eaten (Bigg and Fawcett 1985). However, the data in Table 2 should be typical of the relative relationship between lactating and nonlactating females if actual feeding rates could be measured for free-ranging seals.

Lactating northern fur seals were estimated to consume 8,960 kcal/d (gross energy), of which 3,520 kcal/d (gross energy) represent the additional intake of food related to lactation. Energy expenditures for maintenance and routine activity not directly attributable to lactation were estimated to be 5,440 kcal/d (gross energy). This estimate is about 5.4 times the amount predicted (1,010 kcal/d metabolizable energy or 49.0 *W*) for basal metabolism by the relationship between metabolic rate (*MR*) in watts (*W*) and body mass (*M*) shown by Kleiber (1961) ($MR\,(W) = 3.39\,M^{0.75}$).

These estimates are not typical of energy expenditure during the first week (7.4 d average) postpartum, a period during which the parturient female does not feed. Lactating seals must metabolize their energy from fat reserves during this period (including the day before parturition when they usually do not feed, although we considered only the postparturition period). The loss in body mass (Table 1) in postpartum females following parturition accounts for some of this metabolism of energy from fat reserves. This loss includes about 0.6 kg (12% of pup mass as in harp seals, Lavigne and Stewart 1979) of placental matter and 3.3 kg (7% preparturient female mass) of amniotic and other fluids during parturition (Costa and Gentry in press). There is a calculated net mass loss of 3.2 kg. Loss of body water, as has been reported for some mammals, e.g., cattle (Degen and Young 1980) is also probably part of this loss. In addition, this loss includes the utilization of fat reserves to satisfy energy requirements for lactation (Sadleir 1969) during the first few days of the pup's life, a period when parturient females remain on shore and do not feed (Bartholomew and Hoel 1953; Peterson 1968; Gentry and Holt in press).

Our estimate of net mass loss, presumably through fat metabolism, is an underestimate because it was derived from mean body mass data from seals taken at sea, and, therefore, includes lactating animals which probably regained some body mass after their first foraging trip at sea. Costa and Gentry (in press) measured an average of 8.75 kg of mass loss, presumably by tissue metabolism and water loss, prior to the female's initial departure to sea, after which they gained additional body mass. This situation is analogous to that in gray seals. The gray seal does not feed during its entire 18-d lactation period from parturition to weaning (Amoroso and Mat-

[8]Perez, M. A. 1981. Unpubl. data. Northwest and Alaska Fish. Cent. Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.

thews 1951, 1952) and over 80% of the female's stored energy reserves are used to feed their pup (Fedak and Anderson 1982).

We conducted similar analyses of data comparing pregnant and nonpregnant adult females (age ⩾4 yr) during June-July, but we did not find any significant difference in relative feeding rates. We, therefore, conclude that the onset of the lactation process, and not pregnancy, initiates increased feeding behavior in parturient fur seals. Pregnant northern fur seals presumably consume more food than required by nonpregnant females (i.e., more than that simply required as a function of body mass). This would be necessary for growth of the fetus, especially during winter and spring months when they are in the North Pacific. This conclusion was based on a preliminary examination of the pelagic fur seal data, although the results were not statistically conclusive. Female northern fur seals probably also store energy in fat reserves for the stresses of birth and the first week of lactation. Nevertheless, any additional food intake required by pregnant females is substantially less than that of lactating seals.

We believe lactating females may reduce their need for additional food intake during the last month prior to weaning of pups because we did not find a significant difference in food consumption between lactating and nonlactating females during October; however, data were few. Weaning does not occur until late October or early November when females abandon their pups; the mean date of weaning is about 2 November (Peterson 1968). It should be noted that births occur over at least a 30-d period (Peterson 1968), and weaning of individual pups will likewise occur over a similar time frame. It is thus possible that pups born earlier will quit nursing earlier than those born later in the season. The total lactation period is about 3-5 mo. Therefore, the feeding rate relationships and energy estimates presented in this paper should typify those during the first three months of lactation only, and not necessarily during July-September.

We assumed that all postpartum females taken during 1958-74 were lactating. We believe that this assumption does not significantly affect our results because only a small percentage of the postpartum females fail to lactate or terminate lactation for one reason or another (such as still birth or death of the pup). Therefore, our estimate of the difference in consumption between lactating and nonlactating females is a conservative indicator of the magnitude of this ratio. This is because inclusion of postpartum females that did not lactate would have decreased the mean value of stomach contents for the lactating group.

Individual northern fur seals show variations in their feeding locations. Differences may occur over location and time. For example, lactating females may travel great distances, e.g., at least 160 km from the Pribilof Islands (Perez[4]), during their sea trips in search of food, and they may dive up to 200 m (Gentry et al. in press) to catch prey. There are, of course, differences in availability (e.g., walleye pollock, *Theragra chalcogramma*, Smith and Bakkala 1982) and energetic density (e.g., Pacific herring, *Clupea harengus pallasi*, Bigg et al. 1978; deepsea smelt, Bathylagidae, Childress and Nygaard 1973) of prey by season, region, and depth. The 95% C.I. for the importance of fish biomass in the fur seal diet in the Bering Sea is 64.0-68.6% (Perez and Bigg[5]). Therefore, the estimated quantity of fish and squid consumed, and their relative energy contribution, may vary ±5%.

It should also be stressed that the estimates presented in this paper also depend heavily on metabolic rate information for adult females which we obtained from the literature. Individual variations among seals will cause differences in results obtained from several experiments, and future research may provide somewhat different metabolic rates. Should feeding rates be revised substantially, then the magnitude of energetic estimates from these data will be affected in a corresponding direction. However, the relative ratio of food consumption between lactating and nonlactating females during the breeding season will be unaffected, and remain about 1.6. We suggest the need for further studies on feeding behavior and energetics of lactating females and pups prior to weaning.

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[4]Perez, M. A., Northwest and Alaska Fisheries Center National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, Seattle WA 98115, pers. observ., 1984.

[5]Perez, M. A., and M. A. Bigg. 1984. Food habits of northern fur seals (*Callorhinus ursinus*) off western North America. Unpubl. rep., 67 p. Northwest and Alaska Fish. Cent. Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE. Seattle, WA 98115.

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LITERATURE CITED

AMOROSO, E. C., AND L. H. MATTHEWS.
1951. The growth of the grey seal (*Halichoerus grypus*) from birth to weaning. J. Anat. 85:427-428.
1952. Reproduction and lactation in the seal. Proc. Int. Congr. Anim. Reprod. Artif. Insemin. 1:193-203.

BALDWIN, R. L., JR.
1978. The initiation and maintenance of lactation. *In* A. Yokoyama, H. Mizuno, and H. Nagasawa (editors), Physiology of mammary glands, p. 5-19. Jpn. Sci. Soc. Press, Tokyo.

BARTHOLOMEW, G. A., AND P. G. HOEL.
1953. Reproductive behavior of the Alaska fur seal, *Callorhinus ursinus*. J. Mammal. 34:417-436.

BIGG, M. A., AND I. FAWCETT.
1985. Two biases in diet determination of northern fur seals (*Callorhinus ursinus*). *In* J. R. Beddington, R. J. H. Beverton, and D. M. Lavigne (editors), Marine mammals and fisheries, p. 284-291. George Allen and Unwin, Publ., Lond.

BIGG, M. A., I. B. MACASKIE, AND G. ELLIS.
1978. Studies on captive fur seals. Progress rep. 2. Can. Fish. Mar. Serv. Manuscr. Rep. 1471, 21 p.

BIGG, M. A., AND M. A. PEREZ.
1985. Modified volume: a frequency-volume method to assess marine mammal food habits. *In* J. R. Beddington, R. J. H. Beverton, and D. M. Lavigne (editors), Marine mammals and fisheries, p. 277-283. George Allen and Unwin, Publ., Lond.

BRODY, S.
1945. Bioenergetics and growth. Reinhold, N.Y., 1023 p.

CHILDRESS, J. J., AND M. H. NYGAARD.
1973. The chemical composition of midwater fishes as a function of depth of occurrence off Southern California. Deep-Sea Res. 20:1093-1109.

COCHRAN, W. G.
1977. Sampling techniques. 3d ed. John Wiley and Sons, N.Y., 428 p.

COSTA, D. P., AND R. L. GENTRY.
In press. Free-ranging energetics of the northern fur seals. *In* R. L. Gentry and G. L. Kooyman (editors), Fur seals: Maternal strategies on land and at sea, p. 79-101. Princeton Univ. Press, Princeton, NJ.

DEGEN, A. A., AND B. A. YOUNG.
1980. Live-weight, total body-water and maternal body-solid changes in pregnant and lactating beef cows. J. Agric. Sci. 95:1-5.

EAGLES, J. A., AND M. N. RANDALL.
1980. Handbook of normal and therapeutic nutrition. Raven Press, N.Y., 323 p.

ENGELS, E. A. N., AND A. MALAN.
1979. Feed intake of non-pregnant, pregnant and lactating ewes on native pasture and lucerne hay. S. Afr. J. Anim. Sci. 9:27-32.

FEDAK, M. A., AND S. S. ANDERSON.
1982. The energetics of lactation: accurate measurements from a large wild mammal, the grey seal (*Halichoerus grypus*). J. Zool. (Lond.) 198:473-479.

FISCUS, C. H., G. A. BAINES, AND F. WILKE.
1964. Pelagic fur seal investigations, Alaska waters, 1962. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 475, 59 p.

FRITZ, E. S.
1974. Total diet comparison in fishes by Spearman rank correlation coefficients. Copeia 1974:210-214.

GENTRY, R. L., AND J. R. HOLT.
In press. Attendance behavior of female northern fur seals. *In* R. L. Gentry and G. L. Kooyman (editors), Fur seals: Maternal strategies on land and at sea, p. 41-60. Princeton Univ. Press, Princeton, NJ.

GENTRY, R. L., G. L. KOOYMAN, AND M. E. GOEBEL.
In press. Feeding and diving behavior of northern fur seals. *In* R. L. Gentry and G. L. Kooyman (editors), Fur seals: Maternal strategies on land and at sea, p. 61-78. Princeton Univ. Press, Princeton, NJ.

GOODALL, D. W.
1973. Sample similarity and species correlation. *In* R. Tuxen (editor), Handbook of vegetation science, Part 5: Ordination and classification of communities, p. 105-106. Dr. W. Junk B. V. Publ., The Hague.

HARRISON, R. J.
1969. Reproduction and reproductive organs. *In* H. T. Andersen (editor), The biology of marine mammals, p. 253-348. Acad. Press, N.Y.

KIZEVETTER, I. V.
1971. Chemistry and technology of Pacific fish. [In Russ.] Dal'izdat, Vladivostok. [Translated by Isr. Program Sci. Transl., 1973, available U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, VA, as TT72-50019, 304 p.]

KLEIBER, M.
1961. The fire of life, an introduction to animal energetics. John Wiley and Sons, N.Y., 454 p.

KLEVEZAL', G. A., AND S. E. KLEINENBERG.
1967. Age determination of mammals from annual layers in teeth and bones. [In Russ.] Izdatel'stvo "Nauka", Moscow. [Translated by Isr. Program Sci. Transl. 1969, available U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, VA, as TT69-55033, 128 p.]

KOZLOFF, P. (editor).
1985. Fur seal investigations, 1982. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-71, 127 p.

LANDER, R. H. (editor).
1980. Summary of northern fur seal data and collection procedures. Vol. 2: Eastern Pacific pelagic data of the United States and Canada (excluding fur seals sighted). U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-4, 541 p.

LANDER, R. H.
1981. A life table and biomass estimate for Alaskan fur seals. Fish. Res. 1:55-70.

LAVIGNE, D. M., AND R. E. A. STEWART.
1979. Energy content of harp seal placentas. J. Mammal. 60:854-856.

LAVIGNE, D. M., R. E. A. STEWART, AND F. FLETCHER.
1982. Changes in composition and energy content of harp seal milk during lactation. Physiol. Zool. 55:1-9.

LOCKYER, C.
1978. A theoretical approach to the balance between growth and food consumption in fin and sei whales, with special reference to the female reproductive cycle. Int. Whaling Comm. Rep. Comm. 28:243-249.
1981a. Growth and energy budgets of large baleen whales from the Southern Hemisphere. *In* Mammals in the seas; 3, General papers and large cetaceans, p. 379-487. FAO

Fish. Ser. 5, Vol. 3.
1981b. Estimates of growth and energy budget for the sperm whale, *Physeter catodon*. *In* Mammals in the seas; 3, General papers and large cetaceans, p. 489-504. FAO Fish. Ser. 5, Vol. 3.
1981c. Estimation of the energy costs of growth, maintenance, and reproduction in the female minke whale, (*Balaenoptera acutorostrata*), from the Southern Hemisphere. Int. Whaling Comm. Rep. Comm. 31:337-343.

MILLAR, J. S.
1978. Energetics of reproduction in *Peromyscus leucopus*: the cost of lactation. Ecology 59:1055-1061.

NORTH PACIFIC FUR SEAL COMMISSION.
1984. Proceedings of the 27th annual meeting. North Pac. Fur Seal Comm., Wash., D.C., 50 p.

PETERSON, R. S.
1968. Social behavior of pinnipeds with particular reference to the northern fur seal. *In* R. J. Harrison, R. C. Hubbard, R. S. Peterson, C. E. Rice, and R. J. Schusterman (editors), The behavior and physiology of pinnipeds, p. 3-53. Appleton-Century-Crofts, N.Y.

SADLEIR, R. M. F. S.
1969. The ecology of reproduction in wild and domestic mammals. Methuen and Co., Lond., 321 p.

SCHUTZ, Y., A. LECHTIG, AND R. B. BRADFIELD.
1980. Energy expenditures and food intakes of lactating women in Guatemala. Am. J. Clin. Nutr. 33:892-902.

SIDWELL, V. D.
1981. Chemical and nutritional composition of finfishes, whales, crustaceans, mollusks, and their products. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/SEC-11, 432 p.

SIEGEL, S.
1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, N.Y., 312 p.

SMITH, G. B., AND R. G. BAKKALA.
1982. Demersal fish resources of the eastern Bering Sea: spring 1976. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-754, 129 p.

SNEDECOR, G. W., AND W. G. COCHRAN.
1980. Statistical methods. 7th ed. Iowa State Univ. Press, 507 p.

SPOTTE, S.
1980. Acclimation of adult northern fur seals (*Callorhinus ursinus*) to captivity. Cetology 36:1-8.

SPOTTE, S., AND B. BABUS.
1980. Does a pregnant dolphin (*Tursiops truncatus*) eat more? Cetology 39:1-7.

STEBBINS, L. L.
1977. Energy requirements during reproduction of *Peromyscus maniculatus*. Can. J. Zool. 55:1701-1704.

STUDIER, E. H., V. L. LYSENGEN, AND M. J. O'FARRELL.
1973. Biology of *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae)—II: Bioenergetics of pregnancy and lactation. Comp. Biochem. Physiol. 44A:467-471.

WATT, B. K., AND A. L. MERRILL.
1963. Composition of foods...raw, processed, prepared. U.S. Dep. Agric., Agric. Handb. 8, 190 p.

ZAR, J. H.
1974. Biostatistical analysis. Prentice Hall, Englewood Cliffs, NJ, 620 p.