

THERMOREGULATION AND RESTING METABOLIC RATE OF CALIFORNIA SEA LION (*ZALOPHUS CALIFORNIANUS*) PUPS¹

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Resting metabolic rate and body temperature of California sea lion pups (*Zalophus californianus*: Otariidae) were measured for 39 animals (12,000 g, mean body mass) captured from breeding areas on San Nicolas Island, California. These 3–5-wk-old pups had a mean specific resting metabolic rate of $0.780 \pm .010 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$, which is 2.380 times the value predicted by Kleiber for adult mammals with similar body mass; mean body temperature was $37.8 \pm .08 \text{ C}$. This level of metabolism is similar to those reported for young seals (Phocidae). The heat-transfer coefficient (h) was 2–4.6 times that predicted from body mass, and it appeared that some individuals were on the verge of hypothermia at ambient air temperatures below 19 C. Although high metabolic rates are typically associated with high growth rates in terrestrial mammals, high heat loss associated with relatively poor insulation in sea lion pups may require allocation of relatively large amounts of energy to thermoregulation (=maintenance), thus limiting the amount of energy available for growth.

INTRODUCTION

The high basal metabolic rates of marine mammals have been considered as compensation for the high potential rate of heat loss attributed to their aquatic habitat (e.g., Irving et al. 1935; Irving, Scholander, and Grinnell 1941; Irving 1973). However, it has recently been suggested that the high metabolic rates of pinnipeds may be due to nonstandard measurement procedures (Lavigne et al. 1986). The most common deviation from these standards is the use of juveniles and subadults rather than mature adults. Because most young birds and mammals display high rates of metabolism relative to the basal metabolic rate of adults (Hissa 1968; Dobler 1976; Piekarczywska 1977; Poczopko 1979), the tendency to use

young animals (because they are easier to work with) makes it probable that most metabolic measurements for marine mammals are greatly inflated and thus do not constitute basal rates of metabolism. However, pinniped metabolic data do convey the important information that, even for growing mammals, young pinnipeds have extremely high rates of metabolism.

The elevated metabolism of young endotherms does not represent increased heat production as compensation for the relatively high surface-to-volume ratios associated with small body size (McNab 1983); rather, it appears to facilitate, or reflect, biosynthetic activity associated with growth (the so-called work of growth; Brody [1945]). Thus, a high resting rate of metabolism in juvenile and subadult mammals is expected to be associated with a high growth rate (McNab 1980, 1986). Seal pups and young seals (Phocidae) have high growth rates (Bowen, Oftedal, and Boness 1985) and show very high rates of metabolism that decline with age (Davydov and Marakova 1965; Miller and Irving 1975; Oritsland and Ronald 1975). There is little information on metabolism in sea lion and fur seal pups (Otariidae; see Blix et al. 1979b), but it is interesting that these species seem to couple relatively slow growth rates (Boness, Oftedal, and Ono, in preparation) with relatively high resting metabolic rates in juveniles or

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subadults (Matsuura and Whittow 1973; South et al. 1976).

The purpose of the present study was to determine the resting metabolic rate (RMR) in young California sea lion pups (*Zalophus californianus*) under basal conditions and over a range of ambient temperatures (T_a) representative of those they experience in the wild. The study is part of a long-term study of growth, behavior, and nutrition in a free-living population of this species. We wanted to test the hypotheses that these young animals (1) have high rates of metabolism relative to older juveniles and yearlings and (2) are capable of thermoregulating over a range of temperatures. Because access to captive animals is limited, and because we wanted our data to reflect the nutritional state of wild animals, we elected to make our determinations using wild-caught, nonacclimated animals.

MATERIAL AND METHODS

The study took place July 7–17, 1986, at the west end of San Nicolas Island, California. Pups were estimated to be about 3–5 wk old, although, at this point in the breeding season, pups can range between 1 and 6 wk in age. Pups were captured each morning between 0730 and 0830 hours and immediately intubated to determine whether they had recently suckled. Any milk present in the stomach was removed, and those animals were held for at least 5 h before metabolic measurements were made. Metabolic measurements were made from 0830 to 2200 hours, with the earliest measurements being made on animals with no milk in the stomach. Blood samples were taken after metabolic measurements were concluded. Blood sera were visually inspected for the presence of chylomicrons that would indicate ongoing lipid absorption. On the basis of the absence of milk at initial intubation ($n = 30$) and/or clarity of serum ($n = 39$), all pups were considered to be postabsorptive at the time of measurement.

Oxygen consumption was measured on pups placed in a metabolic chamber (114 × 46 × 51 cm) constructed of epoxy-coated plywood and with a clear Plexiglas lid. The chamber was housed in a small room fitted with heat lamps and an air conditioner

equipped with a thermostat. Chamber temperature could be regulated to produce a range of ambient temperatures between 15.8 and 26.0 C. Air was drawn through the chamber at 55–75 liters/min using a vacuum cleaner fitted with a variable speed control. Water and CO₂ were absorbed from a subsample that was continuously pumped into a Beckman 744 Gas Oxygen Analyzer; data were output on a Linear Instruments strip-chart recorder. The system was calibrated with nitrogen gas as described by Fedak, Rome, and Seeherman (1981). Accuracy of the measurement was determined to be $\pm 2.1\%$.

Pups were held in portable pet kennels throughout the day. When placed in the chamber, some pups struggled initially, but most became calm or went to sleep within 50 min. Pups remained in the chamber for an average of 148.8 ± 9.3 min until the chart record held constant for at least 10 min. Chart records were transposed by using a planimeter to determine the average rate of metabolism for the lowest 10-min period. Body temperature (T_b) was determined immediately after each metabolic measurement with a Fisher digital thermometer and a YSI type 400 probe inserted 16 cm into the rectum; probes were calibrated before and after the study.

Some pups were measured twice each day to examine possible effects of time from capture, acclimation to chamber, and in some cases change in ambient temperature (T_a), on metabolic rate. Prior to their release at the end of each day, animals were individually tagged in the posterior edge of the fore flippers (Jumbo Riese Tags, Dalton, Ltd.) and marked with water-resistant paint (Lenmar Paint Co., Baltimore) to facilitate location and identification on subsequent days. Previous studies indicate that pups removed from the breeding area for this period of time (~ 14 h) experience no difficulty in reuniting with their mothers (Ofstedal, Iversen, and Boness, unpublished data).

We examined the relationships among several measures of experience that might affect RMR in wild-caught animals. Holding time was calculated as the number of minutes that elapsed from the time an animal was captured until the time it was first placed in the chamber. We also examined

the effects of sex, day of measurement, time of day when each measurement began, duration of each measurement, and two quantitative measures of activity during a measurement: the number of times VO_2 exceeded the scale on the chart recorder, and the number of times consecutive maximum and minimum chart points were separated by more than 10% of the final (resting) chart displacement. Some animals had milk or milky mucus in their stomachs when first examined, and some animals were slightly wet or damp when removed from the chamber. Thus, we compared RMR and T_b among (1) animals with measurable amounts of milk, trace amounts of milk, and no milk and (2) animals that were wet, damp, or dry at the end of a measurement.

Data were log transformed and analyzed using least-squares linear regression, multiple regression (to control for mass effects), and stepwise regression with .150 as entry/exit level of significance. Means are reported as \pm SE.

RESULTS

Thirty-nine pups (19 males, 20 females) were measured a total of 60 times: 21 were measured only once, 16 twice, one three

times, and one twice on each of two different days. To avoid the statistical complications associated with repeated measurements on only some of the individuals, we separated the analyses into (1) the first measurement for each individual ($N = 39$), (2) paired first and subsequent measurements ($N = 21$), (3) and all measurements combined ($n = 60$).

Body mass ranged from 8,333 to 14,512 g with a mean of $12,000 \pm 231$ ($n = 39$). Total oxygen consumption (fig. 1) scaled similarly to $\text{mass}^{0.75}$ (Kleiber 1961) but at a level nearly twice that predicted by Kleiber ($t_{\text{intercept}} = 1.771$, 37 df, $P < .05$). After mass was controlled for, T_b was positively correlated with total metabolic rate in liter/h ($\text{VO}_2 = 0.006 + \text{mass}^{0.817} + T_b^{1.822}$, $r = .807$, $P < .0477$); T_b accounted for 10.77% of the mass-independent variability (r^2) of RMR. T_b declined slightly as a function of T_a (fig. 2a). Mean T_b was $37.8 \pm .08$ C ($n = 39$). Although T_b declined with T_a , specific resting metabolic rate (RMR) did not show any significant change as a function of T_a (fig. 2b). The mean specific RMR over the entire range of T_a was $0.780 \pm .010$ ml $\text{O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ($n = 39$), equivalent to a mean of $2.380 \pm .029$ times the value predicted by Kleiber's relationship. The mean specific

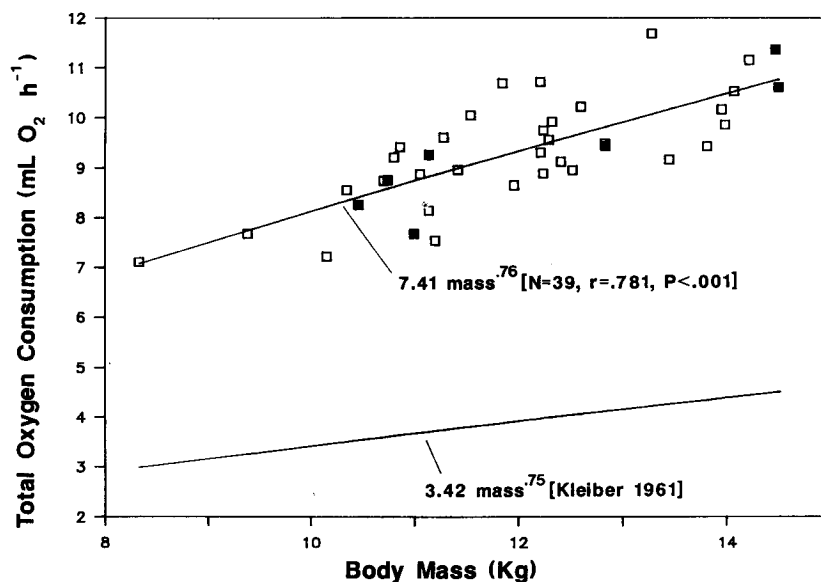


FIG. 1.—Relationship between body mass and total liters of oxygen consumed per animal per hour for first measurements on 39 pups. Solid squares = measurements below 19 C.

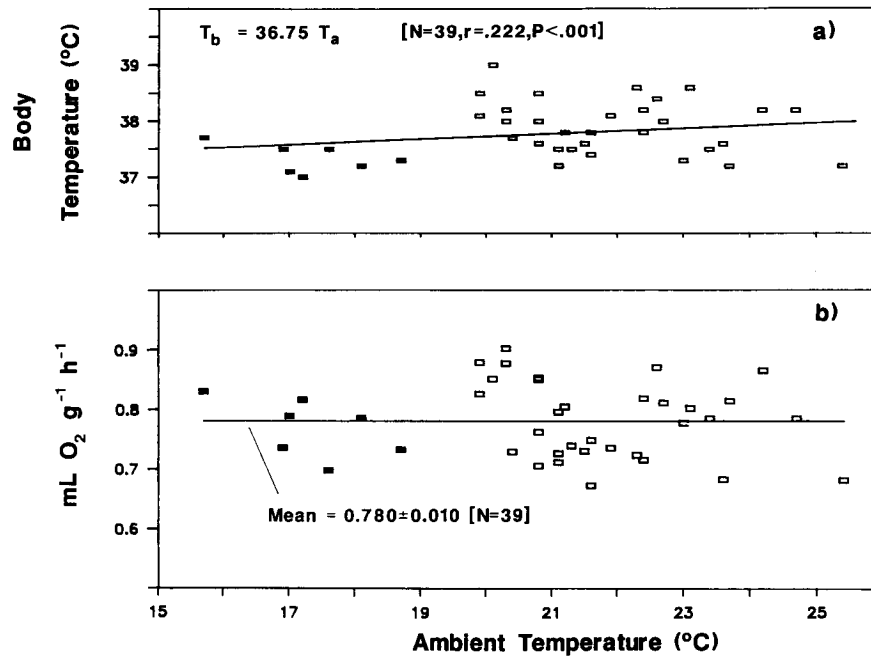


FIG. 2.—Relationship between T_a and (a) T_b and (b) mass-specific metabolic rate (oxygen consumption in ml $g^{-1} h^{-1}$) for first measurements on 39 pups. Symbols as in fig. 1.

RMR for the 39 first measurements was not significantly different from the specific metabolic rate for all data combined ($0.773 \pm .008$ ml O₂ g⁻¹ h⁻¹ [$n = 60$]).

The coefficient of heat transfer (=thermal conductance; see Thompson [1985]), calculated as $h = \text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1} / (T_b - T_a)$, increased approximately linearly as a function of T_a (see below). This observation, along with the independence of RMR and T_a , suggests that most of our measurements were within thermoneutrality. Mean h in this region is $0.0477 \pm .001$ ml O₂ g⁻¹ h⁻¹ C ($n = 39$). It is possible that some of the measurements lie outside thermoneutrality; h appears to become independent of T_a for points ($n = 7$) below 19 C (fig. 3). To determine the presence of an inflection point in this region (i.e., a deviation from linearity), we used piecewise linear regression (Neter, Wasserman, and Kutner 1985), with all possible points of inflection and used the R^2 statistic to determine the best-fit point of inflection; this revealed a discontinuity in the region of 19 C. Unfortunately, the small number of measurements below 19 C makes it difficult to determine

whether this is truly the lower limit of thermoneutrality or merely a transient adjustment in h (see McNab 1979). For the seven values below 19 C, mean $h = 0.384 \pm .001$ ml O₂ g⁻¹ h⁻¹ C; this is 2.76–4.93 times greater than predicted from mass alone (Aschoff 1981; Bradley and Deavers 1980). Our only other measurements in this temperature range, repeated measurements from pups 5 and 2, also conform to this pattern (fig. 3).

Six pups had 100 ml or more of milk and two pups had milky mucus in their stomachs at intubation. Seven pups were either damp or wet when removed from the chamber. Neither the amount or presence of milk at intubation nor whether a pup was wet or damp had any significant effect on either T_b or the level of RMR. When body mass was controlled for, there was no significant relationship between either T_b or specific RMR and sex, time of day, date of measurement, duration of measurement, activity during the measurement, or holding time. Second measurements were usually made at a different T_a , but there was no significant trend for oxygen consump-

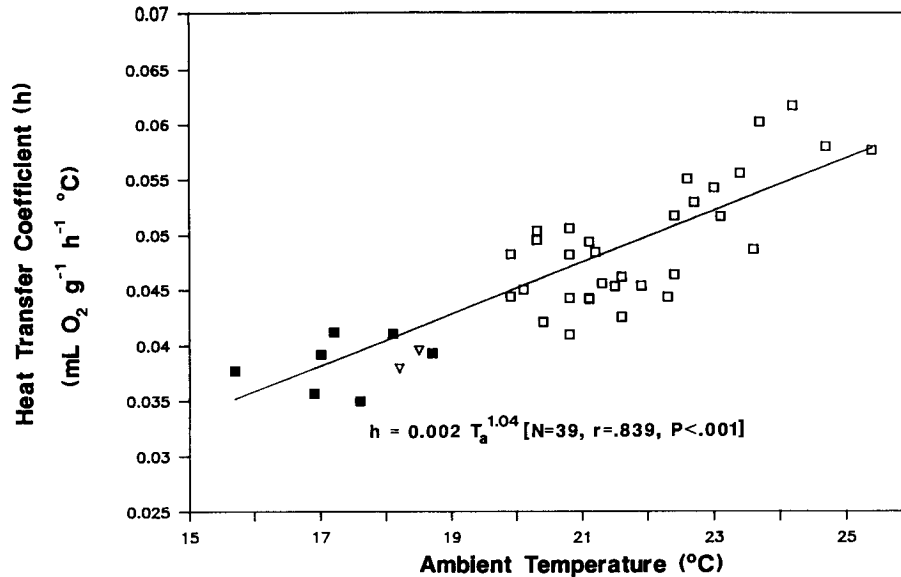


FIG. 3.—Heat-transfer coefficient as a function of T_a for first measurements on 39 pups. Inverted triangles are second measurements on pups 2 and 5; other symbols as in fig. 1.

tion to be either higher or lower at the second measurement in response to an increase or decrease in T_a ($\chi^2 = 0.448$, 1 df, $P > .10$).

DISCUSSION

It is not surprising that very young California sea lions have RMRs two times that predicted by the Kleiber relationship since young mammals typically have mass-independent RMRs 1.2–3.0 times those of adults (Piekarczywska 1977; Poczopko 1979; McNab 1983). The single measurement on a neonatal northern fur seal (*Callorhinus ursinus*) is also about twice the value predicted by Kleiber (Blix et al. 1979b). Young phocids have particularly high RMRs (e.g., Davydov and Marakova 1965; Iversen and Krog 1973; Miller and Irving 1975; Blix, Grav, and Ronald 1979a), and RMRs in our study fall within the range of metabolic rates reported for pinnipeds in general (Lavigne et al. 1986). What is somewhat surprising is that these RMRs do not scale differently than the Kleiber relationship. Intraspecific studies of metabolic rate typically yield scaling coefficients closer to 0.66 than to Kleiber's interspecific value of 0.75 (see Huesner 1982). Because RMR in precocial

mammals seems to decline with age, and because our size range may reflect several weeks' difference in age, we might have predicted RMR to scale at less than 0.75.

Two alternative explanations for our data are: (1) California sea lion pups have a metabolic rate that is similar to the high level presumed to exist in adults, or (2) the high RMRs of pups decline substantially with age to an adult level that is substantially lower than the two times Kleiber's predicted that is typically attributed to pinnipeds. We have some evidence in support of 2. Pups in our study were 5%–12% of adult size and had an average RMR of 2.38 times the value predicted by the Kleiber relationship. RMR for pups captured from the same population in late August 1984 averaged 1.93 times the Kleiber relationship (mean pup size 16.77 kg, $N = 10$; K. Ono and S. Feldcamp, unpublished data). Mass-independent RMRs of lightly restrained 60–70 kg subadult *Zalophus californianus* (Matsuura and Whittow 1973), 25%–75% of adult size (dependent on sex), were about 25% lower than RMRs for 12-kg animals in our study. Since adult BMR is usually attained by the time an individual attains about 90% of adult body size (e.g., Chew and Spencer 1967; Piekarczywska 1977;

McNab 1983), it is possible that RMR gradually declines over 5–10 yr in a late-maturing species such as *Z. californianus* (see also Matsuura and Whittow 1973). A similar decrease in mass-independent RMR is evident for harp seals (*Phoca groenlandica*; Davydov and Marakova 1965; Oristland and Ronald 1975) and harbor seals (*Phoca vitulina*; Miller and Irving 1975).

Although a slight decline in T_b within thermoneutrality is not uncommon (e.g., McNab 1978; Hennemann, Thompson, and Konecny 1983) the lack of an accompanying increase in RMR of pups in our study (solid symbols, fig. 2) suggests that these pups might have been having some trouble maintaining T_b . The lowest T_b 's recorded in our study (37.1 C) are among the lowest reported for neonatal pinnipeds not under extreme thermal (cold) stress (Bartholomew and Wilke 1956; Miller and Irving 1975; Miller, Rosenmann, and Morrison 1976; Elsner et al. 1977; Blix et al. 1979a, 1979b). Perhaps sea lion pups of this age have a relatively thin layer of subcutaneous fat and, thus, limited insulation, and a relatively high lower critical temperature compared with other pinnipeds (e.g., *Phoca groenlandica*; Iversen and Krog 1973). Extrapolation of the relationship in figure 3 to predicted levels of heat loss for mammals (Bradley and Deavers 1980; Aschoff 1981) yields a lower critical temperature of 3.6–6.4 C. However, pup T_b 's at T_a 's below 19 C imply that the lower critical temperature in these sea lion pups is probably above 3.6–6.4 C; this would mean that minimal h is probably at least twice that predicted by either Aschoff (1981) or Bradley and Deavers (1980); and, if 19 C does reflect the true lower critical temperature, h is 2.76–4.93 times that predicted by body mass. Despite indications that lower critical temperature and h are high, it is clear that more work is needed to determine precisely what the lower critical temperature is in sea lion pups of this age.

High h in air should be exacerbated by periodic or prolonged exposure to water. Water temperature is ~12–15 C at the time of this study, so immersion would increase heat loss via either conductance or evaporation upon emergence (Blix et al. 1979a). High rates of heat loss, rather than the "work of growth," could explain the high allocation of energy to maintenance observed in this study. Milk intake data for similar aged pups at the same study site are consistent with this hypothesis: milk and caloric intakes are very high, growth is slow, and most energy is expended for maintenance (Ofstedal, Iversen, and Boness 1987).

We suggest that, in contrast to offspring of most terrestrial mammals, sea lion pups, and perhaps pups of other otariids and aquatic mammals in general, may need to devote much of their energy intake to maintenance of T_b rather than to growth per se and the work of growth. High maintenance costs may impose a significant constraint on the growth rate of young California sea lions.

Finally, it should be emphasized that the data in the present study were gathered on wild-caught, nonacclimated individuals existing on a natural diet. Previous metabolic measurements of wild-caught vertebrates measured shortly after capture have yielded surprising patterns (e.g., MacMillen 1981) and/or somewhat elevated levels of metabolism (e.g., Goldstein and Nagy 1984). Yet the present data not only are consistent with other data on pinniped metabolism but show remarkably low variability; the coefficient of variation for mass-independent (%Kleiber) metabolic rate is less than 5% ($n = 39$). This suggests that studies of wild-caught suckling mammals are reasonable alternatives to the more traditional approach of holding a few individuals in captivity for long periods, often on artificial diets. When possible, metabolic measurements should be made under as near to field conditions as possible.

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