

Seasonal Variability in Otariid Energetics: Implications for the Effects of Predators on Localized Prey Resources

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ABSTRACT

Otariids, like other wild mammals, contend with a wide variety of energetic demands across seasons. However, due to the cryptic behaviors of this marine group, few studies have been able to examine longitudinal energetic costs or the potential impact of these costs on seasonal or annual prey requirements. Here we evaluated the changes in energy demand and intake of female California sea lions (*Zalophus californianus*) during reproductive ($n = 2$ sea lions) and nonreproductive ($n = 3$) periods. Monthly measurements included resting metabolic rate, blood hormone levels, body condition (blubber thickness and body mass), and caloric intake for adult sea lions throughout molting, late pregnancy, lactation, and postweaning. We found that maintenance energy demands decreased from 32.0 to 23.1 MJ d⁻¹ before pupping, remaining stable at 19.4 ± 0.6 MJ d⁻¹ during lactation and postweaning. Energy intake rates to meet these demands showed marked changes with activity level and the reproductive cycle, reaching a peak intake of 3.6 times baseline levels during lactation. Translating this into prey demands, we find that 20,000 reproductively active females on San Nicolas Island rookeries would maximally require 4,950 metric tons of Pacific whiting during a month of the breeding season. This localized impact is reduced significantly with post-breeding dispersal and demonstrates the importance of considering spatial and temporal factors driving the energetic re-

quirements of predators when designing marine protected areas.

Introduction

To survive, wild adult animals must contend with a wide variety of energetic demands that can change markedly between seasons and years (McNab 2002). For marine mammals, the foundation of these demands is represented by basal or maintenance requirements on which the costs associated with thermoregulation, activity, assimilation of food, growth, and reproduction may be overlaid (Costa and Williams 1999). Of these, reproductive costs pose extraordinary prolonged demands in some species, particularly while provisioning for young (Costa et al. 1986). For example, the fasting, lactating gray seal (*Halichoerus grypus*) maintains one of the highest sustained rates of energy expenditure measured for any wild mammal to date (Mellish et al. 2000). This marine mammal sustains a daily energetic expenditure that is 7.4 times basal values for several weeks. By comparison, maximum-intensity exercise in mammals result in levels of energy expenditure that are six to 10 times basal rates but can be maintained only for a few minutes (Taylor et al. 1980; Brooks et al. 2000).

Because pinnipeds exhibit marked behavioral differences in provisioning for young (Costa 1991), the extraordinary daily energetic expenditure reported by Mellish et al. (2000) for a phocid seal may not be observed for other pinniped groups. Unlike phocid seals, the otariids (sea lions and fur seals) exhibit a comparatively long period of pup dependency potentially resulting in a prolonged annual pattern of energy demand. For one temperate region otariid, the California sea lion, seasonal energetic demands include a suite of overlapping costs associated with the reproductive cycle (Fig. 1). In adult female sea lions, this involves breeding in June–July, delayed implantation of the embryo, and a 9-mo gestation period from October through May to early July. Following birth of a single pup is a period of offspring dependency and lactation that may last 10–12 mo (Heath 2002). A consequence of this prolonged period of pup dependency is a period greater than 8 mo during which reproductively active sea lions are simultaneously pregnant and lactating (Fig. 1).

Other energetic challenges, in addition to these maintenance and reproductive costs, are the protein requirements and energy expended during an annual molt (Noren et al. 2003). For Cal-

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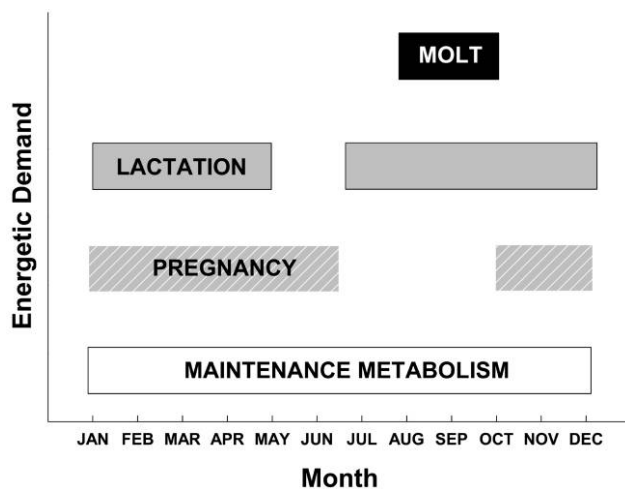


Figure 1. Annual energetic demands during the reproductive cycle for adult female California sea lions. Length of the bars denotes the months during which each energetic event occurs. Note that exact dates for implantation at the initiation of pregnancy, birth, weaning, and molt may vary among individuals. Details are provided in the text.

ifornia sea lions, the molt may be spread across several months during August–November (Berta and Sumich 1999; Yochem and Stewart 2002). The energetic consequences of this hair loss and replacement as well as the impact of these on reproductive costs are unknown for this species. However, for another California pinniped, the elephant seal (*Mirounga angustirostris*), molting costs represent a significant energetic demand in adults (Worthy et al. 1992) as well as pups (Noren et al. 2003), in which molting accounts for 9%–16% of the total energy lost during fasting.

In contrast to other mammalian species (see Kurta et al. 1989; Renouf and Gales 1994; McNab 2002) and despite a reasonable understanding of the timing of reproductive and nonreproductive events for sea lions, little is known regarding the accompanying annual cycle of energetic costs for otariids. This is due in part to the mobility and cryptic at-sea behaviors of these animals, which make long-term energetic measurements difficult. To circumvent this problem and provide insight regarding seasonal energy requirements of an otariid, we assessed longitudinal changes in energy demand and intake of reproductive and nonreproductive California sea lions in captivity. Resting metabolic rate, food consumption rate, body condition (body mass, lean and lipid masses, blubber thickness), and serum hormone (estrogen, progesterone) concentrations were measured monthly before, during, and after pregnancy and lactation. These values were compared with similar measurements made for a nonreproductive group. Using the relative changes in energetic requirements for each period, we were able to compare the likely seasonal changes in the amount

of fish necessary to support a population of sea lions at a rookery in Southern California.

Material and Methods

Experimental Design

The study was conducted at Long Marine Laboratory (University of California, Santa Cruz) from July 2002 to May 2004 to include natural seasonal nonreproductive, molting, pregnancy, lactation, and weaning periods of California sea lions. Measurements were taken monthly for sea lions that were in either a nonreproductive or a reproductive group. Parameters included resting metabolic rate measured in triplicate for each month, daily caloric intake, serum progesterone and estrogen concentrations, and body condition (fat mass and lean mass). As a result of animal availability, measurements were conducted across 13 sequential months for the reproductive group and 18 mo for the nonreproductive group. Monthly veterinary blood panels included reproductive hormone analyses (Greig et al. 2007). Morphometrics (body mass, length, and girth) and ultrasound examination (SonoSite, Bothell, WA) of uterine and fetal condition as well as ovary diameter (T. M. Williams, unpublished data) were also used to evaluate the health and reproductive status of the subjects each month. Milk samples were taken monthly from lactating females during the period of nursing. Veterinary, hormonal, and body condition evaluations were conducted for each animal within 2–14 d of the corresponding metabolic measurements.

Animals

Five adult, female California sea lions (*Zalophus californianus*) were used in these studies. Three captive trained animals (nonreproductive group, body mass = 89.2 ± 0.8 kg) on loan from a zoological park (Brookfield Zoo, Brookfield, IL) were neither pregnant nor lactating during the study period. Two wild sea lions (reproductive group, body mass = 98.3 ± 1.6 kg) from a rookery on San Nicolas Island (California) were transferred to Long Marine Laboratory. The wild animals were 5 mo pregnant at the time of transfer and successfully bore, nursed, and weaned their pups during the course of the study. All sea lions were housed in saltwater pools maintained at local ambient water temperatures ($T_{\text{water}} = 11.2^{\circ}\text{--}20.4^{\circ}\text{C}$) and provided with access to dry haul-outs. General activity patterns and behavior of each animal, including proportion of the time hauled out or swimming, were recorded by observers in a daily log during daylight hours. The animals were fed daily a mixed fish diet (herring and capelin) supplemented with multivitamins (Mammal-Tab, Mazuri, Richmond, IN). All procedures involving the animals were approved by the University of California, Santa Cruz, Animal Care and Use Committee before initiation of the study.

Body Condition

Monthly assessments of body condition included measuring total body mass (Altralite platform scale, Rice Lake Weighing Systems, Rice Lake, WI) and standard length and girth. Lipid mass and lean mass were also assessed by the stable isotope dilution method using deuterium oxide (Pace and Rathbun 1945; Webb 1999). Isotope delivery depended on the training status of the animal. Following an initial blood sample, an intramuscular injection of sterile deuterium-labeled water (99.9% deuterium oxide, 0.05 g kg⁻¹ body mass; Sigma-Aldrich) was given to each sea lion in the reproductive group. For the nonreproductive animals, deuterium oxide was administered orally using a gelatin capsule (12EL, Torpac, Fairfield, NJ) hidden in a single weighed herring. Labeled water was added to the capsule from a pre- and postweighed syringe. Water contributed by the fish, determined by freeze-drying sample fish from the same lot, was subtracted from subsequent calculations. For all sea lions, final blood samples were drawn after a 3-h equilibration period (Costa 1987) and frozen until analysis at Metabolic Solutions (Nashua, NH) via isotope ratio mass spectrometry. Enrichment relative to standard mean ocean water was used to determine the dilution space of the animal and corrected by 1.7% to account for the overestimation of total body water (TBW) using deuterium oxide (Arnould et al. 1996). Lean tissue hydration was assumed to be the same as adult female Antarctic fur seals (*Arctocephalus gazella*), 70.7%, as this is the most closely related species for which this has been measured (Arnould et al. 1996). Using this value, we calculated mass of total body lipid (TBL in kg) as

$$\text{TBL} = M_b - 1.41\text{TBW},$$

where M_b is body mass (kg) and TBW is total body water (kg; Pace and Rathbun 1945). Values of total body lean tissue and percentages were subsequently calculated using TBL.

Fat deposition was evaluated by measuring blubber thickness of the animals each month using a scanning ultrasound machine (Sonosite). For these measurements the thickness of the subdermal blubber layer between the skin and skeletal muscle was measured in triplicate dorsally, ventrally, and laterally at the level of the neck, at the axillary region at the insertion of the fore flipper, and at maximum abdominal girth, according to standard protocols developed for otariid morphometrics (T. M. Williams, unpublished data). The reproductive sea lions were sedated for these measurements using isoflourane (Forane, Zeneca Pharma, Mississauga, Ontario) and oxygen. The nonreproductive group was trained to lie quietly on a deck without sedation during the measurements.

Metabolic Rate

Metabolic rate was measured using open-flow respirometry for sea lions resting in water. Details of the respirometry system for marine mammals have been described previously (Williams et al. 2001). During the respirometry tests, sea lions were placed in a saltwater pool (183 cm long × 119 cm wide × 91 cm deep, $T_{\text{water}} = 16.1^{\circ}\text{--}16.4^{\circ}\text{C}$) covered with a Plexiglas metabolic hood (138 cm long × 91 cm wide × 38 cm high) mounted on the water surface. A parallel thermoregulation study with the same animals showed that these water temperatures were within the sea lions' thermal neutral zone (lower critical temperature <10°C; H. Mostman-Liwanag, unpublished data).

Air was drawn through the dome with a vacuum pump (Sable Systems, Henderson, NV) and monitored electronically. Flow rates were adjusted so that the fractional concentration of oxygen in the respirometry chamber remained above 0.2000 and averaged 255 L min⁻¹. Samples of the air from the exhaust port were dried (Drierite, Hammond Drierite, Xenia, OH) and scrubbed of carbon dioxide (Sodasorb, Chemetron, St. Louis, MO) before entering the oxygen analyzer (Sable Systems). The percentage of oxygen in the exhaust air was monitored continuously during the experiments and recorded with a personal computer using Sable Systems software. The output from the oxygen analyzer was monitored every second and averaged each minute. These values were converted to rates of oxygen consumption ($\dot{V}O_2$) using previously developed equations (Fedak et al. 1981; Davis et al. 1985) and an assumed respiratory quotient of 0.77. The lowest value of $\dot{V}O_2$ averaged over 10–30 min during each 20–60-min experimental session was used in the analysis of resting metabolic rate. All values were corrected to STPD, and the entire system was calibrated before and after the tests with ambient air and nitrogen gas according to Fedak et al. (1981).

The sea lions were fasted overnight before the measurements and therefore were considered postabsorptive. Metabolic measurements for three independent trials conducted on nonsequential days were averaged for each sea lion per month. Monthly values for the reproductive and nonreproductive groups are reported.

Caloric and Energy Intake

Energy intake of each sea lion was calculated from daily feeding records and the caloric value of fish in the diet. The animals were fed in multiple sessions (2–8 meals day⁻¹) depending on reproductive status, behavior, and maintenance of body mass. Additional meals were provided if the animals maintained interest in feeding or if body mass declined by >10% in 1 mo. Comparisons of length/girth ratios to those of wild California sea lions at San Nicolas Island and Monterey Bay (T. M. Williams, unpublished data) were used to avoid overfeeding. At each meal, each sea lion was fed independently until satiated.

Total amount of fish offered and consumed was based primarily on the feeding behavior/attitude of the sea lion. The mass and type of fish (herring or capelin) ingested were recorded for each meal and subsequently summed for each day. Daily summaries were averaged over each month and then converted to caloric equivalents for each fish type.

Caloric value and water content were determined using adiabatic bomb calorimetry (1341 Oxygen Combustion Bomb, Parr Instrument, Moline, IL) on samples of fish taken periodically throughout the study period. Sample analyses followed the procedures of Williams et al. (2004) where frozen fish were ground whole, subdivided into three aliquots, and freeze-dried to a constant mass over 48 h. Dried subsamples (approximately 1 g) were pulverized, compressed into pellets, and immediately analyzed. The calorimeter was calibrated between samples using benzoic acid standards and was accurate to 0.1%. The resulting caloric value for each dry tissue sample was converted to wet mass energy values using a conversion factor of 4.186 J cal^{-1} , and water content was determined from the difference between initial and final subsample mass during drying.

Blood Samples for Health and Reproductive Status Evaluations

Blood samples were taken each month from the caudal gluteal venous plexus and used for general health screening as well as evaluation of serum hormone levels to assess reproductive status of each animal. Samples for the hormonal analyses were placed in sterile tubes (Vacutainer, BD, Franklin Lake, NJ) and immediately centrifuged for 5 min, and the serum was subdivided for archiving and analysis. Samples were either analyzed immediately or stored at -80°C for less than 6 mo. Hormonal analyses on the subsamples were conducted at both commercial (Antek Diagnostics, San Francisco, CA) and noncommercial (Greig et al. 2007) laboratories to cross-check for accuracy.

Statistics

Relationships between metabolic rate and water temperature or serum hormone concentrations were determined by least squares linear regressions using statistical software (SigmaStat 2000, Jandel Scientific Software, San Rafael, CA). A two-way ANOVA (SYSTAT, SPSS) was run to test differences in metabolic rates between reproductive and nonreproductive groups between time periods (pregnant, lactating, and postweaning) and to evaluate potential interactive effects. Similarly, a two-way ANOVA (Tukey test) was used to assess differences in the body mass during prebirth and postbirth periods for the two groups. The effect of molt on metabolic rate within each group was determined by comparing metabolic rates measured during August–September (peak molt period) with rates for October–November (postmolt period). Because the test for normality failed, a Mann-Whitney nonparametric test was used. Interannual differences in metabolic rate for nonreproductive sea

lions were determined by standard *t*-tests (Zar 1974). All means for metabolic rate, total body mass, blubber thickness, energy and caloric intake, and reproductive hormones are reported as ± 1 SEM unless otherwise noted.

Results

Body Condition

Total body mass ranged from 71.1 to 108.0 kg in the nonreproductive group and from 85.5 to 117.1 kg for the reproductive sea lions during the study. Body mass, lipid mass, and blubber thickness showed similar general trends across months for both groups of sea lions, with a few notable exceptions (Fig. 2). From January, body mass increased to a peak level in May

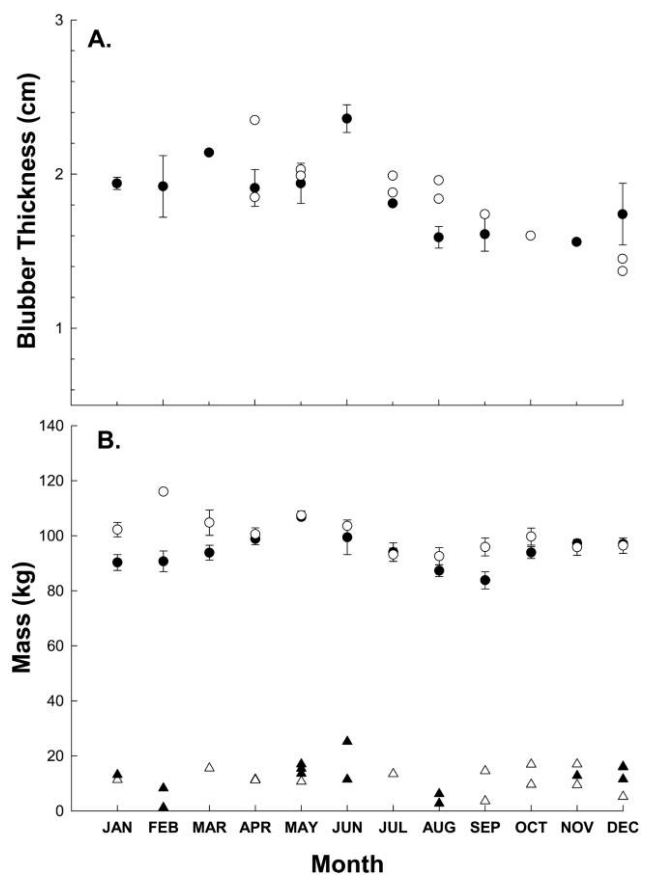


Figure 2. Seasonal changes in body condition for reproductive (*open symbols*) and nonreproductive (*solid symbols*) California sea lions. Blubber thickness in the lateral axillary area (A) as well as body mass and lipid mass (B) are compared for each month. In B, total body mass is shown by the circles, while lipid mass is shown by the triangles. Mean values ± 1 SEM are shown by the symbols and lines; $n = 3$ sea lions in the nonreproductive group, and $n = 2$ sea lions in the reproductive group, with four body mass measurements per month each. Symbols with no error bars represent the average value for each month for an individual. Note that the difference between total body mass and lipid mass is the lean body mass of the animal.

and was followed by a 13.8% (reproductive group) to 21.6% (nonreproductive group) decline to the lowest level during the molt in August to September. Body mass gradually increased during the winter months. An exception to this general trend occurred during the postweaning period (January–February) for the reproductive group in which body mass showed a marked elevation compared with the nonreproductive group (Fig. 2B). In a two-way ANOVA evaluating mean body mass of reproductive and nonreproductive groups during January–June before birth of the pup and during the July–December postbirth period, the effects of reproductive status ($F_{1,20} = 8.697$, $P = 0.008$) and of period ($F_{1,20} = 11.906$, $P = 0.003$) were highly significant, while the interaction between the two was not ($F_{1,20} = 1.834$, $P = 0.191$).

We found that the presence of milk resulted in inconsistent blubber thickness values for the ventral measurement sites. Therefore, we report the data for one representative, easily accessible site outside of the area of the mammary tissues. Blubber thickness in the lateral axillary area (Fig. 2A) and to a lesser extent lipid mass (Fig. 2B) reflected the patterns in body mass with season; that is, the highest values occurred during May–June and the lowest values during the period of molt. Lipid mass ranged from 3.5% to 23.9% of total body mass for nonreproductive sea lions and from 4.0% to 17.4% for the reproductive group. Consequently, lean body mass calculated from the difference between total body mass and lipid mass ranged from 64.9 to 91.0 kg in the nonreproductive group and from 76.4 to 101.6 kg for the reproductive sea lions.

Metabolic Rate and Energy Demand

Both nonreproductive and reproductive groups showed a consistent 17%–18% decline in resting metabolic rate from the beginning to the end of the study period (Fig. 3) that was attributed in part to training effects. This was demonstrated by comparing the metabolic rates of the nonreproductive group during January–April in sequential years. Resting metabolic rate for this period was 8.48 ± 0.27 mL O₂ kg⁻¹ min⁻¹ ($n = 4$ mo) in 2003 and 6.47 ± 0.17 mL O₂ kg⁻¹ min⁻¹ ($n = 4$) in 2004, representing a 23.7% decline that correlated with the behavioral consistency of the animals in the metabolic chamber.

With our recognition that approximately 2% of the decrease in metabolic rate observed per month could be attributed to training effects as shown above, California sea lions resting in water showed little variation in metabolism with reproductive status (Fig. 3). In a two-way ANOVA, the effect of period was significant ($F_{2,162} = 18.932$, $P < 0.001$) for both groups, while the period by reproductive status interaction term was not ($F_{2,162} = 1.898$, $P = 0.153$). Average metabolic rate for the reproductive group was 7.53 ± 0.33 mL O₂ kg⁻¹ min⁻¹ during late pregnancy (May–July), 6.87 ± 0.13 mL O₂ kg⁻¹ min⁻¹ during lactation (August–January), and 5.94 ± 0.20 mL O₂ kg⁻¹ min⁻¹ during the postweaning period (February–May). Values

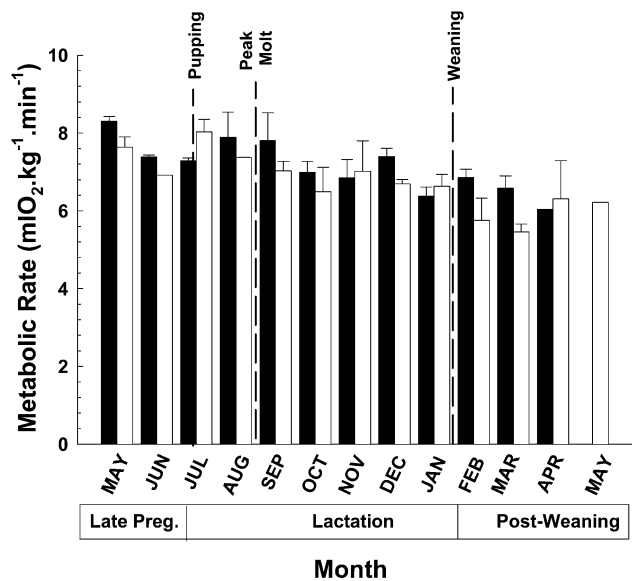


Figure 3. Resting metabolic rate in relation to month for adult California sea lions. Reproductive (open bars, $n =$ mean values for three monthly measurements for two sea lions) and nonreproductive (solid bars, $n =$ mean values for three monthly measurements for three sea lions) animals are compared. Height of each bar represents the mean + 1 SEM. Bars with no error lines are months in which only one animal was measured. Data span from May 2003 to May 2004 and include late pregnancy, birth, lactation, and weaning for the reproductive animals. Vertical dashed lines indicate the timing of major energetic events observed for the sea lions in this study.

for the nonreproductive group were 7.66 ± 0.32 , 7.22 ± 0.24 , and 6.49 ± 0.24 mL O₂ kg⁻¹ min⁻¹ for the same periods and were not statistically ($F_{1,162} = 2.243$, $P = 0.136$) different from metabolic rates measured for the reproductive group. These trends for resting metabolic rate were independent of seasonal changes in ambient water temperatures ($n = 143$, $r^2 = 0.003$, $P = 0.364$) that ranged from 11.2°C to 20.4°C during the study.

The highest recorded resting metabolic rate for the nonreproductive sea lions was measured during the period of molting (August–September) and averaged 10.31 ± 0.40 mL O₂ kg⁻¹ min⁻¹ ($n = 6$). This value was 1.3 times higher than that measured during the postmolt period. In contrast, there was no statistical difference (Mann-Whitney U -test, $U = 21$, $P = 0.486$) between resting metabolic rates of the reproductive sea lions during and immediately after molting.

Translating these metabolic rates into maintenance energy demand (using a conversion factor of 4.8 kcal L O₂⁻¹ and 4.186 J cal⁻¹), we find that the last trimester of pregnancy resulted in a decline in energy demand for the two reproductive sea lions (Fig. 4A). Maintenance energy demand decreased from an average of 7,644 kcal d⁻¹ (32.0 MJ d⁻¹) to 5,512 kcal d⁻¹ (23.1 MJ d⁻¹) in the weeks before pupping. Maintenance energy demand of these animals remained stable throughout the period

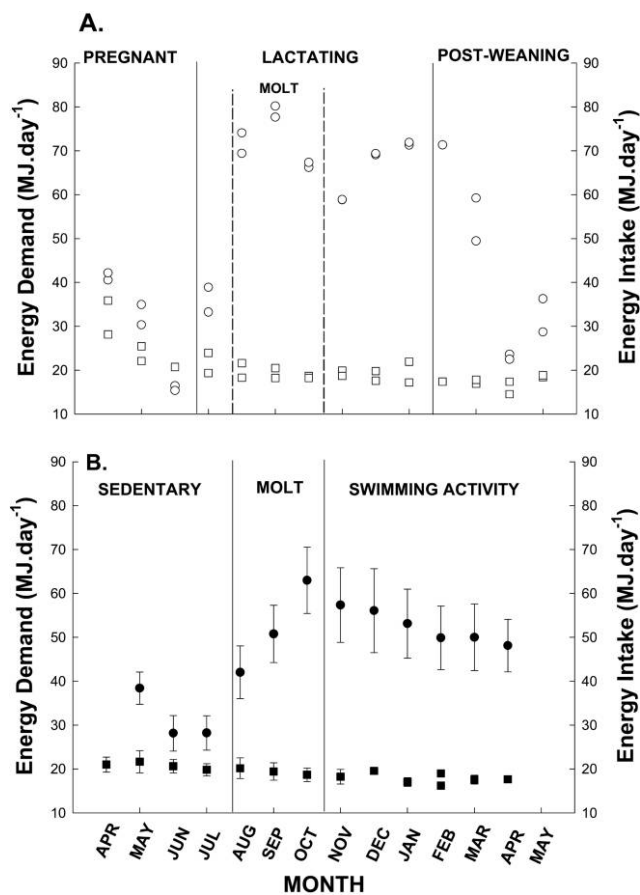


Figure 4. Daily energy demand (*squares*) and energy intake from fish ingestion (*circles*) in relation to month during different reproductive and activity stages of California sea lions. Each point represents the average monthly value for individual sea lions. Results for two reproductive individuals (*A*, *open symbols*) are shown during the last trimester of pregnancy, lactation, and pup weaning. The period between the dashed black lines indicates when the reproductive animals were simultaneously lactating and molting. These values are compared with those of three nonreproductive sea lions (*B*, *solid symbols*) during different levels of activity and molt. Symbols and error bars in *B* denote mean ± 1 SEM for $n = 3$ sea lions. Note in particular the marked increase in energy intake during lactation and activity despite little change in the maintenance energy demand of the females.

of lactation and postweaning, averaging $4,639 \pm 152$ kcal d⁻¹ (19.4 ± 0.6 MJ d⁻¹; $n = 21$) over 11 mo. The average value for the nonreproductive group (Fig. 4B) was similar over the same period at $4,380 \pm 85$ kcal d⁻¹ (18.3 ± 0.3 MJ d⁻¹; $n = 30$).

Caloric and Energy Intake

Unlike maintenance energy demands, energy intake to meet basic metabolic demands based on daily fish consumption showed marked changes with activity level as well as with the reproductive cycle, particularly during lactation and postwean-

ing (Fig. 4). For the two reproductively active sea lions, energy intake during the last trimester of pregnancy and late postweaning ranged from 0.8 to 2.0 times the maintenance energy demand. Mean energy intake from fish ingestion during these periods was $42.0\% \pm 28.0\%$ ($n = 9$ feeding periods) higher than the measured energy demand determined from metabolic rate, which likely represents the minimum maintenance energy intake for a sedentary sea lion (Fig. 4A). Similarly, minimum energy intake for the nonreproductive sea lions, which occurred during June–July when the animals tended to haul out, was $38.3\% \pm 0.01\%$ ($n = 6$ feeding periods) higher than maintenance energy demands (Fig. 4B).

Energy intake for the reproductive group increased markedly during peak lactation (August–January). During this 6-mo period, energy intake of the two sea lions reached a maximum of $18,546$ kcal d⁻¹ (77.6 MJ d⁻¹); mean energy intake was 3.6 ± 0.4 ($n = 12$) times the maintenance energy demand for this time period. Energy intake of the reproductive group declined to prelactation levels within 2 mo of weaning their pups. The nonreproductive group also showed an increase in energy intake during August–January but for different reasons. Energy intake increased markedly during the period of molt (August–October). Maximum intake during October was $15,042 \pm 1,811$ kcal d⁻¹ (63.0 ± 7.6 MJ d⁻¹), approximately 3.4 times the maintenance energy demand. Following this period, as temperatures decreased during the winter months, the nonreproductive sea lions tended to increase swimming activity, resulting in a concomitant increase in energy intake. Maximum swimming activity occurred during November–March following the period of molt and corresponded to the highest energy intakes. On average, the increased activity resulted in an $89.1\% \pm 0.1\%$ ($n = 5$ mo) increase in energy intake over minimum levels.

Reproductive Hormones

Serum progesterone concentration changed with reproductive status of the California sea lions and averaged 15.27 ± 2.06 ng mL⁻¹ ($n = 16$) during the year for reproductive animals and 10.72 ± 1.70 ng mL⁻¹ ($n = 21$) for nonreproductive animals, including one aged female that we discovered was anoestrous (mean progesterone levels = 2.50 ± 0.42 ng mL⁻¹; $n = 13$). Conversely, serum estrogen concentration was lowest for the reproductive group (range = 0.75 – 1.85 ng mL⁻¹) compared with the nonreproductive group (range = 1.26 – 4.82 ng mL⁻¹), which included the aged female (range = 1.30 – 3.13 ng mL⁻¹). Seasonal changes occurred in these hormones and are reported elsewhere (Greig et al. 2007).

For females in the nonreproductive group, metabolic rate was positively correlated with serum progesterone concentration but not estrogen concentration (Fig. 5). For all three sea

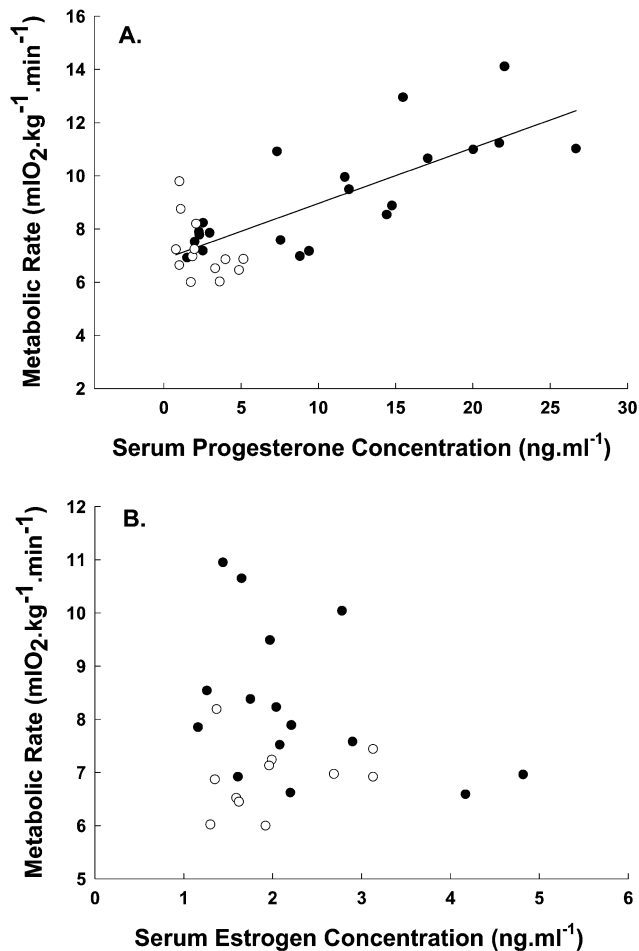


Figure 5. Resting metabolic rate in relation to serum progesterone (A) and estrogen (B) concentration of nonpregnant, nonlactating California sea lions. Each point represents the monthly averages for individual animals; reproductively viable sea lions ($n = 2$, solid circles) are compared to an aged, anoestrous female ($n = 1$, open circles). The thin black line is the least squares linear regression through the data points as described in the text.

lions comprising this group, the relationship between metabolic rate and progesterone was

$$\text{metabolic rate} = 6.87 + 0.21 \text{ progesterone}$$

($n = 34$, $r^2 = 0.59$, $P < 0.001$; metabolic rate in $\text{mL O}_2 \text{ kg}^{-1} \text{ min}^{-1}$ and progesterone concentration in ng mL^{-1}). The older female with the lowest progesterone levels maintained correspondingly low metabolic rates (Fig. 5) in a pattern similar to the simultaneous decline metabolism and reproductive hormone levels in human females (Van Pelt et al. 1997). Due to the low number of blood samples available for the reproductive group, it was not possible to determine whether a similar re-

lationship between metabolic rate and reproductive hormone concentrations occurred for pregnant and lactating animals.

Discussion

Energetic Demands and Limits in Otariids

In an earlier study, we reported that the maintenance energetic costs for a variety of marine mammal species range from 1.4 to 2.8 times that predicted for domestic terrestrial mammals of similar body mass (Williams et al. 2001). Likewise, the California sea lions here maintained resting metabolic rates that were 2.2 times Kleiber (1975) predictions for basal metabolic rates of domestic mammals and 1.2 times levels expected for carnivorous mammals (McNab 1986). A consequence of these elevated maintenance costs is a higher energetic foundation on which reproductive costs must be imposed, compared to many terrestrial mammals. However, several physiological and behavioral mechanisms appear to mitigate compounding energetic costs in reproductively active sea lions.

The basal metabolic requirements of adult female California sea lions were remarkably invariant across individuals and an annual cycle that included changes in reproductive events as well as environmental temperature (Fig. 3). Regardless of reproductive status, mean monthly metabolic rate ranged between approximately 5.0 and $9.9 \text{ mL O}_2 \text{ kg}^{-1} \text{ min}^{-1}$ and showed a 60.7%–74.2% change across seasons with the exception of one nonreproductive animal that demonstrated only a 35.8% change. Although ambient water temperatures changed by 9.2°C during the year, no subsequent changes in metabolism were recorded for nonreproductive and reproductive groups. This response was expected based on the thermal neutral zone and upper and lower critical temperatures of California sea lions in water (Liao 1990; H. Mostman-Liwanag, T. M. Williams, and R. W. Davis, unpublished data). Our findings are also consistent with the maintenance costs and reproductive metabolic overhead reported for other mammals (McNab 2002) and species of wild otariids (Costa and Gentry 1986; Perez and Mooney 1986; Costa and Trillmich 1988; Costa 1991). In another otariid, the northern fur seal (*Callorhinus ursinus*), fasting metabolic rates were similar for lactating and nonlactating females during the period of maternal attendance on rookeries, indicating little additional cost to milk synthesis (Costa and Gentry 1986). Likewise, the lactating and nonlactating California sea lions in this study demonstrated comparable maintenance metabolic rates during this period as well as throughout the year. It should be noted, however, that all of our metabolic measurements were conducted on postabsorptive animals; therefore, the cost of processing fish was not accounted for in this study.

In contrast to other phases of the life cycle, the period of molting resulted in a significant increase in resting metabolic rate for the nonreproductive sea lions; this was not observed for the animals in the reproductive group (Fig. 3). It is unlikely

that this response was due to the poor condition of the fur per se because blubber is the primary thermal barrier of California sea lions (Whittow et al. 1972). Rather, changes in the underlying subdermal blubber layer including cardiovascular, metabolic, and hormonal factors associated with molting (Berta and Sumich 1999) may have contributed to the metabolic response. During peak molt, the blubber layer along the lateral body was at its thinnest (1.61 ± 0.11 cm), and body lipid content was at its lowest (3.5%–6.5% of total body mass) for the nonreproductive sea lions (Fig. 2). Although the reproductive sea lions showed similar trends, lactating and weaning simultaneously contributed to changes in lipid stores and the insulating blubber layer during this period, making differentiation of the effects of molting difficult.

Despite the relative consistency of maintenance metabolic requirements for sea lions across seasons, energy intake to meet the added cost of reproduction and activity varied markedly during the year. As found for other mammals (Hammond and Diamond 1992), provisioning for young represented the highest energetic demand during the annual cycle for female California sea lions (Fig. 4). Sea lions in the reproductive group increased energy intake by nearly four times maintenance levels during peak lactation, sustaining this level for 6 mo as the pups grew. The 3.6-fold increase for lactating otariids is within the range of peak levels of intake reported for other lactating mammals including domestic dogs (*Canis familiaris*; Case 1999), free-ranging African lions (*Panthera leo*; Schaller 1972), and Antarctic fur seals (Costa et al. 1989), but it is nearly double that of captive bottlenose dolphins (*Tursiops truncatus*; Kastelein et al. 2002). As might be expected based on differences in the pattern of maternal provisioning, the metabolic scope associated with lactation in California sea lions was considerably less than the observed 6.0–7.4-fold increase in energetic costs for lactating phocid seals (Costa et al. 1986; Mellish et al. 2000). In addition to distinct provisioning patterns, these differences in scope for nursing otariids and phocids likely correspond to differences in the ability to utilize stored energy at parturition by each of these pinniped groups (Costa 1991).

The California sea lions in this study did not further increase energy intake in response to the elevated demands of older pups. By 6 mo of age, the energetic demands of the pups appeared to exceed the energy that could be provided solely by milk, as evidenced by a decrease in pup body mass (T. M. Williams, unpublished data). This energetic limit instigated weaning as the pups began to preferentially eat fish provided by husbandry personnel. The initiation of weaning at 6 mo was earlier than that reported for wild California sea lions in which pups remain with their mothers for up to 12 mo, nursing periodically until the birth of the subsequent pup (Heath 2002). It is unlikely that the shortened nursing period for captive pups was necessarily due to differences in the quality of the diet between wild and captive sea lions. Rather, the results suggest that energy intake from milk must be supplemented by inde-

pendent feeding on fish after 6 mo of age to maintain maximum growth. Because the provisioning of pups by females in the wild is interrupted by trips to sea (see next subsection) and inexperience makes independent foraging a slower process for wild pups compared to captive animals, supplemental nursing and consequent energetic demand on the mother may be longer in the wild than found in this study.

As suggested for other mammals by Gittleman and Thompson (1988), behavioral compensation during gestation and lactation may be an important strategy for minimizing these various energetic demands for reproductively active sea lions. A noticeable behavioral difference between the reproductive and nonreproductive sea lions in this study was the level of activity, with the former tending to be more sedentary, particularly during late pregnancy and nursing. The result was similar values for peak energy intake (3.4–3.6 times basal) for both reproductive and nonreproductive groups (Fig. 4), although the factors driving intake differed between the groups. Such factors included molting (Fig. 3) and reproductive hormone levels (Fig. 5) as well as lactation and swimming activity (Fig. 4). Similar patterns of behavioral compensation to reduce total costs have been reported for smaller reproductively active mammals. Thus, the allocation of daily energy from activity or other costly behaviors to reproduction by rats (Slonaker 1925) and bats produce nearly identical food consumption rates for reproductive and nonreproductive females (Gittleman and Thompson 1988).

Implications for the Impact of California Sea Lions on Prey Resources

The balance between energetic demand as identified above and energy intake through foraging will dictate the survival of individuals and the stability of wild populations (Stephens and Krebs 1986). By examining the underlying cycle of energetic costs associated with molting and reproduction from this study and then assigning a caloric requirement to those costs, we can evaluate how seasonal changes in prey requirements occur for wild sea lions. Figure 6 illustrates the relative amount of energy in prey required for supporting energetic costs in wild California sea lions. The cost of activity at sea and on land during initial pup rearing was based on field metabolic rates of adult *Zalophus* measured while provisioning pups (35.4 MJ d^{-1} ; Costa et al. 1991). Note that this particular field rate does not include lactation costs. For all energetic values we added a 0.42 factor to account for the difference between energy demand and actual energy intake of sea lions in this study (Fig. 4), as described in “Caloric and Energy Intake” in “Results.”

We assumed that food consumption for the sea lions was limited by a metabolic ceiling equivalent to 3.6 times maintenance levels. This ceiling was consistent with trends for food intake by lactating sea lions as well as the molting, nonreproductive animals (Fig. 4). The use of a metabolic ceiling is also consistent with the energetic-behavioral trade-offs to reduce

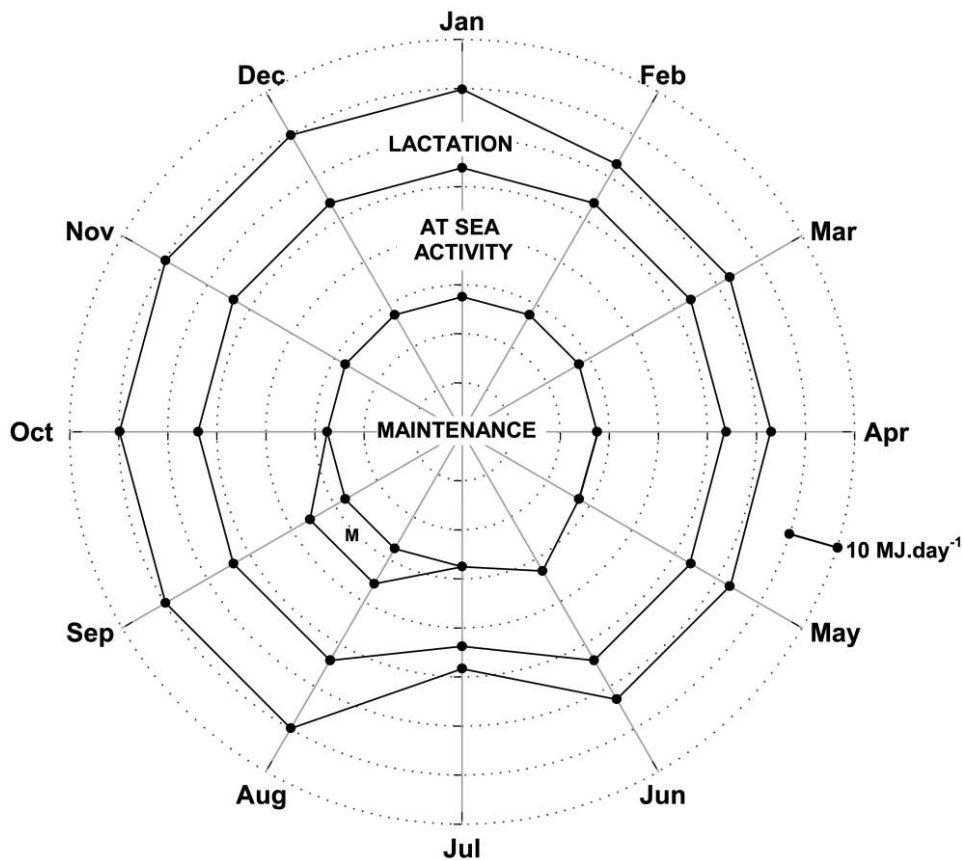


Figure 6. Predicted annual energy intake required for reproductive adult, female California sea lions. Monthly costs (radial lines) for maintenance and pregnancy events, molting (designated as *M*), at-sea activity, and lactation are shown as successive rings. Each ring gradation represents 10 MJ d⁻¹ in required energy consumption by individuals. Energy calculations for each are described in the text.

total costs observed for other lactating mammals (Gittleman and Thompson 1988). For the California sea lion, this results in a predicted maximum energy intake of 69.8 MJ d⁻¹ that is maintained until weaning for a lactating, pregnant female (Fig. 6).

The effect of these energetic requirements on local prey may be sudden and enormous when the reproductive life history of wild California sea lions is considered. For example, each year nearly 20,000 reproductively active females occupy rookeries on San Nicolas Island off of the California coast from late May to early August (Lowry 1999), during which time the animals give birth, breed, and nurse pups (Bartholomew 1951). During a single month of the breeding season in which females alternate between 4 d at sea and 3 d nursing pups on land (Costa et al. 1991), this population of females would maximally ingest 23.9×10^6 MJ in prey items ($69.8 \text{ MJ d}^{-1} \times 17.1 \text{ d at sea} \times 20,000 \text{ females}$), according to the costs identified in this study. Translating these numbers into the amount of fish required, we see that each female sea lion would consume 14.5 kg d⁻¹ of Pacific whiting (*Merluccius*

productus), a common prey item in this area (Costa et al. 1991; NMFS 1997), to support itself and its pup. This assumes a caloric value of 3.67 kJ g⁻¹ wet weight of fish and that whiting comprises 76.0% of the sea lion's diet (Costa et al. 1991). At this energetic value, the population of reproductively active sea lions around San Nicolas Island would consume more than 4,950 metric tons of whiting per month during lactation, with correspondingly lower values as the animals disperse after breeding.

Admittedly, these intake rates represent maximum values based on animals fed ad lib. in captivity. Calculations by Costa et al. (1991) using water turnover rates indicate a prey intake range of 5.0–11.7 kg d⁻¹ of mixed prey for wild sea lions provisioning pups. This difference in ingestion rates probably reflects the caloric value of prey as well as the trade-offs between foraging maximally and the timing of nursing dependent pups left on rookeries. Interestingly, this difference may explain the faster weaning times for the pups in this study compared to wild sea lion pups.

Regardless, data concerning seasonal changes in the energy

requirements of these large predatory animals allow managers to identify critical periods in life history and vulnerable segments of the population (see York 1994). Unlike phocid seals that are capable of buffering cyclic energetic events by storing energy in the form of fat (Costa 1991; McNab 2002), temperate-region sea lions with their comparatively thin blubber layers must meet immediate energy needs through prey consumption. Thus, we might expect a closer association between seasonal energetic demands and changes in foraging behavior in otariids compared to other pinnipeds. As noted for other marine predators (see Boyd and Murray 2001; Barlow et al. 2002; Boyd 2002), the spatial scale on which these energetic demands occur adds an important component to understanding the impacts of these species on localized prey resources. Management schemes that take these unique demands and limitations into account, particularly on the spatial and temporal scales used by foraging predatory animals, provide an energetic foundation on which to develop flexible marine reserves.

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Literature Cited

- Arnould J.P.Y., I.L. Boyd, and J.R. Speakman. 1996. Measuring the body composition of Antarctic fur seals (*Arctocephalus gazella*): validation of hydrogen isotope dilution. *Physiol Zool* 69:93–116.
- Barlow K.E., I.L. Boyd, J.P. Croxall, K. Reid, I.J. Staniland, and A.S. Brierley. 2002. Are penguins and seals in competition for Antarctic krill at South Georgia? *Mar Biol* 140:205–213.
- Bartholomew G.A. 1951. Spring, summer, and fall censuses of the pinnipeds on San Nicolas Island, California. *J Mammal* 32:15–21.
- Berta A. and J.L. Sumich. 1999. *Marine Mammals: Evolutionary Biology*. Academic Press, San Diego, CA.
- Boyd I.L. 2002. Estimating food consumption of marine predators: Antarctic fur seals and macaroni penguins. *J Appl Ecol* 39:103–119.
- Boyd I.L. and A.W.A. Murray. 2001. Monitoring a marine ecosystem using responses of upper trophic level predators. *J Anim Ecol* 70:747–760.
- Brooks G.A., T.D. Fahey, T.P. White, and K.M. Baldwin. 2000. *Exercise Physiology*. McGraw-Hill, New York.
- Case L.P. 1999. *The Dog: Its Behavior, Nutrition and Health*. Iowa State University Press, Ames.
- Costa D.P. 1987. Isotopic methods for quantifying energy and material intake of free-ranging marine mammals. Pp. 43–66 in A.C. Huntley, D.P. Costa, G.A.J. Worthy, and M.A. Castellini, eds. *Approaches to Marine Mammal Energetics*. Allen, Lawrence, KS.
- . 1991. Reproductive and foraging energetics of pinnipeds: implications for life history patterns. Pp. 300–344 in D. Renouf, ed. *The Behavior of Pinnipeds*. Chapman & Hall, London.
- Costa D.P., G.A. Antonelis, and R.L. DeLong. 1991. Effects of El Niño on the foraging energetics of the California sea lion. Pp. 156–165 in F. Trillmich and K.A. Ono, eds. *Pinnipeds and El Niño: Responses to Environmental Stress*. Springer, Berlin.
- Costa D.P., J.P. Croxall, and C.D. Duck. 1989. Foraging energetics of Antarctic fur seals in relation to changes in prey availability. *Ecology* 70:596–606.
- Costa D.P. and R.L. Gentry. 1986. Free-ranging energetics of northern fur seals. Pp. 79–101 in R.L. Gentry and G.L. Kooyman, eds. *Fur Seals: Maternal Strategies on Land and at Sea*. Princeton University Press, Princeton, NJ.
- Costa D.P., B.J. Le Boeuf, A.C. Huntley, and C.L. Ortiz. 1986. The energetics of lactation in the northern elephant seal, *Mirounga angustirostris*. *J Zool (Lond)* 209:21–34.
- Costa D.P. and F. Trillmich. 1988. Mass changes and metabolism during the perinatal fast: a comparison between Antarctic (*Arctocephalus gazella*) and Galapagos fur seals (*Arctocephalus galapagoensis*). *Physiol Zool* 61:160–169.
- Costa D.P. and T.M. Williams. 1999. Marine mammal energetics. Pp. 176–217 in J. E. Reynolds III and S. A. Rommel, eds. *Biology of Marine Mammals*. Smithsonian Institution, Washington, DC.
- Davis R.W., T.M. Williams, and G.L. Kooyman. 1985. Swimming metabolism of yearling and adult harbor seals, *Phoca vitulina*. *Physiol Zool* 58:590–596.
- Fedak M.A., L. Rome, and H.J. Seeherman. 1981. One-step N₂ dilution technique for calibrating open-circuit O₂ measurement systems. *J Appl Physiol* 51:772–776.
- Gittleman J.L. and S.D. Thompson. 1988. Energy allocation in mammalian reproduction. *Am Zool* 28:863–875.
- Greig D.J., K. Mashburn, M. Rutishauser, F. Gulland, T. Wil-

- liams, and S. Atkinson. 2007. Seasonal changes in circulating progesterone and estrogen concentrations in the California sea lion (*Zalophus californianus*). *J Mammal* 88:67–72.
- Hammond K. and J. Diamond. 1992. An experimental test for a ceiling on sustained metabolic rate in lactating mice. *Physiol Zool* 65:952–977.
- Heath C.B. 2002. California, Galapagos, and California sea lions. Pp. 180–186 in W.F. Perrin, B. Wursig, and J.G.M. Thewissen, eds. *Encyclopedia of Marine Mammals*. Academic Press, San Diego, CA.
- Kastelein R.A., N. Vaughan, S. Walton, and P.R. Wiepkema. 2002. Food intake and body measurements of Atlantic bottlenose dolphins (*Tursiops truncatus*) in captivity. *Mar Environ Res* 53:199–218.
- Kleiber M. 1975. *The Fire of Life*. Krieger, Huntington, NY.
- Kurta A., G.P. Bell, K.A. Nagy, and T.H. Kunz. 1989. Energetics of pregnancy and lactation in free-ranging little brown bats *Myotis lucifugus*. *Physiol Zool* 62:804–818.
- Liao J.A. 1990. An Investigation of the Effect of Water Temperature on the Metabolic Rate of the California Sea Lion (*Zalophus californianus*). MSc diss. University of California, Santa Cruz.
- Lowry M.S. 1999. Counts of California sea lion (*Zalophus californianus*) pups from aerial color photographs and from the ground: a comparison of two methods. *Mar Mammal Sci* 15:143–158.
- McNab B.K. 1986. The influence of food habits on the energetics of eutherian mammals. *Ecol Monogr* 56:1–19.
- . 2002. *The Physiological Ecology of Vertebrates*. Comstock, Ithaca, NY.
- Mellish J.E., S.J. Iverson, and W.D. Bowen. 2000. Metabolic compensation during high energy output in fasting, lactating grey seals (*Halichoerus grypus*): metabolic ceilings revisited. *Proc R Soc B* 267:1245–1251.
- NMFS (National Marine Fisheries Service). 1997. Investigation of scientific information on the impacts of California sea lions and Pacific harbor seals on salmonids and on the coastal ecosystems of Washington, Oregon, and California. U.S. Dept. of Commerce. NOAA Technical Memo NMFS-NWFSC-28.
- Noren D.P., D.E. Crocker, T.M. Williams, and D.P. Costa. 2003. Energy reserve utilization in northern elephant seal (*Mirounga angustirostris*) pups during the postweaning fast: size does matter. *J Comp Physiol B* 173:443–454.
- Pace N. and E.N. Rathbun. 1945. Studies on body composition. III. The body water and chemically combined nitrogen content in relation to fat content. *J Biol Chem* 158:685–691.
- Perez M.A. and E.E. Mooney. 1986. Increased food and energy consumption of lactating northern fur seals *Callorhinus ursinus*. *Fish Bull* 84:371–382.
- Renouf D. and R. Gales. 1994. Seasonal variation in the metabolic rate of harp seals: unexpected energetic economy in the cold ocean. *Can J Zool* 72:1625–1632.
- Schaller G.B. 1972. *The Serengeti Lion: A Study of Predator-Prey Relations*. University of Chicago Press, Chicago.
- Slonaker J.R. 1925. The effect of copulation, pregnancy, pseudopregnancy and lactation on the voluntary activity and food consumption of the albino rat. *Am J Physiol* 71:362–394.
- Stephens D.W. and J.R. Krebs. 1986. *Foraging Theory*. Princeton University Press, Princeton, NJ.
- Taylor C.R., G.M.O. Maloiy, E.R. Weibel, V.A. Langman, J.M.Z. Kamau, H.J. Seeherman, and N.C. Heglund. 1980. Design of the mammalian respiratory system. III. Scaling maximum aerobic capacity to body mass: wild and domestic mammals. *Respir Physiol* 44:25–37.
- Van Pelt R.E., P.P. Jones, K.P. Davy, C.A. Desouza, H. Tanaka, B.M. Davy, and D.R. Seals. 1997. Regular exercise and the age-related decline in resting metabolic rate in women. *J Clin Endocrinol Metab* 82:3208–3212.
- Webb P.W. 1999. Effects of Buoyancy and Body Composition on the Diving Behavior and Swimming Effort of Northern Elephant Seals, *Mirounga angustirostris*. PhD diss. University of California, Santa Cruz.
- Whittow G.C., D.T. Matsuura, and Y.C. Lin. 1972. Temperature regulation in the California sea lion (*Zalophus californianus*). *Physiol Zool* 45:68–77.
- Williams T.M., J.A. Estes, D.F. Doak, and A.M. Springer. 2004. Killer appetites: assessing the role of predators in ecological communities. *Ecology* 85:3373–3384.
- Williams T.M., J. Haun, R.W. Davis, L. Fuiman, and S. Kohin. 2001. A killer appetite: metabolic consequences of carnivory in marine mammals. G. L. Kooyman Symposium. *Comp Biochem Physiol A* 129:785–796.
- Worthy G.A.J., P.A. Morris, D.P. Costa, and B.J. Le Boeuf. 1992. Moulting energetics of the northern elephant seal (*Mirounga angustirostris*). *J Zool (Lond)* 227:257–265.
- Yochem P.K. and B.S. Stewart. 2002. Hair and fur. Pp. 548–547 in W.F. Perrin, B. Wursig, and J.G.M. Thewissen, eds. *Encyclopedia of Marine Mammals*. Academic Press, San Diego, CA.
- York A. 1994. The population dynamics of northern sea lions, 1975–1985. *Mar Mamm Sci* 10:38–51.
- Zar J.H. 1974. *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs, NJ.