

# MILK AND ENERGY INTAKES OF SUCKLING CALIFORNIA SEA LION ZALOPHUS CALIFORNIANUS PUPS IN RELATION TO SEX, GROWTH, AND PREDICTED MAINTENANCE REQUIREMENTS<sup>1</sup>

OLAV T. OFTEDAL,\* SARA J. IVERSON,\*† AND DARYL J. BONESS\*

\*Department of Zoological Research, National Zoological Park, Smithsonian Institution, Washington, D.C. 20008; and †Graduate Program in Nutritional Sciences, University of Maryland, College Park, Maryland 20742  
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Isotope dilution was used to measure milk intake of 43 California sea lion pups on San Nicolas Island, California, from 1982 to 1984. Deuterium concentration was monitored in serial blood samples collected at about 5-day intervals for 3 wk after isotope administration. Estimated milk intakes differed significantly between male ( $723 \pm 31.0 \text{ g} \cdot \text{day}^{-1}$ ) and female ( $609 \pm 24.0 \text{ g} \cdot \text{day}^{-1}$ ) pups but did not increase from the first to second month postpartum. On a metabolic size basis ( $\text{weight}^{0.83}$ ), gross energy intakes did not differ between male and female pups but did differ between years, apparently as a consequence of the 1983 El Niño. The mean energy intakes ( $\text{kcal} \cdot \text{day}^{-1}$ ) of sea lion pups in the first ( $361 \cdot \text{W}^{0.83}$ ) and second ( $308 \cdot \text{W}^{0.83}$ ) months were high relative to terrestrial species. Regression of energy intake on growth rate predicted that maintenance energy requirements ( $\text{kcal} \cdot \text{day}^{-1}$ ) were also high (168 and  $252 \cdot \text{W}^{0.83}$  in the first and second months). The fact that California sea lion pups devote a large proportion of energy to maintenance rather than to growth or to blubber deposition may reflect both the energetic demands of an aquatic environment and limitations in the ability of lactating females to increase the rate of energy transfer to pups.

## INTRODUCTION

Although adapted to an aquatic environment and food supply, pinnipeds seek out solid substrate (land or ice) for giving birth and for nursing of young (Oftedal,

Boness, and Tedman 1987). This behavior may be related in part to reduction of thermal losses by young pups on submergence in water. Given the thin blubber layer of newborn pinnipeds (Blix et al. 1979; Worthy and Lavigne 1983; Bowen, Boness, and Oftedal 1987), rapid acquisition of milk energy may be important to offset costs of thermoregulation in cold and wet environments and for deposition of body fat. It has been suggested that marine mammals produce milks high in fat because of the high energy requirements of the young (Jenness and Sloan 1970; Bonner 1984). Although young pinnipeds do not exhibit unusually high resting metabolic rates (Lavigne et al. 1986), the hypothesis that young pinnipeds have high maintenance requirements has not been directly tested.

Unlike neonatal seals (family Phocidae) that deposit large amounts of blubber during a short lactation period, neonatal fur seals and sea lions (family Otariidae) grow slowly over a lactation period of 4–12 mo or more (Kovacs and Lavigne 1986; Oftedal et al. 1987). The maintenance component of pup energy requirements is particularly important when the period of dependence is long and is presumed to underlie the high

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total energy cost of lactation in otariids (Oftedal et al. 1987).

Growth rate is another important component of energetic strategies, especially for male pinnipeds that must achieve large size to attain social status in a polygynous mating system. Parental investment theory predicts that mothers in polygynous species should invest more heavily in male than female offspring if the reproductive return from investment in males is greater (Trivers 1972; Maynard Smith 1980). This could occur if larger, more robust male offspring gain a position of social dominance or an advantage in male-male competition on reaching maturity and thereby mate with many females and produce a disproportionate number of descendants. Measurement of milk and energy intakes of pinniped pups serves as a useful indicator of maternal investment (Ortiz, Le Boeuf, and Costa 1984).

The availability of hydrogen isotope methods for determination of milk intake under field conditions has recently stimulated a number of studies on pinniped lactation (Ortiz et al. 1984; Costa and Gentry 1986; Oftedal et al. 1987; Costa et al. 1986; Tedman and Green, in press). Pinnipeds are well suited for isotope studies because of relative ease of capture when out of water, site tenacity even when disturbed, and a tendency to aggregate in large numbers. Solid food consumption by pups occurs only in the latter part of lactation in otariids and after complete weaning in most phocids (Oftedal et al. 1987), such that complications owing to ingestion of water from non-milk sources are largely avoided. Although most intake studies have been on phocids, Costa and Gentry (1986) examined milk intakes of northern fur seal *Callorhinus ursinus* pups during the first 2 mo postpartum.

In this study, we measured milk intake of pups of the California sea lion *Zalophus californianus* during early lactation. The California sea lion breeds on relatively accessible islands off the coast of southern California and Mexico (Peterson and Bartholomew 1967; Odell 1981). Pregnant females haul out onto breeding sites in late May and June to give birth to a single precocial pup. At about 6–8 days postpartum, females depart from the rookery to begin

periodic feeding trips that average 1–3 days in duration, interspersed with periods of pup attendance of about 1.5 days average duration (Boness et al. 1985). One objective of our study was to determine whether the difference in growth rate of male and female pups (Boness et al. 1983) could be attributed to differential maternal investment. A second objective was to study the relation of milk intake to growth rate independent of pup sex and to predict the energy intake required for maintenance.

## MATERIAL AND METHODS

### FIELD PROCEDURES

Data were collected from a wild population of California sea lions on San Nicolas Island, California (33° N lat., 119° W long.). Our initial intent was to study the first month of lactation in June 1982 and the second month in July 1983, but, since an unusually strong El Niño occurred in 1983 (Cane 1983; Barber and Chavez 1983), measurements were repeated with sea lion pups in June and July 1984. Over the 3-yr period, isotope studies were conducted on 43 pups. Pups captured in June 1982 were estimated to average 5 days of age (range = 0.5–10 days) based on known ( $n = 7$ ) or estimated ( $n = 10$ ) birth dates. Pups in June 1984 were captured on the same dates, had similar weights ( $P > .1$ ,  $t$ -test), and were considered to be of comparable age. Based on information on mean birth dates and growth rates for sea lions on the island (Boness et al. 1983; Ono, Boness, and Oftedal, in press, and unpublished data), July pups were about 3–4 wk old at the initial capture. Henceforth, June and July pups will be referred to as first and second month postpartum, respectively.

After capture, each pup was placed in a restraining device constructed of a plywood board to which netting was attached on one side and secured over the pup's back on the other side with nylon ropes. Stomach contents of pups in 1983 and 1984 (but not 1982) were evacuated by gastric intubation with a 3/8" Veterinary Stomach Tube (Kallayjian Industries, Inc.) prior to isotope administration. A preweighed amount of deuterium oxide ( $D_2O$ , 99.8% purity, Stable Isotopes Division, ICN Biomedicals, Inc., Cambridge, Mass.) was administered via a 12 French stomach tube, at approximately

3 g per kg body weight. Syringe and stomach tube were flushed with small quantities of water ( $2 \times 5 \text{ cm}^3$ ) and air to complete  $\text{D}_2\text{O}$  delivery. The pup was then transferred to a portable kennel and partially wetted to prevent overheating. Pups were bled from the caudal gluteal vein (Geraci and Sweeney 1986) at the following times after isotope administration: 2, 4, and 6 h in 1982, 0.5, 1, 2, and 3 h in 1983, and 3 and 4 h in 1984. Pups were weighed on a hanging spring scale (60 lb. by 1 oz., John Chatillion & Sons, Inc., Kew Gardens, N.Y.); weights were converted to metric units prior to calculations. Pups were individually marked with hair bleach and water-resistant paint (Lenmar Paint Co., Baltimore) prior to release. All pups reunited successfully with their mothers.

Sequential blood samples and body weights were obtained on recaptures of isotope-labeled pups at about 5-day intervals (range = 3–6 days) over a period of 20–21 days. An extended study period of 3 wk was selected to minimize the influence of individual suckling sessions on estimated milk intake in a species characterized by infrequent suckling. A second dose of  $\text{D}_2\text{O}$  was administered at the completion of the 3-wk period to eight pups in June 1982 and to four pups in July 1983.

Two apparently healthy pups that died of accidental causes in September 1982 were frozen for subsequent chemical analysis. Body water content was concurrently determined for five similar-aged pups by  $\text{D}_2\text{O}$  dilution, as described above.

#### LABORATORY ANALYSES

Blood samples (2–5 cc) were centrifuged to isolate sera that were frozen until analysis. Free water was collected from thawed blood sera by heat distillation (Oftedal 1981).  $\text{D}_2\text{O}$  concentration of samples was determined by infrared spectrophotometry (Model 599B double-beam grating infrared spectrophotometer, Perkin Elmer Corp., Norwalk, Conn.), at a wavelength of 3.98  $\mu$ , using matched barium fluoride cells (path length 0.11 mm) (Stansell and Mojica 1968). A baseline reading with distilled water was obtained before each sample reading, and all samples from an individual pup were read on the same day. A complete range of  $\text{D}_2\text{O}$  standards was read at the be-

ginning and end of each day of analysis to construct standard curves and account for possible daily fluctuations in machine response. For each pup, equilibration was defined by achievement of stable isotope levels in at least two successive samples after isotope administration.

Pups obtained for carcass analyses were partially thawed and ground in toto in a 25-horsepower whole-body grinder equipped with a 10-inch diameter screw drive and a die with  $\frac{7}{8}$ -inch holes (Autio Model 801B, Paul Autio, Astoria, Oreg.). Total water content of the ground material was determined by drying to constant weight (18 h) in a forced convection oven at 100 C. The two carcasses were assayed for total nitrogen (TN) by a macro-Kjeldahl procedure using a copper catalyst (Horwitz et al. 1975); crude protein was calculated as  $\text{TN} \times 6.25$ . Total lipid was determined on dried samples by petroleum ether extraction in Soxhlet extractors (Horwitz et al. 1975).

#### ESTIMATION OF WATER TURNOVER AND INTAKE

In computations, the isotope level ( $C_t$ ) of samples must be corrected because increase in body water pool size causes a decline in isotope concentration not owing to water turnover (Dove and Freer 1979; Nagy and Costa 1980; Oftedal 1984b). We assume that pool size constitutes a constant proportion of body weight over the study period, such that body weight can be used to calculate a corrected isotope concentration ( $C_t^*$ ):

$$C_t^* = C_t \times \frac{W_t}{W_0}, \quad (1)$$

where  $W_t$  is body weight at time  $t$  and  $W_0$  is body weight at time 0 (time of isotope administration). Minor deviations from constancy in body water proportion have little effect on water intake calculations (see p. 570).

Body water turnover of each pup was determined from regression of  $\ln C_t^*$  against  $t$ , with the absolute value of the slope providing an estimate of fractional water turnover rate ( $k$ ) and the intercept providing an estimate of isotope level at 0 h. In calculation of initial pool size ( $P_0$ ), this 0 h regression value was used in place of the equilibration value because some isotope

loss may occur during the equilibration process owing to urination, defecation, and respiration, leading to overestimation of pool size (Panaretto 1968; Nagy and Costa 1980).

Pup weight was regressed on elapsed time after isotope administration to determine daily gain ( $\Delta g$ ) and predicted weight ( $W_{1/2}$ ) for each pup at the midpoint of the study period. Body water pool size at this midpoint ( $P_{1/2}$ ) was calculated from the initial percent body water ( $\%BW = 100 \times P_0/W_0$ ) and predicted weight. The following equations were used to calculate daily water loss ( $L$ ), water storage owing to gain in pool size ( $G$ ), and total daily water intake (TWI):

$$L = k \times P_{1/2}, \quad (2)$$

$$G = \Delta g \times \frac{\%BW}{100}, \quad (3)$$

$$TWI = L + G. \quad (4)$$

#### CALCULATION OF MILK INTAKE

Conversion of TWI to milk intake (MI) required estimation of free water content of milk consumed by the pup as well as the amount of metabolic water produced from catabolism of milk components. Milk composition data were obtained from a concurrent study (Ofstedal, Boness, and Iverson 1983, and unpublished data). Since milk composition did not differ between samples collected at several days postpartum and 2 mo postpartum ( $P > .1$ ,  $n = 9$  animals), the following average values were used for the present study: 59.0% water ( $\%W_M$ ), 31.7% fat ( $\%F_M$ ), 8.58% protein ( $\%P_M$ ), 0.317% sugar ( $\%S_M$ ), and 3.41 kcal per g gross energy.

Oxidation of 1 g each of fat, protein, and sugar yields approximately 1.07 g, 0.42 g, and 0.58 g of water, respectively (Van Es 1969). While sugar can be assumed to be completely catabolized ( $S_C$ ), fat and protein catabolism ( $F_C$ ,  $P_C$ ) may be estimated from the difference between intake ( $F_I$ ,  $P_I$ ) and deposition in growing tissue ( $F_D$ ,  $P_D$ ) of these nutrients:

$$F_C = F_I - F_D = \frac{MI \times \%F_M}{100} - F_D, \quad (5)$$

$$P_C = P_I - P_D = \frac{MI \times \%P_M}{100} - P_D, \quad (6)$$

$$S_C = S_I = \frac{MI \times \%S_M}{100}. \quad (7)$$

Total water intake derives from milk water intake (MWI) and metabolic water production (MetWP):

$$TWI = MWI + MetWP, \quad (8)$$

$$TWI = \frac{MI \times \%W_M}{100} + 1.07F_C + 0.42P_C + 0.58S_C. \quad (9)$$

Substituting equations (5), (6), and (7) into equation (9) leads to

$$TWI = \frac{MI \times \%W_M}{100} + 1.07 \left[ \frac{MI \times \%F_M}{100} - F_D \right] + 0.42 \left[ \frac{MI \times \%P_M}{100} - P_D \right] + 0.58 \left[ \frac{MI \times \%S_M}{100} \right]. \quad (10)$$

Rearranging equation (10) gives

$$TWI = \frac{MI}{100} \times (\%W_M + 1.07\%F_M + 0.42\%P_M + 0.58\%S_M) - (1.07F_D + 0.42P_D). \quad (11)$$

Therefore milk intake can be expressed as follows:

$$MI = 100 \times \frac{TWI + 1.07F_D + 0.42P_D}{\%W_M + 1.07\%F_M + 0.42\%P_M + 0.58\%S_M}. \quad (12)$$

$F_D$  and  $P_D$  were estimated from changes in body water content and body weight (see, e.g., Ortiz, Costa, and Le Boeuf 1978; Ortiz et al. 1984). Since both the water and the protein content of lean body mass (LBM) tend to be relatively constant among ani-

mals of a given species and age (Widdowson 1950; Reid, Wellington, and Dunn 1955; Reid et al. 1963; Roubicek 1969), ratios of water and protein to LBM determined by direct carcass analysis of 3-mo-old pups were applied to isotope-labeled pups to determine LBM, protein, and fat content (body weight - LBM) in June. Calculated deposition rates of fat and protein were entered into equation (12) along with milk composition data and average water intake to determine the ratio of milk intake to water intake. Gross energy intakes of pups were calculated as 3.41 kcal per g  $\times$  milk intake (g). Predicted maintenance requirements for gross energy were determined by the regression of daily gain against energy intake, both on a metabolic body weight basis.

Data were tested by two-way ANOVA (sex  $\times$  year or sex  $\times$  month) using the Statistical Package for the Social Sciences (SPSS) (Nie et al. 1975). Since both months were not studied in all years, the following three comparisons could be made: June 1982 versus June 1984; July 1983 versus July 1984; and June 1984 versus July 1984. Sex differences tested in the first two independent comparisons were used to generate a combined probability statistic that was compared to a  $\chi^2$  distribution with 4 df (Sokal and Rohlf 1969). Regression analyses were performed using a graphic statistics package (StatView<sup>TM</sup>) for the Macintosh<sup>TM</sup>. Regression analyses were tested for differences between slope, intercept, and  $r^2$  value by multivariate analysis (Kleinbaum and Kupper 1978). Mean values are presented as mean  $\pm$  SEM unless otherwise indicated.

## RESULTS

### EQUILIBRATION AND WATER KINETICS

In the first year of study (1982), pups' stomachs were not evacuated prior to isotope administration. Isotope equilibration occurred prior to the initial bleed at 2 h in three pups but not until  $5.1 \pm 0.34$  h in the remaining 14 pups. The latter pups had all been observed suckling before capture, or recent suckling was evident on intubation from the appearance of milk in stomach tubes. By contrast, the three pups in which isotope equilibrated rapidly were observed

alone before capture, and their stomach tubes contained no milk. In an attempt to reduce equilibration time, stomach contents were evacuated before isotope administration in all pups in 1983. In these pups, isotope equilibrated by  $1.1 \pm 0.25$  h ( $n = 9$ ). In 1984, gastric contents of all pups were evacuated, and isotope equilibration occurred prior to the first bleed at 3 h.

Semilogarithmic regressions of corrected isotope concentration ( $\ln C_t^*$ ) on time ( $t$ ) were highly linear (e.g., fig. 1). Correction for change in body weight resulted in a flatter slope but had little effect on intercept. Estimates of isotope levels at 0 h obtained from regression were closely correlated to the measured equilibration levels ( $r = .958$ ,  $P < .001$ ). Initial body water content estimated from regression averaged  $70.2\% \pm 0.60\%$  for first-month and  $68.2\% \pm 1.07\%$  for second-month pups, whereas equilibration data yielded slightly higher estimates of  $72.2\% \pm 0.40\%$  and  $69.0\% \pm 1.28\%$  for these respective age groups ( $P < .001$  for both months combined, paired  $t$ -test).

In order to validate the estimation of body water content by isotope dilution, carcass analysis data on two pups at about 3 mo (table 1) were compared to isotope dilution estimates of body water content for pups of similar age. The mean value of 60.0% body water by oven drying was not significantly different from either regression ( $61.3\% \pm 1.07\%$ ,  $n = 5$ ) or equilibration estimates ( $61.2\% \pm 0.60\%$ ,  $n = 5$ ), nor were the two isotope estimates significantly different from each other. Although sample sizes for these comparisons are small, it appears that isotope methods give reasonably accurate estimates of body water content in sea lion pups.

Changes in body water over the course of 3 wk were assessed in 12 pups (table 2). Pups studied in the first month of life exhibited a significant increase in body weight and body water pool size, but body water percentage declined. The small set of pups studied in the second month showed no significant changes, but trends were in the same direction. A comparison of initial body water percentage of pups in the two age groups in 1984 (tables 3, 4) also indicates that younger pups were significantly higher in %BW ( $P < .01$ ); yearly differences in %BW in the first month (table 3) preclude

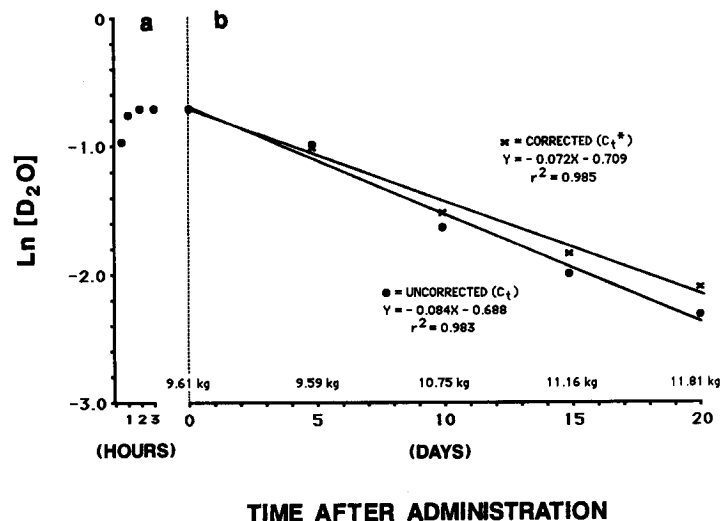


FIG. 1.—An example of changes in isotope concentration in the body water of a suckling sea lion pup. *a*, Changes during the equilibration period. *b*, Semilog linear decline in concentration over the 3-wk study period. The effect of correction for body weight change on isotope concentration is indicated by the symbol "x." Numbers above X-axis are body weights at the corresponding sampling times. Fractional turnover rate is estimated at 0.072 for corrected data and 0.084 for uncorrected data. For all 43 pups, the  $r^2$  averaged  $.990 \pm .002$ .

interyear comparisons of the two age groups. Thus, although initial pool size ( $P_0$ ) was highly correlated to body weight ( $W_0$ ) among all pups studied ( $r = .926$ ,  $P < .001$ ,  $n = 43$ ), use of body weight to estimate change in pool size may overestimate the magnitude of change since %BW declines with age.

Male pups were consistently larger than female pups (tables 3, 4). In the first two months, males had larger water pool size ( $P < .01$ ), but %BW did not differ between the sexes. Fractional turnover rate of body

water ( $k$ ) did not differ by sex or between the first and second months in 1984 ( $P > .1$ ). Calculated water intake was greater for males ( $651 \pm 27.9 \text{ g} \cdot \text{day}^{-1}$ ) than for females ( $549 \pm 21.6 \text{ g} \cdot \text{day}^{-1}$ ;  $\chi^2 = 10.77$ ,  $P < .05$ ) but did not differ with age or by year. There were no significant differences in weight gain of isotope-labeled pups between males and females, between the first and second months ( $P > .1$ , 1984 data only), or between years (tables 3, 4).

#### MILK AND ENERGY INTAKE

Conversion of water intake to milk intake required estimation of the fat and protein content of weight gain. Given that LBM contains 74% water (table 1), LBM was estimated to be 95% pup weight shortly after birth and 81% pup weight at 3 mo. Based on relationships of protein and fat to LBM (table 1), 3-mo-old pups averaging about 18 kg contain 14.6 kg LBM, 2.9 kg protein, and 3.4 kg fat, as compared to 8.3-kg pups shortly after birth that contain 7.9 kg LBM, 1.6 kg protein, and 0.4 kg fat. Over the first 3 mo of life, pups deposit approximately 15 g protein and 33 g fat per day. Given an average water intake of 606 g (all pups,  $n = 43$ ), the corresponding milk intake (calculated by eq. [12]) is 670 g. This ratio of milk to water intake (1.11:1) was

TABLE 1  
CHEMICAL ANALYSIS OF CALIFORNIA SEA LION PUPS  
AT ABOUT 3 MO

	Pup 763 (female)	Pup 767 (male)
Weight (kg) . . . . .	15.0	22.7
Body water content (BW) (%) . . . . .	59.9	60.1
Fat (%) . . . . .	19.3	18.7
Protein (%) . . . . .	16.2	16.2
Lean body mass (LBM) (%) . . . . .	80.7	81.3
Ratios:		
BW:LBM . . . . .	.742	.739
Protein:LBM . . . . .	.201	.199

TABLE 2  
COMPARISON OF INITIAL VERSUS FINAL EQUILIBRATION DATA  
IN CALIFORNIA SEA LION PUPS

Month Postpartum <sup>a</sup>	Initial	Final	Paired <i>t</i> -test <i>t</i>
Weight (kg):			
1st .....	8.44 ± .233	10.48 ± .401	-6.085***
2d .....	9.20 ± .455	9.86 ± .554	-1.151
Pool size (kg):			
1st .....	6.06 ± .202	6.79 ± .279	-4.004**
2d .....	6.61 ± .245	6.83 ± .477	-.497
Body water (%):			
1st .....	71.8 ± .83	64.9 ± 1.40	4.136**
2d .....	72.0 ± 1.31	69.6 ± 5.33	.509

NOTE.—Values are means ± SEM. Data were obtained at the beginning (initial) and end (final) of the 20- to 21-day study period for each pup.

<sup>a</sup> Month postpartum: 1st = June 1982, *n* = 8; 2d = July 1983, *n* = 4.

\*\* *P* < .01.

\*\*\* *P* < .001.

used to calculate milk intake for each pup. Free milk water accounted for 65% of total water intake, while metabolic water supplied 35%.

Daily milk and energy intakes were greater for male pups than for female pups, but milk and energy intakes did not differ with age (*P* > .1, 1984 data only) or between

TABLE 3  
BODY WATER TURNOVER AND MILK INTAKE IN SUCKLING CALIFORNIA SEA LION PUPS  
IN THE FIRST MONTH OF LIFE

	JUNE 1982		JUNE 1984		TWO-WAY ANOVA <sup>a</sup>	
	Male ( <i>n</i> = 9)	Female ( <i>n</i> = 8)	Male ( <i>n</i> = 5)	Female ( <i>n</i> = 4)	Sex Effects ( <i>F</i> )	Year Effects ( <i>F</i> )
Initial weight ( <i>W</i> <sub>0</sub> ) (kg) .....	8.79 ± .240	7.76 ± .306	8.53 ± .398	7.84 ± .435	7.92**	.09
Daily gain ( $\Delta$ g) (g)	120.6 ± 20.06	109.1 ± 12.97	92.4 ± 15.74	95.0 ± 11.75	.14	1.37
Body water (BW) (%) .....	70.2 ± 1.08	68.1 ± .88	73.0 ± 1.08	71.1 ± .81	3.73	6.72*
Fractional water turnover ( <i>k</i> ) .....	.088 ± .0030	.083 ± .0030	.073 ± .0040	.076 ± .0025	.72	10.52**
Milk intake (MI) (g/ day) .....	773 ± 47.5	631 ± 34.7	629 ± 64.5	596 ± 40.4	4.64*	3.53
MI as % of pup body weight <sup>b</sup> .....	7.78 ± .278	7.19 ± .275	6.75 ± .459	6.82 ± .207	1.28	4.80*
Energy intake (GE), kcal/day .....	2636 ± 161.9	2152 ± 118.2	2144 ± 219.8	2032 ± 137.8	4.64*	3.53
GE per MBS <sup>c</sup> (kcal/ <i>W</i> <sub>1/2</sub> <sup>0.83</sup> ) .....	391.7 ± 15.49	354.6 ± 14.08	336.2 ± 24.43	335.9 ± 9.73	2.04	4.75*

NOTE.—Values are means ± SEM.

<sup>a</sup> No significant interactions (sex × year) were present. The  $\chi^2$  values for combined probabilities of sex effects for both age groups (tables 3, 4) were *W*<sub>0</sub>, 17.8\*\*;  $\Delta$ g, 7.5; BW, 7.2; *k*, 2.0; MI, 10.8\*; MI% 2.9; GE, 10.8\*; GE per MBS, 4.7.

<sup>b</sup> Weight at midpoint of study period for each pup predicted by regression; all other values expressed on this basis.

<sup>c</sup> Metabolic body size (MBS) taken as *W*<sup>0.83</sup> for suckling young.

\* *P* < .05.

\*\* *P* < .01.

years (tables 3, 4). Mean daily milk intake for all male pups was  $723 \pm 31.0$  g and for all female pups was  $609 \pm 24.0$  g. When milk intake was expressed as a percentage of body weight, however, milk intakes did not differ between sexes (tables 3, 4) or with age ( $P > .05$ , 1984 data only); annual differences were apparent between 1982 and 1984 but not between 1983 and 1984 (tables 3, 4). Similarly, gross energy intake expressed per metabolic body size ( $W^{0.83}$  in suckling young; see Discussion, below) did not differ between sexes or with age ( $P > .1$ ), and annual differences were only found between 1982 and 1984.

Estimates of maintenance requirements for milk energy were obtained by regression of energy intake on weight gain in the first and second months postpartum (fig. 2a, 2b). Both variables were expressed on a metabolic size basis to compensate for differences in body weight among pups. Data for all years were included, since maintenance requirements would not be expected

to vary substantially between years. There was no significant difference in either slope ( $P > .1$ , both months) or intercept ( $P > .1$ , both months) between male and female pups in the two age groups. Regression lines for first and second months postpartum differed significantly in slope and intercept (fig. 2). Zero gain was equated to maintenance energy requirement ( $\text{kcal} \cdot \text{day}^{-1}$ ), which was calculated to be  $167.6 \cdot W^{0.83}$  and  $251.5 \cdot W^{0.83}$  for first- and second-month pups, respectively. Thus, the estimated daily maintenance requirements of pups in the first and second months postpartum were  $1060 \pm 21.4$  kcal and  $1848 \pm 57.4$  kcal, respectively.

## DISCUSSION

### BODY WATER AND COMPOSITION OF GAIN

In several species, differences have been reported between body water estimates derived from isotope dilution and those obtained by direct carcass desiccation. Isotope

TABLE 4  
BODY WATER TURNOVER AND MILK INTAKE IN SUCKLING CALIFORNIA SEAL LION PUPS  
IN THE SECOND MONTH OF LIFE

	JULY 1983		JULY 1984		TWO-WAY ANOVA*	
	Male (n = 5)	Female (n = 4)	Male (n = 5)	Female (n = 3)	Sex Effects (F)	Year Effects (F)
Initial weight ( $W_0$ ) (kg) . . . . .	10.32 ± .715	9.12 ± .128	11.52 ± .533	9.26 ± .642	8.10*	1.75
Daily gain ( $\Delta g$ ) (g) . . . . .	109.2 ± 41.62	75.8 ± 62.56	117.8 ± 20.01	39.7 ± 42.60	1.54	.05
Body water (BW) (%) . . . . .	66.9 ± 3.57	68.8 ± 1.42	67.9 ± .59	70.0 ± 1.12	.74	.22
Fractional water turnover (k) . . . . .	.073 ± .0054	.071 ± .0045	.072 ± .0018	.073 ± .0052	.01	.02
Milk intake (MI) (g/ day) . . . . .	681 ± 87.9	600 ± 67.6	769 ± 47.2	582 ± 88.9	2.97	.37
MI as % of pup body weight <sup>b</sup> . . . . .	5.96 ± .405	5.93 ± .467	6.11 ± .217	6.00 ± .533	.03	.09
Energy intake (GE), kcal/day . . . . .	2323 ± 299.8	2046 ± 230.6	2624 ± 160.9	1986 ± 303.0	2.97	.37
GE per MBS <sup>c</sup> (kcal/ $W_{1/2}^{0.83}$ ) . . . . .	306.8 ± 23.44	299.4 ± 25.30	320.3 ± 12.46	300.7 ± 29.91	.33	.14

NOTE.—Values are means ± SEM.

\* No significant interactions (sex × year) were present. The  $\chi^2$  values for combined probabilities of sex effects for both age groups (tables 3, 4) were  $W_0$ , 17.8\*\*;  $\Delta g$ , 7.5; BW, 7.2; k, 2.0; MI, 10.8\*; MI%, 2.9; GE, 10.8\*; GE per MBS, 4.7.

<sup>b</sup> Weight at midpoint of study period for each pup predicted by regression; all other values expressed on this basis.

<sup>c</sup> Metabolic body size (MBS) taken as  $W^{0.83}$  for suckling young.

\*  $P < .05$ .

\*\*  $P < .01$ .



dilution usually overestimates body water by 2–5 percentage points, probably owing to incorporation of hydrogen isotopes into exchangeable sites in organic constituents (Pinson 1952; Panaretto 1968; Houseman, McDonald, and Pennie 1973; Oftedal 1984a). Isotope may also be lost to nonexchangeable sites during synthetic processes associated with rapid growth (Ussing 1938). In the present study, such error could not be detected in comparison of isotope dilution and carcass desiccation data for 3-month-old sea lion pups, but sample sizes were small. The relatively slow growth rate of sea lion pups indicates low anabolic rates and may contribute to the accuracy of isotope estimates in this species (Nagy and Costa 1980; Oftedal 1984b).

The average body water content of sea lion pups in the first and second months postpartum (tables 3, 4) are similar to reported values of 67%–83% for neonates of terrestrial mammals (Wood and Groves

1965; Norton 1968; Oftedal 1981; Oftedal, Hintz, and Schryver 1983; Oftedal 1984a). The fact that body water percentage was significantly lower in first-month pups in 1982 than in 1984 suggests that the 1982 pups were higher in fat content. This may reflect annual variation in fat content at birth; it is unlikely that pups in these years differed in age. The subsequent decline in body water percentage with age is consistent with observed trends in other mammals (Moulton 1923; Spray and Widdowson 1950; Adolph and Heggenes 1971).

In the first 3 mo postpartum, body weight gain of sea lion pups was estimated to contain about 14% protein and 31% fat—that is, lean body mass constituted about 69% of gain. Given the precocial condition of sea lion pups at birth, the error involved in assuming a constant water content of lean body mass is probably small (see, e.g., Moulton 1923; Adolph and Heggenes 1971) but would cause lean body mass at

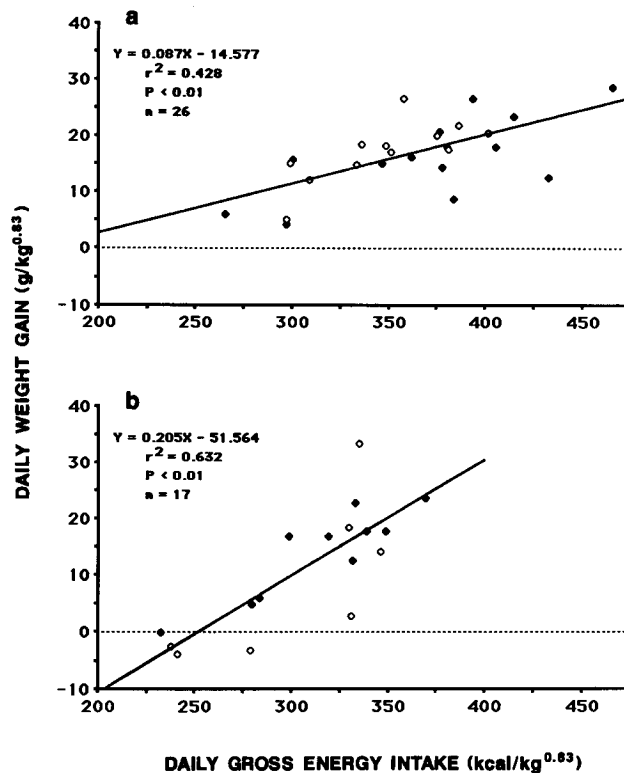


FIG. 2.—The relationship between daily weight gain and daily gross energy intake in suckling sea lion pups in the first, *a*, and second, *b*, months postpartum. Regression lines are significantly different in both slope ( $P < .01$ ) and intercept ( $P < .01$ ). Predicted maintenance ( $\text{kcal} \cdot \text{day}^{-1}$  at zero growth) is  $167.6 \cdot W^{0.83}$  and  $251.5 \cdot W^{0.83}$  for first and second months, respectively. Symbols as follows:  $\blacklozenge$  = males,  $\diamond$  = females.

birth, and hence fat content of gain, to be underestimated. Nonetheless, the fat content of gain in sea lions is considerably lower than that seen in phocid pups in which weight gain is as much as 70% blubber (Worthy and Lavigne 1983; Bowen et al. 1987). In suckling young of most terrestrial species, fat constitutes about 7%–13% of weight gain (Sheng and Huggins 1971; Roy 1980; Oftedal 1981; Oftedal et al. 1983).

#### ESTIMATION OF WATER TURNOVER RATE

In the first 2 mo postpartum, fractional turnover rates of sea lion pups (tables 3, 4) are about one-third to one-half those measured for suckling dogs, skunks, mink, sheep, and horses (0.15–0.25; Oftedal 1981; Oftedal et al. 1983; Oftedal 1984a). The slow turnover rates for sea lion pups undoubtedly reflect the consumption of a highly concentrated milk.

Some investigators have utilized a two-point model for determining water turnover (e.g. Ortiz et al. 1984; Costa and Gentry 1986; Costa et al. 1986) rather than regression of several sampling points to demonstrate linearity. Our data confirm linearity of the semilogarithmic decline in isotope concentration but indicate fluctuations in turnover rate over short time intervals owing to periodic suckling. We calculated a series of two-point fractional turnover rates ( $k^*$ ) for each pup using the equilibration point as the first point and each of the subsequent recaptures as the end point. The deviation of  $k^*$  from  $k$  as determined by regression of all data points for each pup was plotted against time interval (fig. 3). A narrow study period (0–5 days) yielded deviations ranging from –42% to +31% of the multiple-point turnover rate (mean =  $5.3\% \pm 17.18\%$  SD). However, when the

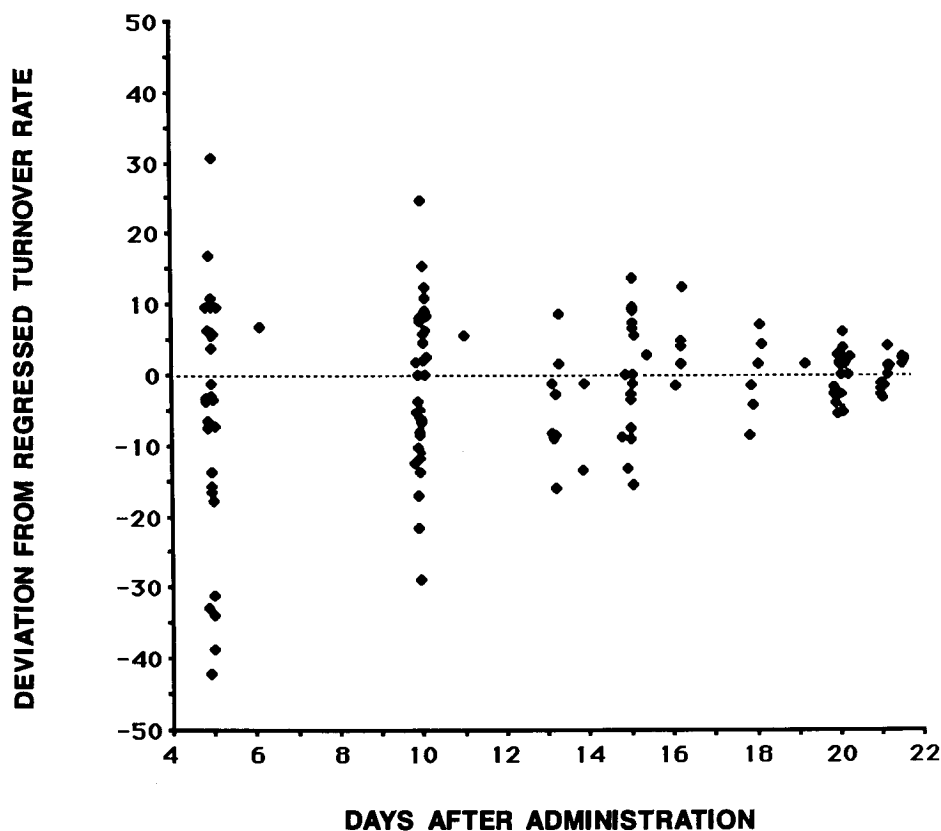


FIG. 3.—Comparison of two-point and multiple-point (regression) estimates of fractional body water turnover rate. Each two-point value was calculated from the isotope concentration at equilibration and at a subsequent recapture of a pup and expressed as the percentage deviation from the regressed turnover rate for that pup. The X-axis indicates the interval between administration and recapture for two-point estimates.

two-point study period was extended to 20–21 days, mean deviation from the multiple-point turnover rate was  $-0.3\% \pm 2.64\%$  and ranged only from  $-5\%$  to  $+6\%$  (fig. 3). Although two-point models are more influenced by error of individual isotope measurements, they yield comparable results if conducted over an extended time interval in species with infrequent suckling.

We have used body weight to correct isotope levels for change in pool size (eq. [1]), even though our data indicate that body weight does not remain at a constant percentage of body weight during the first month postpartum. The body weight correction overestimates change in pool size, such that calculated fractional turnover rate is somewhat underestimated, while pool size at the midpoint of study ( $P_{1/2}$ ) is somewhat overestimated. In calculation of water loss (eq. [2]), these effects counteract each other. To determine the degree of overall error, water intakes of the eight first-month pups in table 2 were calculated by the two-point method, using either initial and final weight, or initial and final pool size, to correct isotope levels. The weight correction results in an estimated daily water intake of  $658 \pm 89.9$  g as compared to  $653 \pm 88.0$  g when the actual pool size data are employed. The error for individual estimates using weight correction ranged from 0.0% to 1.4% (mean =  $0.6\% \pm 0.5\%$  SD) and is thus negligible.

The measurement of milk intake in suckling young by isotopically labeled water involves several other possible sources of error, including influx of respiratory water and fractionation effects, but these tend to cancel each other (Lifson and McClintock 1966; Nagy and Costa 1980; Oftedal 1984*b*; Costa et al. 1986; Schoeller and Fjeld 1986). The premise that milk is the sole source of ingested water is perhaps the most critical concern. Several studies have investigated the magnitude of seawater drinking in pinnipeds. Simultaneous measurements of water turnover and sodium intake in fed and fasted juvenile harbor seals (Depocas, Hart, and Fisher 1971) and in suckling Weddell seals (Tedman and Green, in press) have demonstrated that seawater ingestion is insignificant and in juveniles is attributable to small quantities that are swallowed while consuming prey. Further validation

may be found in the correspondence between milk consumption measured by isotope dilution and actual weighed amounts of milk fed to fur seal pups (Costa and Gentry 1986), as well as the close relationship of measured milk intake and mass gain in Weddell and elephant seal pups (Ortiz et al. 1984; Tedman and Green, in press).

In preliminary studies that we conducted in July 1981, two deuterium-labeled sea lion pups showed no significant change in isotope level and no weight gain when recaptured after 2 days (unpublished data). Over a 1-wk period, water turnover appeared to be normal, however. We interpret these observations to indicate that no milk or water was consumed during intervals that the mothers were feeding at sea. Oxidative water probably satisfies body water needs during fasting without requiring seawater ingestion, as in adult elephant and harbor seals (Depocas et al. 1971; Huntley, Costa, and Rubin 1984). As the pup gets older, an increasing proportion of time is spent in the water such that the chances of accidental water ingestion increase. Evidence of feeding was first noted in 7-month-old pups (unpublished data); thereafter, hydrogen isotope dilution is not a reliable measure of milk intake.

#### MILK AND ENERGY INTAKE IN RELATION TO AGE, SEX, AND YEAR

Data on milk intake were obtained over 3 yr in order to increase sample size and to account for annual variation. The relative constancy of the mean date of birth on San Nicolas Island during this period (Ono et al., in press) implies that the ages of pups studied in June 1982 and June 1984 should be comparable, as should those studied in July 1983 and July 1984. In 1983, an unusually severe El Niño occurred, with consequent effects on food supply, maternal foraging patterns, suckling patterns, pup growth, and pup behavior (Ono et al., in press). Effects of this El Niño on California sea lions persisted into 1984. One might expect the present study to reveal effects of El Niño, with both growth rate and milk intake reduced in comparison to more normal years.

Comparison of growth rates of isotope-labeled pups did not reveal any significant year effects (tables 3, 4) despite the fact that

more extensive studies of relatively undisturbed animals on San Nicolas Island indicate a significant reduction of growth rate in both 1983 and 1984 (Ono et al., in press). Similarly, the growth rate of male sea lion pups in the present study was not significantly different from that of female pups, although information from the larger data set revealed higher growth rates of male than of female pups in 1982, 1984, and 1985 (unpublished data). A time interval of 3 wk may be too brief to accurately assess long-term growth performance in a species characterized by infrequent suckling and periodic surges in weight. Nonetheless, mean growth rates for isotope-labeled pups were similar to population norms for these years.

Unfortunately, it is not possible to compare milk intakes in 1982 to those in 1983, when the greatest growth depression occurred in the population (Ono et al., in press) since our data represent different lactation stages in these 2 yr. Data for the first month of lactation in 1982 and in 1984 indicate that daily milk intakes were somewhat reduced in 1984, but the difference was not quite significant at the .05 level ( $P = .073$ ) unless expressed as a percentage of body weight ( $P = .039$ , table 3). No significant differences were found between 1983 and 1984 in milk intake in the second month of lactation, either on an absolute or on a percent body weight basis. Thus, our data support the hypothesis that milk intake was higher in 1982 than in the years influenced by El Niño, but relatively small sample sizes in each year and the lack of comparable data for 1982 and 1983 do not permit an accurate assessment of the magnitude of difference.

The finding that daily milk intake was not affected by age was surprising, since one would expect milk intake to increase with pup age in early lactation. Our age comparison was restricted to 1984, when El Niño effects were still evident. It may be that lactating sea lion mothers were unable to increase milk yields during early lactation owing to nutritional and environmental constraints in this year. In ungulates confined to poor pasture, milk yields do not exhibit the normal postpartum rise but rather begin to decline shortly after birth (Ofstedal 1985). Further study is needed to

determine whether milk yields of California sea lions normally increase during lactation.

California sea lions are highly polygynous and exhibit great sexual dimorphism in adult size (Peterson and Bartholomew 1967). If male offspring that rapidly attain large size have an advantage in male-male competition and hence in gaining access to many reproductive females, mothers may achieve a reproductive benefit from investing more milk energy and nutrients in male than in female offspring. The milk intake of male sea lion pups was in fact greater than that of female pups, but the sex difference disappears if milk intake is expressed as a percentage of body weight (tables 3, 4). This raises the question of causality: do lactating females invest more in males to promote greater growth rates or are males simply more successful at obtaining milk owing to larger size from birth (Boness et al. 1983, and unpublished data)? A similar pattern of milk intake has been reported in the northern fur seal (Costa and Gentry 1986): male pups consume more milk than females on an absolute basis but not in relation to body weight.

Daily milk intake in the present study encompasses a 3-wk study period and thus includes periods of maternal presence and absence. Given that the maternal feeding/nursing cycle is of about 4 days' duration on average (Boness et al. 1985, and unpublished data), the study period was equivalent to about five cycles. Male and female sea lion pups consumed about 3.0 kg and 2.6 kg milk per period of maternal presence, respectively. Northern fur seals have longer cycles—of about 8 days' duration (Gentry and Holt 1986)—but the amounts of milk consumed by pups per period of maternal presence (4.3 kg for males and 2.6 kg for females; Costa and Gentry [1986]) are similar to those of sea lion pups of the same age. Pups of the northern fur seal are smaller but suckle less frequently than California sea lion pups; if milk intakes are averaged over the entire maternal cycle, they represent a similar proportion of body weight in both species (about 5.4% per day in northern fur seals vs. 6.0%–7.8% per day in California sea lions). These milk intakes are very low by comparison to typical values of 10%–25% per day for offspring of terrestrial mammals at peak lactation (Of-

tedal 1981, 1984b) but are compensated for by the high energy density of milks of sea lions and fur seals (Ofstedal et al. 1983; Costa and Gentry 1986).

Energy intakes are best compared among species on a metabolic size basis to account for effects of body mass (Brody 1945; Kleiber 1975). While the energetics of adult mammals scale to body weight (kg) to the 0.75 power, in suckling neonates of terrestrial species, the scaling factor for energy intake has been determined to be  $0.83 \pm 0.013$  ( $n = 15$  species) when compared at peak lactation (Ofstedal 1981, 1984b). Although the appropriate scaling factor for young otariid pups is not known, data have been expressed in relation to  $W^{0.83}$  to facilitate interspecies comparison. Gross energy intakes ( $\text{kcal} \cdot \text{day}^{-1}$ ) of sea lion pups averaged  $361 \cdot W^{0.83}$  in the first month and  $308 \cdot W^{0.83}$  in the second month. These values are 60% and 37% higher than the value predicted for suckling young of terrestrial species at peak lactation,  $225 \cdot W^{0.83}$  (Ofstedal 1984b), but considerably lower than reported energy intakes of phocid pups (Ortiz et al. 1984; Costa et al. 1986; Tedman and Green, in press; Ofstedal et al. 1987). The reported daily energy intake of northern fur seals in the first 2 mo postpartum ( $372 \cdot W^{0.83}$ ) is quite similar to that of California sea lion pups, in part owing to the higher energy content ( $4.76 \text{ kcal} \cdot \text{g}^{-1}$ ) of northern fur seal milk at this lactation stage (Costa and Gentry 1986).

#### MAINTENANCE REQUIREMENTS FOR MILK ENERGY

The energy intake of a young animal must cover requirements for both maintenance and growth. Maintenance refers to an equilibrium condition in which energy is neither stored nor withdrawn from body stores and is thus equivalent to the energy required for metabolic processes, including those associated with activity and thermoregulation (Brody 1945). Although a growing animal is never strictly at maintenance, an estimate of maintenance requirements can be obtained by regression of energy retention on energy intake and extrapolation to zero retention (Blaxter and Wood 1952; Van Es 1972; CAB 1980; Hudson and Christopherson 1985). Since energy retention is closely correlated to weight gain, gain

can be used as a first estimate of energy retention in the absence of direct data on changing body energy content (Hudson and Christopherson 1985).

In the present study maintenance requirements for gross energy ( $\text{kcal} \cdot \text{day}^{-1}$ ) were predicted to increase from  $168 \cdot W^{0.83}$  in the first month to  $252 \cdot W^{0.83}$  in the second month (fig. 2), values equivalent to 47% and 82% of total energy intake in these 2 mo, respectively. Given the considerable scatter about the regression lines (fig. 2), these estimates cannot be considered precise. The predicted maintenance requirement for the first month represents extrapolation beyond the range of measured values and may therefore be less reliable than the second-month estimate. These maintenance requirements for gross energy are considerably higher than estimated values for domestic calves (about  $83 \cdot W^{0.83}$ ; data of Roy 1980) and lambs ( $130 \cdot W^{0.83}$ ; data of Jagusch and Mitchell 1971) in the first month postpartum.

High maintenance requirements of sea lion pups could stem from elevated resting metabolic rates or from energetic demands associated with activity and thermoregulation. Although the resting metabolic rates of young sea lion and other otariid pups are high, they fall within the expected range for young animals (Lavigne et al. 1986; Thompson et al., in press). The daily resting metabolic rate of second-month sea lion pups is  $137 \cdot W^{0.83}$  or 54% of maintenance in the second month. Assuming that 5% of ingested milk energy is lost in urine and feces (Jagusch and Mitchell 1971; Roy 1980), the remaining 40% must be primarily due to the energetic costs of activities and thermoregulatory responses that pups must bear even if insufficient energy is available to support growth. An increase in activity and time spent in water as pups mature is the most likely explanation for the large increases in estimated maintenance requirement from the first to second month. Available evidence suggests that ambient water temperatures at San Nicolas Island (12–15 C) are below thermoneutrality for sea lion pups such that heat losses owing to conductance and evaporation during and after submergence must be great (Thompson et al., in press).

The increased proportion of energy in-

take devoted to maintenance in the second month may reflect the effects of El Niño on energy intake as well as changes in maintenance requirements with age. Both growth rates and activity levels of pups were reduced in 1983 and 1984 (Ono et al., in press), indicating that pups curtailed these energetically expensive processes in the face of reduced availability of milk energy. Swimming time was not reduced, however, perhaps because development of swimming skills is required for self-feeding and may be too critical to curtail (Ono et al., in press). If energy intakes of pups are higher in normal years than they were in 1983 and 1984, maintenance will constitute a smaller proportion of total energy intake than our data indicate.

The high maintenance requirements and slow growth rates of sea lion pups by comparison to terrestrial mammals result in a low efficiency in the conversion of milk energy to energy in mass gain. The mean energy intake of sea lion pups was equivalent to 22.7 kcal per g gain, while energy deposition was calculated as 3.7 kcal per g gain, assuming energy equivalents of 9.3 kcal per g fat and 5.65 kcal per g protein

in gain (Brouwer 1965). Thus, the gross efficiency of energy deposition was only 16% in sea lions, as compared to 26%–34% for foals, lambs, puppies, and mink kits at 3–4 wk postpartum (Ofstedal 1981). By contrast, phocid pups that are depositing large amounts of blubber would be expected to have high gross efficiencies. Costa et al. (1986) estimate that 82% of milk energy is deposited in tissue stores by northern elephant seal pups.

In conclusion, despite the relatively high rate of energy transfer from mother to pup in the California sea lion, a large proportion of this energy is required for maintenance and relatively little is deposited in growth. Given the spatial separation of foraging sites from rookeries, and the need to store milk secreted during maternal foraging trips in mammary glands of finite capacity (Ofstedal et al. 1987), lactating otariid females may be limited in their ability to increase energy investment rate in offspring and thereby increase growth efficiency. By contrast, lactating phocids typically remain with or near their pups, refrain from feeding, and achieve phenomenal rates of energy transfer (Ofstedal et al. 1987).

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