

The energetics of lactation in the Northern elephant seal, *Mirounga angustirostris*

D. P. COSTA, B. J. LE BOEUF, A. C. HUNTLEY AND C. L. ORTIZ

*Long Marine Laboratory, Center for Marine Studies and Biology Board,
University of California, Santa Cruz, CA 95064, USA*

(Accepted 14 May 1985)

(With 3 figures in the text)

The energy and material transferred from Northern elephant seal mothers to their pups during the 26.5-day lactation interval was measured using mass change and water influx data. The dilution of tritium- and deuterium-labelled water was monitored in six female elephant seals and their pups. During the nursing period, pup mass increased by 10.4% of the initial body mass per day while females lost 4.19% of their initial body mass per day. Over the entire nursing period, females lost $42.2 \pm 4.9\%$ of their initial body mass. Maternal mass transfer to the pup was efficient; pups gained 54.9% of the mass lost by their mothers. Females lost only 14.9% of their lean mass compared to 57.9% of their adipose mass. The fasting metabolic rate of females was 66.2 ± 7.5 MJ/day, 2.41 times the predicted standard metabolic rate (SMR) of a terrestrial mammal of equal size; the total energy output was 163 ± 11 MJ/day, 5.98 times the predicted SMR. Energy consumption for the entire lactation interval was 4330 ± 460 MJ. Milk production accounted for 60% of this energetic expenditure. This efficient milk production was made possible by temporal separation of lactation and feeding. Separation of feeding from lactation confers several energetic and ecological advantages: reduction in the metabolic overhead used for maintenance metabolism onshore, reduction of foraging effort required to meet the demands of lactation, since feeding can be spread out over a significantly longer interval, and a greater flexibility while foraging at sea due to the absence of the pup.

Contents

	Page
Introduction	21
Materials and methods	22
Subjects and field procedures	22
Sample analysis	24
Data analysis and calculations	24
Results	25
Changes in mass	25
Milk transfer	25
Maternal water and energy flux	26
Discussion	28
Error analysis	29
References	32

Introduction

The allocation of resources to maintenance, growth and reproduction is a central issue in theories of life history strategies of animals (Williams, 1966; Giesel, 1976; Pianka, 1976; Stearns, 1976, 1980; Calow, 1979; Fleming, 1979; Ricklefs, 1979). Among female mammals, lactation is

the major energetic component of parental investment, requiring approximately three times more energy than gestation (Millar, 1977). Furthermore, lactation is expensive, requiring increases in maintenance metabolism ranging from 66 to 266% above non-lactating maintenance levels (Brody, 1945; Nelson & Evans, 1961; Arman *et al.*, 1974; Randolph, Randolph, Mattingly & Foster, 1977; Millar, 1978). However, the amount and pattern of energy transferred during lactation varies widely among species (Millar, 1977).

Most large mammals lactate for a relatively long period (months or years), feed during lactation, produce milk with relatively low energy content and wean their pups gradually, e.g. many ungulates (Fraser, 1968), wolves, *Canis lupus* (Mech, 1970), many primates (van Lawick-Goodall, 1971; Altmann, 1980) and the African lion, *Panthera leo* (Schaller, 1972). In addition, the young of many of these species supplement their diet of mother's milk with food acquired by them or by a parent. In contrast, some phocids deviate from this standard terrestrial pattern (Grey seals, *Halichoerus grypus*, Fedak & Anderson, 1982; Harp seals, *Phoca groenlandica*, Stewart & Lavigne, 1984; elephant seals, *Mirounga angustirostris* and *M. leonina* (Laws, 1959; Le Boeuf, Whiting & Gantt, 1972). Females of these species lactate for relatively brief periods (four weeks or less), fast from food and water during lactation, produce an energy-rich milk with a high fat content and wean their pups abruptly. Prior to weaning, the sole source of nutrients in the developing pup is mother's milk. The nutrients gained during this interval supply the pup during the subsequent 2.5-month postweaning fast. What physiological mechanisms enable these species to accomplish this feat? What are the advantages of a concentrated nursing period? Why is the lactation pattern so different in these seals?

In a previous study (Ortiz, Le Boeuf & Costa, 1984), we estimated the energetic value of milk received by pups, using isotopically labelled water methodologies for measuring milk intake. In the present study, we extend our investigation and simultaneously quantify the female's energy consumption and mass loss, as well as the pup's milk intake and mass increase, to arrive at a measure of the total energy expenditure during a major portion of the lactation interval. We estimate the energetic cost to the female of nurturing her pup from parturition to weaning, a major component of what Trivers (1972) termed the period of parental investment, and examine the physiological processes underlying this reproductive strategy and discuss their ecological implications.

Materials and methods

Subjects and field procedures

Experiments were conducted on 6 free-ranging females (4–6 years old) and their suckling pups at Año Nuevo Point, California, during the 1982 breeding season. Subjects were selected from marked, known-age females that were observed daily after their arrival (Reiter, Panken & Le Boeuf, 1981).

First procedure

The first experimental procedure was performed within 4 days of parturition. Solitary females or females located on the periphery of small harems were selected for study to minimize disturbance to the colony. Solitary females were immobilized directly; those on the edge of the rookery were herded away from the harem prior to immobilization. Ketamine hydrochloride (4–6 mg/kg) was introduced into the rear flank with 10 and 15 cc (100 mg/ml) injection darts fired from a distance of 2–3 m with a CO₂-powered pistol (Cap-Chur Darts and Pistol, Palmer Chemical Co.) (Briggs, Henrickson & Le Boeuf, 1975). Immobilization occurred within 15–20 min. Additional 5 cc injections of ketamine HCl were administered as necessary

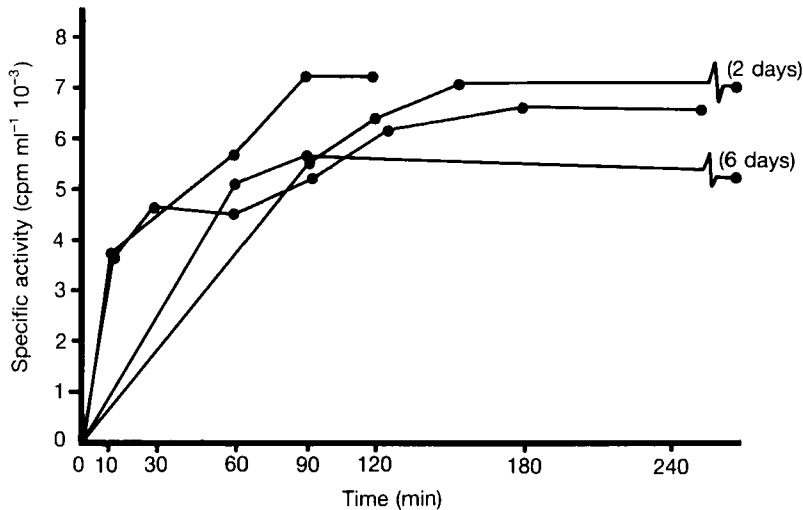


FIG. 1. The time required for equilibration of HTO determined by blood sampling four female elephant seals at various time intervals after the initial intramuscular injection of HTO. The equilibration point was determined from the asymptotic value obtained within three hours. Samples taken at two and six days should be slightly lower due to the production of metabolic water, but are included to further confirm equilibration.

to maintain restraint throughout the equilibration period (approximately 3–4 h). Based on behavioural observations, recovery was virtually complete within 1–2 h after the procedure. After immobilization, females were administered 8 ml of tritiated water (HTO), 0.25 mCi/ml, via intramuscular or intravenous injection. The time required for isotopic equilibration was determined in 4 females by blood sampling at various time intervals after intramuscular injection. Equilibration of HTO in the body water occurred within 3 h (Fig. 1). Therefore, all initial blood samples were collected 3–4 h after administration of HTO. During the equilibration period, each female was weighed by rolling her on a 2.1 m × 2.5 m sling, which was lifted with 2.306 m × 5 cm schedule 40 aluminium poles fitted along its short length. Once in position, an aluminium tripod was placed over the animal. The sling poles were brought around and over the midline of the animal and attached to a cable-puller hand winch hung from a dynamometer (Chatillon Co. 1000 kg ± 2.5 kg) attached to the apex of the tripod.

While the female was being treated, her pup was restrained manually and given 90–150 ml of deuterated water (HDO, 99.9%, Norell Inc., California) via a stomach tube. Like females, serial samples indicated that equilibrium was reached within 3 h following oral administration of HDO in pups. Pups were weighed, blood sampled 3 h after administration of isotopes, measured, and then marked with paint or bleach (Le Boeuf & Peterson, 1969). Subsequently, mother and pup usually began suckling within a few minutes. Mother and pup were observed daily, but were otherwise left undisturbed until the second procedure, a few days prior to weaning. In all cases, normal behaviour was observed during this interval. Tritiated water was used in previous measurements of milk intake in elephant seal pups (Ortiz *et al.*, 1984). In these measurements, deuterated water (HDO) was used, since pups would be receiving HTO in their mother's milk.

Final procedure

Four to seven days before the expected weaning date, predicted by the age of the mother (Reiter *et al.*, 1981), each female was isolated from other females, immobilized, blood sampled, injected, weighed, measured and blood sampled as before. Pups were then bled again, weighed, measured and tagged. The day

TABLE I
Ingestion rates of total milk mass, its major components and energy content over the experimental interval. Values are derived from pup water influx and milk composition data

Pup no.	Experiment interval (days)	Milk material ingested by pups					Milk Energy Transfer Rate* (MJ/day)
		Total mass (kg/day)	Water (kg/day)	Fat (kg/day)	Protein (kg/day)	Other solid (kg/day)	
1	2-24	5.08	2.17	2.13	0.60	0.18	94.8
2	0-22	4.63	2.20	1.81	0.55	0.07	81.3
3	2-21	5.50	2.43	2.23	0.65	0.18	100.0
4	2-24	5.27	2.27	2.22	0.63	0.16	99.3
5	4-23	6.05	2.51	2.65	0.72	0.17	118.0
6	0-21	5.45	2.56	2.09	0.65	0.15	94.3
Mean		5.50	2.36	2.19	0.63	0.15	98.0
± S.D.		0.66	0.17	0.27	0.06	0.04	11.9

* Derived from fat and protein content since elephant seal milk is virtually devoid of carbohydrate (Reidman & Ortiz, 1979).

after weaning, pups were again blood sampled, injected with 750 μ Ci HTO in 3 ml saline, blood sampled 3 h later and released. This procedure was used to assess the change in body composition during the experimental interval (Ortiz, Costa & Le Boeuf, 1978).

The experimental period, the number of days between the first and second procedure ($x = 20.8$ days, see Table I), was shorter than the female's lactation period ($x = 26.5$ days). We present data for the daily rate, measured over approximately 80% of the female's lactation interval, and then extrapolate those data to the entire lactation interval, to estimate the female's costs during the onshore period of parental investment. This extrapolation is valid, since the rate of milk intake is linear over the entire lactation period (Ortiz, Le Boeuf & Costa, 1984).

Sample analysis

Tritium specific activity was determined in triplicate by scintillation spectrometry of 300 μ l of water distilled from the serum samples in 10 ml of Betaphase cocktail (Westchem, San Diego, California) (Ortiz *et al.*, 1978). The specific activity of HDO was determined by mass ratio spectrometry of distilled serum water using standard mean ocean water as a reference (Global Geochemistry, Canoga Park, California). Replicate errors in both methods were less than 1%.

Data analysis and calculations

Changes in body composition were estimated from changes in total body water (TBW) and body mass incurred during the experimental period. TBW was determined from the initial dilution of HTO (females) (Foy & Schneiden, 1960) or HDO (pups). Adipose tissue mass (M_{adi}) was calculated from TBW and body mass as:

$$M_{adi} = 1.16 M - 1.59 W \quad (1)$$

where M_{adi} is the total body mass in kg and W is the total body water in litres where adipose and lean tissue are 10% and 73% water, respectively (Ortiz, Costa & Le Boeuf, 1978).

The total energetic expenditure E_t of the female during lactation is equal to the sum of her metabolic costs (E_{met}) and the caloric value of the milk transferred to the pup (E_{milk}), thus:

$$E_t = E_{met} + E_{milk} \quad (2)$$

The metabolic energy expended, E_{met} , while lactating and fasting was determined from:

$$E_{\text{met}} = r_{\text{in}} \cdot k \cdot t \quad (3)$$

where r_{in} is the mean daily water influx, in l/kg-day, k is the stoichiometric constant 35.3 MJ/ml H₂O (Schmidt-Nielsen & Schmidt-Nielsen, 1952), and t is days of lactation. Metabolic rates of lactating, fasting females were derived from estimates of water influx rates for animals with linearly changing body mass, as in Nagy & Costa (1980) as modified from Lifson & McClintock (1966). In fasting non-drinking animals, metabolic water production is the primary component of water influx and is therefore an index of metabolism (Ortiz, Costa & Le Boeuf, 1978). If fat is the sole metabolic substrate, the fasting metabolic rate is 35.3 MJ/ml H₂O produced; this assumes that 1 ml of water was produced when 0.909 g of stored fat or 0.99 g of adipose tissue was oxidized. In our calculations, we assume fat metabolism provides 98% of the energy in fasting females, similar to that seen in weaned pups (Pernia, Hill & Ortiz, 1980; Costa & Ortiz, 1980).

The energy of milk ingested by pups, E_{milk} was determined from:

$$E_{\text{milk}} = r_{\text{milk}} \cdot C \cdot t \quad (4)$$

where r_{milk} is the mean daily intake of milk by the pup in kg/day, C is the average caloric value of ingested milk in MJ/kg and t is days of nursing. The method for estimating r_{milk} from HDO kinetics in pups and the values of C are similar to those described by Ortiz, Le Boeuf & Costa (1984). In this method, the milk intake is derived from body water turnover; the only components of water influx are metabolic water and preformed water in the milk. The difference between total water turnover, quantified by the dilution of HDO through time, and metabolic water production, previously determined on fasting weaned pups (Ortiz, Costa & Le Boeuf, 1978), yields the rate of milk water ingestion. Total milk input was calculated from milk water input and the water content (and energetic composition) of elephant seal milk (Riedman & Ortiz, 1979).

Results

Changes in mass

The mass loss of females and daily gain of their pups during the experimental period is shown in Fig. 2. Pups gained a mean of 10.4 ± 0.7 while mothers lost $4.19 \pm 0.62\%$ of their initial body mass per day. Thus, pups gained $54.9 \pm 3.3\%$ of the mass lost by their mothers.

Over the experimental interval, total body water (as % of body mass) of females increased from a mean of $48.6 \pm 2.3\%$ to $57.9 \pm 4.5\%$. These data indicate that mean total mass of females was 195 ± 26 kg adipose tissue and 309 ± 47 kg lean mass early in lactation, which declined to 82 ± 25 kg adipose tissue and 265 ± 51 kg lean mass near weaning; the percentage of adipose tissue in body mass decreased from 39% to 24% while lean mass increased from 61% to 76%. The $57.9 \pm 10.3\%$ decline in adipose tissue was significantly greater than the $14.4 \pm 6.4\%$ decrease in lean mass.

Milk transfer

Females transferred a mean of 5.50 ± 0.66 kg/day of milk to their pups during the experimental period, consisting of primarily fat (41%), water (44%) and protein (12%). The mean rate of milk energy transfer was 98.0 ± 11.9 MJ/day (Table I), calculated from the fat and protein components only.

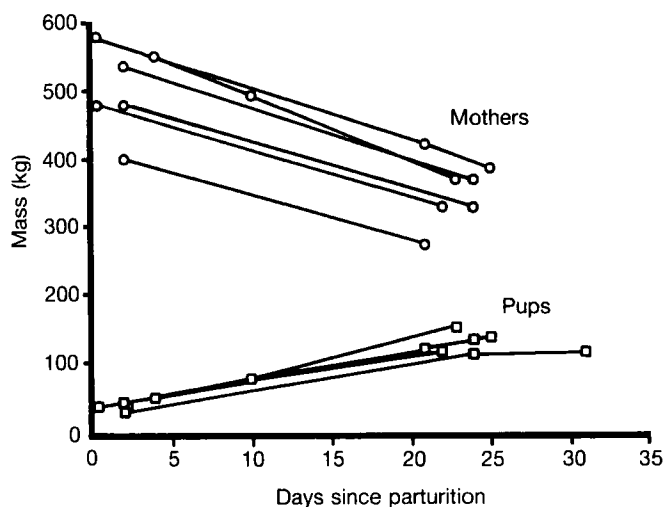


FIG. 2. The mass loss of the six female elephant seals and the mass gain of their pups plotted over the measurement interval. Additional mass determinations were made for the pups at weaning, the day after their mothers departed.

TABLE II

Changes in total and component mass loss of Northern elephant seal females during the experiment interval. Mean mass is the mean of the first and second procedure masses. Mass loss was estimated from the adipose tissue necessary to account for the water influx and the amount of milk consumed by pups in Table I. The correspondence of the observed mass change as determined by weighing to the mass change predicted from metabolism and milk production is an independent confirmation of these data

Female no.	Age (yr.)	Mean mass (kg)	Water influx (l/day)	Components of mass loss onshore			Observed mass (kg/day)	Predicted mass change
				Adipose tissue (kg/day)	Milk mass (kg/day)	Total mass (kg/day)		Observed mass change
1	4*	403	1.73	1.75	5.08	6.83	6.95	0.98
2	4*	403	1.96	1.98	4.74	6.72	6.76	0.99
3	4	356	1.66	1.58	5.50	7.07	6.79	1.04
4	6	452	1.88	1.90	5.27	7.17	7.64	0.94
5	6	459	1.75	1.77	6.05	7.82	9.61	0.81
6	6	499	2.24	2.27	5.45	7.72	7.57	1.02
Mean		425	1.87	1.87	5.35	7.22	7.55	0.97
± S.D.		57	0.19	0.22	0.40	0.42	0.98	0.08

* Indicates age estimated from standard length (Reiter *et al.*, 1981)

Maternal water and energy flux

The water influx rate, the rate of adipose tissue loss due to metabolism and the rate of milk mass transferred to the pup are shown in Table II. Predicted mass loss was calculated as the adipose tissue catabolism necessary to sustain a female's estimated metabolism plus the measured mass of milk ingested by her pup. The observed rate of total mass loss is in close agreement with the sum of losses due to metabolism and milk production. Given the assumptions inherent in these calculations, the agreement is remarkably good and is consistent with the observed body compositional changes.

TABLE III

The metabolic rate of fasting, lactating females derived from water influx compared to the energy contained in the milk produced. The total energy expenditure is the sum of the metabolic and milk energies. For comparison, the ADMR (average daily metabolic rate) and the total energy output is compared to the SMR (standard metabolic rate) of a terrestrial animal of equal size (Kleiber, 1975)

Female no.	Metabolic rate (MJ/day)	Milk energy produced (MJ/day)	Total energy expenditure (MJ/day)	ADMR	Total energy output
				SMR	SMR
1	61.1	94.8	156	2.32	5.81
2	69.1	81.3	150	2.62	5.63
3	58.6	100.0	159	2.55	6.92
4	66.2	99.3	165	2.30	5.80
5	61.5	118.0	180	2.12	6.15
6	79.1	94.3	173	2.56	5.53
Mean	66.2	96.3	163	2.41	5.98
± S.D.	7.5	12.6	11	0.20	0.51

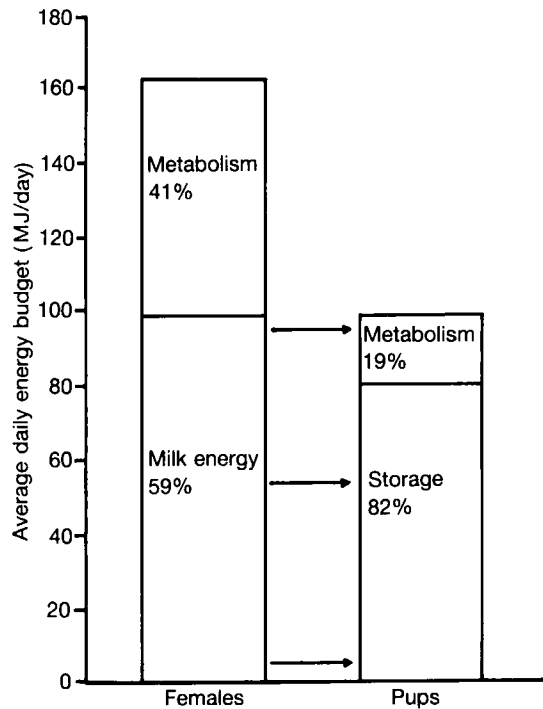


FIG. 3. The daily energy budget of Northern elephant seal females and pups is summarized. The relative importance of maintenance metabolism vs. milk production for females and maintenance metabolism vs. stored energy for pups is given for comparison.

The energy expenditure of the six lactating females derived from metabolic and milk transfer measurements is presented in Table III. Milk energy represents the largest proportion of the female's energy expenditure during lactation (Fig. 3). In addition, the average daily metabolic rate (ADMR) is only 2.4 times the predicted standard or basal metabolism (SMR) of a terrestrial

TABLE IV
The total energetic investment of females for the entire lactation period extrapolated from experiment interval data. Data are presented in both absolute and mass specific units for comparison

Female no.	Lactation interval (Days)	Metabolic rate		Milk energy produced (MJ)	Total energy (MJ)	Expenditure (MJ/kg)
		MJ	MJ/kg			
1	30	1830	4.55	2840	4680	11.6
2	27	1870	4.63	2200	4050	10.0
3	23	1350	3.79	2300	3660	10.3
4	28	1850	4.10	2780	4620	10.2
5	23	1410	3.08	2710	4140	9.0
6	28	2220	4.44	2640	4840	9.7
Mean	26.5	1760	4.10	2580	4330	10.1
± S.D.	2.9	320	0.60	270	460	0.9

animal of equal size, whereas the total energy expenditure is six times the predicted SMR (SMR from Kleiber, 1975).

The total amount of milk and metabolic energy expended by the females during the entire lactation period was calculated by extrapolating the daily milk and metabolic expenditure rates (Tables I & III) over the total observed lactation period of each female. Females expended a mean of 4330 ± 460 MJ or 10.1 ± 0.9 MJ/kg and lost $42.2 \pm 4.9\%$ of their initial mass over the mean 26.5-day nursing interval (Table IV).

Discussion

During the 26.5 days of lactation, Northern elephant seal females lose approximately 42% of their body mass and expend 4330 MJ. Pups incorporate 55% of their mothers mass loss into body tissue. Since few terrestrial mammals employ this reproductive pattern, direct comparisons are difficult. However, Grey seal pups, *Halichoerus grypus*, gain 46% of the mass lost by their mothers, which expend 2260 MJ (Fedak & Anderson, 1982). Perhaps the significantly larger size of the Northern elephant seal, as compared to Grey seals, makes this higher transfer efficiency possible. Large body size decreases the mass specific maintenance metabolism and lowers the 'metabolic overhead', releasing a larger share of the female's energy stores for milk production (Fedak & Anderson, 1982). The larger size of elephant seal pups similarly reduces their metabolic overhead, allowing more of the ingested milk to be used for growth instead of maintenance. This relationship can be seen in the graphic summary of female and pup energy budgets in Fig. 3.

However, due to variations in the energy, water and metabolic components of species with differing reproductive patterns, discussions of mass transfer alone are misleading. The high rate of energy and material transfer in phocids can be attributed to the important role of fat in both metabolism and material and energy transfer. Fat is the primary component in elephant seal milk (Le Boeuf & Ortiz, 1977; Riedman & Ortiz, 1979) and allows for rapid growth of the pup in a limited time interval (Ortiz *et al.*, 1984).

Although we did not directly assess the relative contribution of fat, carbohydrate and protein to metabolism and milk production, we can examine the relative importance of each by comparing changes in body mass to material transferred in milk. Table I indicates that pups consumed

45 kg of fat and 13 kg of protein over the measurement period. Fat, stored as adipose tissue, contained 10% water and protein, stored as lean mass, contained 73% water. Therefore, the equivalent of 49.5 kg of adipose tissue and 48 kg of lean mass was transferred to the pup. The experimental females lost 113 kg of adipose tissue and 44 kg of lean mass over the experimental period. Subtracting the portion transferred to the pups as milk leaves 63 kg adipose tissue and -4 kg protein. Obviously, negative protein transfer does not occur. However, this derivation indicates that most, if not all, of the protein mobilized during lactation was used in milk production with little contributing to the female's maintenance metabolism. This is consistent with measurements of fasting metabolism in other lactating and non-lactating pinnipeds, which show that protein contributes less than 5% to overall metabolism (Pernia *et al.*, 1980; Costa, Feldkamp, & Gentry, 1983).

Error analysis

Lifson & McClintock (1966) and Nagy & Costa (1980) discuss the errors inherent in the measurement of water influx with isotopically labelled water. Of the five potential sources of error discussed, we consider only three to be of possible significance to the present study. Errors may result from inaccurate measurement of total body water, exchange of unlabelled inspired water vapour for labelled water vapour in the respiratory tract and physical fractionation of the isotopes.

Although we were unable to directly validate the accuracy of our total body water measurement in elephant seals by body dehydration, other studies indicate that this error may range from -5.7 to +12.0, with a mean of 3.7% (Nagy & Costa, 1980). If we assume a mean error of 3.7%, our estimate of water influx, and therefore maintenance metabolism, would be overestimated by no more than 3.7%.

The errors due to water vapour exchange and physical fractionation effects tend to increase as total water flux rates decrease. The theoretical maximum error assumes complete exchange of inspired unlabelled water vapour for labelled water vapour (Lifson & McClintock, 1966). In fasting elephant seals, this is the water vapour contained in the air volume inhaled to supply metabolism. In this study, we estimated this error by assuming an oxygen extraction efficiency of 10% (Costa & Huntley, unpubl. data) and data on nasal water exchange for elephant seals (Huntley, Costa & Rubin, 1984). In fasting females, this error could lead to a maximum overestimate of water influx and maintenance metabolism of 20%. However, physical fractionation effects lead to a 9% underestimate of water influx (Nagy & Costa, 1980). Since these errors tend to cancel each other out, it is likely that the maximum overestimate of fasting metabolism does not exceed 10-15%. Despite these possible errors, our basic conclusions are unaffected, since even a 20% overestimate of maintenance metabolism results in only an 8% error in the total energy expended by a female during lactation. Furthermore, the excellent agreement between actual mass change, and mass loss of females predicted from metabolic and milk intake measurements, suggests that the errors of measurement are small.

Similar errors may occur in suckling pups. However, as with the females, our work with suckling pups shows that actual and predicted mass gains were within 5% (Ortiz *et al.*, 1984). The greater water flux in suckling pups results in a proportional reduction in the error of vapour exchange and fractionation effects. Furthermore, validation studies on Northern fur seal pups indicate that milk intake measured with HTO influx is within -4 to 7% of actual milk intake (Costa & Gentry, 1986).

The relative efficiency of milk production in lactating elephant seals is the ratio of the energy content of the milk ingested by pups to the total energy expenditure of the female (average metabolism and milk energy). In elephant seals, milk production represents 60% of the total energy expenditure, a value close to the 57% reported for the Grey seal using a different method (Fedak & Anderson, 1982) and lower than the 69% for Northern fur seals, *Callorhinus ursinus*, suckling during the two-day nursing intervals between feeding trips (Costa & Gentry, 1986). Comparisons with terrestrial animals are possible, but the conditions are different and comparisons are difficult. Brody (1945) defined the gross efficiency of milk production as the ratio of milk energy produced to total energy consumed. He reported efficiencies of 31% for milk cows, 44% for laboratory rats and 35% for goats. The total energy input for these animals is a measure of their total food energy intake and includes energy lost in the assimilation and digestion of food. Since studies of pinnipeds do not include these costs, direct comparisons may be misleading. Pinnipeds generally incur these metabolic costs while feeding at sea prior to arrival onshore.

The high efficiency of milk transfer of these marine mammals results from both a high rate of energy transfer between mother and pup and the low metabolic rates of females. Rapid transfer of energy between mother and pup is made possible by the high lipid content of marine mammal milk (Fedak & Anderson, 1982; Ortiz *et al.*, 1984). Rapid transfer of energy in the form of lipid-rich milk reduces the total energy expended by the female for maintenance (Fedak & Anderson, 1982). Additional reductions in the female's metabolism also increase her milk production efficiency.

Several mechanisms decrease fasting metabolism during lactation. Unlike terrestrial animals that synthesize milk from ingested food and body stores, these marine mammals must produce their milk from stored body fat and protein alone. Mobilization of body fat and protein, and subsequent incorporation into milk should be efficient, since direct recruitment, rather than *de novo* synthesis of lipid, is possible. However, milk caseins must be synthesized from body proteins. In addition, the lack of dietary carbohydrate may be of some consequence to the developing pup. Again, the cost of synthesizing lipids and proteins from ingested food has already been paid while the animal was at sea. However, the cost of milk synthesis does not appear to increase overall metabolism significantly. Several investigators report no significant differences in the overall metabolic rate of lactating and non-lactating Cotton rats, *Sigmodon hispidus* (Randolph *et al.*, 1977), laboratory mice, *Mus musculus* (Studier, 1979) and fur seals, *Callorhinus ursinus* (Costa & Gentry, 1986).

Further metabolic savings are achieved by minimizing onshore activity. Female elephant seals spend considerable amounts of time asleep and remain within a few metres of the parturition site for the entire lactation cycle (J. Reiter, pers. comm.). Final energy savings may be derived from a reduction in basal metabolism obtained by periodic sleep apnoeas. Such periodic apnoeas during sleep results in up to a 48% reduction of metabolism in fasting weaned pups (Huntley & Costa, 1983; Huntley, 1984). The ratio of fasting metabolism in female elephant seals, to the predicted standard metabolism of a terrestrial mammal of equivalent mass, is 2.4, virtually identical to the value reported for weaned fasting pups (Ortiz *et al.*, 1978). In contrast, lactating Northern fur seals, which are more active on the rookery and do not exhibit prolonged sleep apnoeas, exhibit a higher metabolic rate that is 3.2 times that predicted for a terrestrial animal of equal size (Costa & Gentry, 1986).

The reproductive pattern employed by elephant seals may confer several non-energetic advantages. For example, a female may forage more efficiently over a larger range without concern for the pup's safety, or ability to follow. This allows spatial and temporal separation of activities

of pupping and nursing from foraging and permits the female to exploit food resources that are far from the rookery and take weeks or months to exploit. In contrast, otariid mothers initially leave their pups on the beach and make frequent foraging trips. Each trip requires considerable expenditure of energy to get to and from the foraging grounds. Furthermore, the duration of each trip is limited by the pup's ability to fast and maintain a net mass gain until the mother returns. In otariids, this appears to limit female foraging trips to seven days or less (Gentry & Holt, 1986). Since elephant seals expend this energy once, they reduce the energy expended getting to and from the feeding grounds per unit of energy delivered to the pup. Moreover, once a good resource patch is discovered, an elephant seal can stay with it, since there is no need to return to a pup fasting onshore. Many otariids eventually take their pups to sea. Here again, the elephant seal has an advantage, since the female's foraging behaviour is not altered by the pup's presence. This is especially important in a diving mammal, where body size, experience and age determine its diving capabilities. Kooyman, Castellini, Davis & Maue (1983) found that the 10–13 min aerobic dive limit (ADL) of young Weddell seals, *Leptonychotes weddelli*, was considerably lower than the 20–25 min ADL for adult animals. Greater experience and large body size were thought to account for these differences. Older, larger animals have a lower mass specific metabolic rate as well as a greater blood and muscle oxygen store (Kooyman *et al.*, 1983). Furthermore, there is no need to develop long-term mother-pup recognition mechanisms like those that exist in otariids. Finally, the concentrated nursing strategy allows a female to amortize the energetic cost of lactation over a longer time interval. This could reduce the foraging intensity and allow the mother to face periodic fluctuations in prey availability without endangering her pup's survival.

The potential magnitude of this reduced foraging effort can be calculated by comparing the food intake necessary to sustain the onshore lactation with the animal's daily food consumption at sea. The total cost of lactation onshore for the 4–6-year-old females in this experiment was 4330 MJ (Table IV). This is the fasting metabolic rate. However, urinary and faecal energy loss associated with prey processing and digestion must be considered. Although no data are available for these factors in elephant seals, another phocid, the Harbour seal, has been shown to store or utilize 80.6% of the ingested food energy for metabolism (Ashwell-Erickson & Elsner, 1981). Based on these data, an elephant seal would need 5370 MJ in food energy to store the 4330 MJ used for milk production and maintenance metabolism during the onshore lactation period. There are no estimates of daily food intake or the free-ranging energy metabolism of elephant seals, but recent studies on Northern fur seals indicate foraging requires 1.75 times the onshore metabolism (Costa & Gentry, 1986). If a similar relationship exists in elephant seals, the estimated average metabolic rate of a free-ranging female is 115 MJ/day. Utilizing the ratio of ingested food energy to metabolism of 80.6%, the at-sea food consumption is 143 MJ/day. Assuming that a female elephant seal spends 302 days at sea, 28 days onshore moulting and 35 days for parturition, lactation and copulation, the average yearly food intake would be 43200 MJ. Since the total cost of onshore lactation is 4330 MJ, a female elephant seal needs only to increase her average daily prey intake by 10% to store sufficient energy for lactation.

This small increase in prey intake in elephant seals is made possible by amortizing the cost of lactation over the entire year. In terrestrial animals, percentage increase in food energy intake during lactation is considerably higher, for example, 47.5% in Pine voles, *Microtus pinetorum* (Lochmiller, Whelan & Kirkpatrick, 1982), 74–146% in *Peromyscus leucopus* (Millar, 1978), 66% in Cotton rats, *Sigmodon hispidus* (Randolph *et al.*, 1977) and 160% in Red deer, *Cervus elaphus* (Arman, Kay, Goodall & Sharman, 1974). Clearly, separation of lactation from feeding appears

to be ecologically and energetically advantageous and may be one of the key strategies underlying the remarkable recovery of this species from near extinction at the turn of the century. Since this unusual lactation pattern is restricted to large marine mammals, it may represent a fundamental component of their life history.

We thank employees of the California Department of Parks and Recreation for cooperation and logistic support at Año Nuevo State Reserve, the National Marine Fisheries Service for a marine mammal permit and Clairol Inc. for providing marking solutions. Many people were involved in the field manipulations, especially J. Reiter, G. McCalla, P. Thorson, R. Wells, R. Spaulding, D. Peton, M. Meade, R. Rubin, J. Vanderlip, D.V.M., S. Feldkamp, J. Herpolsheimer, D. De Master and E. Keith. Thanks are extended to K. Nagy for assistance with the HDO analysis and for helpful suggestions with methodology. This work was supported by NIH fellowship AM 06093-01, NOAA-grants ABC-000164 and NA80AA-D-00120, NSF-grants DPP 83-11799, DEB 77-17063 and BSR 8117024, and MBS-NIH-grant DRR S06-RR08132-04.

REFERENCES

- Altmann, J. (1980). *Baboon mothers and infants*. Cambridge, Mass. & London: Harvard University Press.
- Arman, P., Kay, R. N. B., Goodall, E. D. & Sharman, G. A. M. (1974). The composition and yield of milk from captive red deer (*Cervus elaphus* L.). *J. Reprod. Fert.* **37**: 67-84.
- Ashwell-Erickson, S. & Elsner, R. (1981). The energy cost of free existence for Bering Sea harbor and spotted seals. In *The Eastern Bering Sea Shelf: oceanography and resources 2*. Seattle: University of Washington Press.
- Briggs, G. D., Henrickson, R. V. & Le Boeuf, B. J. (1975). Ketamine immobilization of northern elephant seals. *J. Am. vet. med. Ass.* **167**: 546-548.
- Brody, S. (1945). *Bioenergetics and growth*. New York: Hafner Press.
- Calow, P. (1979). The cost of reproduction, a physiological approach. *Biol. Rev.* **54**: 23-40.
- Costa, D. P., Feldkamp, S. D. & Gentry, R. L. (1983). Bioenergetics of lactation in the northern fur seal. *Physiologist* **25**: 279.
- Costa, D. P. & Gentry, R. L. (1986). Free ranging and reproductive energetics of the northern fur seal. In *Fur seals: maternal strategies on land and at sea*. Princeton: Princeton University Press. In press.
- Costa, D. P. & Ortiz, C. L. (1980). Water electrolyte and nitrogen balance of fasting weaned elephant seal pups, *Mirounga angustirostris*. *Physiologist* **23**(4): 516.
- Fedak, M. A. & Anderson, S. S. (1982). The energetics of lactation: accurate measurements from a large wild mammal, the Grey seal (*Halichoerus grypus*). *J. Zool., Lond.* **198**: 473-479.
- Fleming, T. H. (1979). Life-history strategies. In *Ecology of small mammals*: 1-61. Stoddart, D. M. (Ed.). New York: Chapman & Hall.
- Foy, J. M. & Schnieden, H. (1960). Estimation of total body water in the rabbit, guinea pig and man, and the biological half-life of tritium in man. *J. Physiol.* **154**: 169-176.
- Fraser, A. F. (1968). *Reproductive behavior in ungulates*. New York: Academic Press.
- Gentry, R. L. & Holt, J. R. (1986). Attendance behavior of northern fur seals. In *Fur seals: maternal strategies on land and at sea*. Princeton: Princeton University Press. In press.
- Giesel, J. T. (1976). Reproductive strategies as adaptations to life in temporally heterogeneous environments. *A. Rev. Ecol. Syst.* **7**: 57-79.
- Huntley, A. C. (1984). *Relationships between metabolism, respiration, heart rate, and arousal states in the northern elephant seal*. Ph.D. Thesis, University of California, Santa Cruz.
- Huntley, A. C. & Costa, D. P. (1983). Cessation of ventilation during sleep: a unique mode of energy conservation in the northern elephant seal. *Proc. int. Union Physiol. Sci.* **15**: 203.
- Huntley, A. C., Costa, D. P. & Rubin, R. D. (1984). The contribution of nasal countercurrent heat exchange to water balance in the northern elephant seal. *J. exp. Biol.* **113**: 447-454.
- Kleiber, M. (1975). *The fire of life*. New York: Krieger Publ. Co.
- Kooyman, G. L., Castellini, M. A., Davis, R. W. & Maue, R. A. (1983). Aerobic diving limit of immature Weddell seals. *J. comp. Physiol.* **151**: 171-174.

- Laws, R. M. (1959). Accelerated growth in seals, with special reference to the Phocidae. *Norsk Hvalfangst tid.* **48**: 425-452.
- Le Boeuf, B. J. & Ortiz, C. L. (1977). Composition of elephant seal milk. *J. Mammal.* **58**: 683-685.
- Le Boeuf, B. J. & Peterson, R. S. (1969). Social status and mating activity in Elephant seals. *Science, Wash.* **163**: 91-93.
- Le Boeuf, B. J., Whiting, R. J. & Gantt, R. F. (1972). Perinatal behaviour of northern elephant seal females and their young. *Behaviour* **43**: 121-156.
- Lifson, N. & McClintock, R. (1966). Theory and use of the turnover rates of body water for measuring energy and material balance. *J. theor. Biol.* **12**: 46-74.
- Lochmiller, R. L., Whelan, J. B. & Kirkpatrick, R. L. (1982). Energetic cost of lactation in *Microtus pinetorum*. *J. Mammal.* **63**: 475-481.
- Mech, L. D. (1970). *The wolf*. New York: The Natural History Press.
- Millar, J. S. (1977). Adaptive features of mammalian reproduction. *Evolution, Lawrence, Kans.* **31**: 370-386.
- Millar, J. S. (1978). Energetics of reproduction in *Peromyscus leucopus*: the cost of lactation. *Ecology* **59**: 1055-1061.
- Nagy, K. & Costa, D. P. (1980). Water flux in animals: analysis of potential errors in the tritiated water technique. *Am. J. Physiol.* **238**: R454-465.
- Nelson, M. M. & Evans, H. M. (1961). Dietary requirements for lactation in the rat and other laboratory animals. In *Milk: the mammary gland and its secretion* **2**: 137-185. Kon, S. K. & Cowie, A. T. (Eds). New York: Academic Press.
- Ortiz, C. L., Costa, D. P. & Le Boeuf, B. J. (1978). Water and energy flux in elephant seal pups fasting under natural conditions. *Physiol. Zool.* **51**: 166-178.
- Ortiz, C. L., Le Boeuf, B. J. & Costa, D. P. (1984). Milk intake of elephant seal pups: An index of parental investment. *Am. Nat.* **124**: 416-422.
- Pernia, S. D., Hill, A. & Ortiz, C. L. (1980). Urea turnover during prolonged fasting in the northern elephant seal. *Comp. Biochem. Physiol. (B)* **658**: 731-734.
- Pianka, E. R. (1976). Natural selection of optimal reproductive tactics. *Am. Zool.* **16**: 775-784.
- Randolph, P. A., Randolph, J. C., Mattingly, K. & Foster, M. M. (1977). Energy costs of reproduction in the cotton rat, *Sigmodon hispidus*. *Ecology* **58**: 31-45.
- Reiter, J., Panken, K. J. & Le Boeuf, B. J. (1981). Female competition and reproductive success in northern elephant seals. *Anim. Behav.* **29**: 670-687.
- Ricklefs, R. E. (1979). Adaptation, constraint and compromise in avian postnatal development. *Biol. Rev.* **54**: 269-290.
- Riedman, M. & Ortiz, C. L. (1979). Changes in milk composition during lactation in the northern elephant seal. *Physiol. Zool.* **52**: 240-249.
- Schaller, G. B. (1972). *The Serengeti lion*. Chicago: The University of Chicago Press.
- Schmidt-Nielsen, K. & Schmidt-Nielsen, B. (1952). Water metabolism in desert mammals. *Physiol. Rev.* **32**: 135-166.
- Stearns, S. C. (1976). Life-history tactics: A review of the ideas. *Q. Rev. Biol.* **51**: 3-47.
- Stearns, S. C. (1980). A new view of life-history evolution. *Oikos* **35**: 266-281.
- Stewart, R. E. & Lavigne, D. M. (1984). Energy transfer and female condition in nursing harp seals *Phoca groenlandica*. *Holarct. Ecol.* **7**: 182-194.
- Studier, E. H. (1979). Bioenergetics of growth, pregnancy and lactation in the laboratory mouse, *Mus musculus*. *Comp. Biochem. Physiol. (A)* **64**: 473-481.
- Trivers, R. L. (1972). Parental investment and sexual selection. In *Sexual selection and the descent of Man*: 135-179. Campbell, B. (Ed.). Chicago: Aldine Publ. Co.
- van Lawick-Goodall, J. (1971). *In the shadow of Man*. Boston: Houghton Mifflin.
- Williams, G. C. (1966). Natural selection, the costs of reproduction and a refinement of Lacks' principle. *Am. Nat.* **100**: 687-690.