No Evidence for Bioenergetic Interaction between Digestion and Thermoregulation in Steller Sea Lions *Eumetopias jubatus*

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ABSTRACT

The increase in metabolism during digestion—the heat increment of feeding—is often regarded as an energetic waste product. However, it has been suggested that this energy could offset thermoregulatory costs in cold environments. We investigated this possibility by measuring the rate of oxygen consumption of four juvenile Steller sea lions (*Eumetopias jubatus*) before and after they ingested a meal in water temperatures of 2°–8°C. Rates of oxygen consumption of fasted and fed animals increased in parallel with decreasing water temperature, such that the apparent heat increment of feeding did not change with water temperature. These results suggest that Steller sea lions did not use the heat released during digestion to offset thermoregulatory costs.

Introduction

The heat increment of feeding (HIF; Harris 1966) denotes the increase in rate of oxygen consumption following ingestion of a meal. This phenomenon is thought to result from both the mechanical and biochemical processes of digestion (Blaxter 1989). HIF has been quantified in numerous species consuming a variety of meal types, including several species of marine mammals (see Rosen and Trites 1997). This increase in metabolism during digestion has often been treated in bioenergetic calculations as an energetic loss from gross energy intake, comparable to subtracting the energy contained in feces and urine to calculate net energy (the energy that is biologically available to the consumer).

It has been suggested that homeotherms might be able to

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use this increase in heat production to offset concurrent thermoregulatory costs (Rubner 1902; Kleiber 1975; Lavigne et al. 1982). Unfortunately, empirical evidence to support this hypothesis is equivocal (Robbins 1993). While some studies have suggested that HIF can substitute for thermoregulatory costs (e.g., Masman et al. 1988; Chappell et al. 1997), others have indicated little or no interaction between these two bioenergetic parameters (e.g., Klassen et al. 1989; MacArthur and Campbell 1994).

The apparent inconsistency in results between studies that have and have not reported thermal substitution poses an interesting dilemma to comparative physiologists. The question of thermal substitution is also critical to those investigating the energy budgets of homeotherms, given that HIF can comprise a significant proportion (up to 20%) of gross energy intake. Uncertainty in whether this energy is strictly a waste product or can be used to offset other components of the animal's energy budget (such as thermoregulation) can introduce significant errors into bioenergetic calculations. The problem may be further amplified in aquatic homeotherms given that rates of heat loss in water are potentially about 25 times greater than in air because of differences in specific heat capacity. Although there is evidence to support thermal substitution among some aquatic mammals (Costa and Kooyman 1984), other experiments have failed to support this hypothesis (MacArthur and Campbell 1994; Campbell et al. 2000).

This study examined the bioenergetic interaction between HIF and thermoregulation in young Steller sea lions (*Eumetopias jubatus*). We sought to determine whether HIF was used to offset thermoregulatory costs by comparing differences between fasted and postprandial metabolic rates of sea lions in water of varying temperature.

Material and Methods

Study Animals

We conducted this study on four juvenile Steller sea lions (age: 2–2.5 yr, mass: 75–159 kg) between January and July 1999. The animals were captured as pups and were held at the Vancouver Aquarium Marine Science Centre (British Columbia, Canada) in an outdoor compound with access to filtered (ambient temperature) seawater and haul-out space. Their normal diet consisted of thawed herring (*Clupea harengus*) fed ad lib. twice per day, supplemented with vitamin tablets (5M26 Vita-zu tablets, Purina Test Diets, Richmond, Ind.). Research was conducted

under University of British Columbia Animal Care Permit A97-0121.

Experimental Equipment

The metabolic testing tank consisted of a swim flume equipped with a 120-L Plexiglas respirometry dome and a large access hatch. The active swim space within the chamber was ∼2,900 L. The sea lions were trained to enter the tank and breathe within the respirometry dome once the hatch was closed. Experimental water temperatures were set at 2°, 4°, 6°, and 8°C (measured at excurrent water flow) and were controlled with an external chilling unit that maintained a constant temperature of ±0.5°C. However, the effective thermal load during the experiments was slightly higher because of forced convection that resulted from circulating the water within the chamber to maintain a constant, even temperature. We initially chose these test temperatures on the basis of prior experiments that indicated that they fell at least partially below the sea lion's thermoneutral zone (D. A. S. Rosen and A. W. Trites, unpublished data), and we specifically tested this assumption by comparing resting metabolism across water temperatures in this experiment (see "Results").

Metabolism was measured using flow-through respirometry, as detailed in Rosen and Trites (2002). In brief, air was drawn through the dome at a rate of 170 L min^{-1}, which was sufficient to maintain oxygen concentrations above 19.5%. A dried subsample of the excurrent airflow was continuously measured for oxygen (S-3A/I analyzer, Ametek, Pittsburgh) and carbon dioxide content (AR-60 analyzer, Anarad, Santa Barbara, Calif.) using a Sable Data Acquisition System (Sable Systems, Henderson, Nev.), and average concentrations were recorded every second. Flow rates were corrected to STPD using recorded flow temperature and barometric values. We only measured CO_2 to correct for estimates of rate of oxygen consumption (using eq. [3b] in Withers 1977) because absolute readings of carbon dioxide are unreliable given its absorption into water. Gas concentration readings were verified against baseline measurements of ambient air taken at the start and end of each measurement, and the entire system was recalibrated through the course of the experiments with gases of known concentrations. The accuracy of the system was measured using a nitrogen dilution technique (Fedak et al. 1981).

Experimental Protocol

The experiment had three phases: (1) measurement of fasted, resting metabolic rate (MR$_F$) in a metabolic testing tank; (2) feeding the animal; and (3) measurement of postprandial metabolism (MR$_P$) 2 h after the meal. Each of the four sea lions completed a minimum of four trials at each of the four water temperatures. Although the trials for each animal took place over several weeks, the experimental conditions were distributed evenly throughout the testing period to minimize potential seasonal effects.

The sea lions were allowed to swim freely within the confines of the closed testing tank for a 25-min acclimation period before their postabsorptive (>14 h) metabolic rates were measured. MR$_F$ was then measured for a 10–15-min period during which the sea lions remained calm and stationary, with their heads in the respirometry dome. Both the trainer and the researcher independently judged the behavior of the sea lions for movement and apparent agitation.

The sea lions were removed from the tank after measuring MR$_F$ and fed a 2-kg meal of herring (their normal meal size) that had been maintained at a constant temperature of 8.5°–10°C to standardize the thermal effects of the food itself (Wilson and Culik 1991). According to our experimental design, the meal had to be eaten within a 5-min period. In practice, the animals either ate the entire meal immediately or consumed very few fish before losing interest (in which case the trial was terminated).

Ideally, the effect of environmental temperature on HIF could be measured by following changes in metabolism over the entire presumed course of digestion. However, limiting the confounding effect of activity in the testing tank over an extended period of digestion is not feasible in these animals. In addition, it is difficult to differentiate between a lack of increase in metabolism because of thermal substitution versus a suspension of digestion resulting from thermoregulatory vasoconstriction. Therefore, in this study, we used an experimental protocol that first ensured digestion was occurring, then measured the effect of environmental temperature on HIF at a set point during the course of digestion.

Following feeding, the sea lions were placed in a dry holding area for 95 min to ensure that sufficient digestive time had passed between metabolic measurements for the potential HIF to be manifest (Rosen and Trites 1997). Removing the sea lions from the water negated the potential interactions between thermoregulation and the course of digestion during this period. It also restricted the movement of the animals in case activity also affected digestion.

The sea lions were returned to the testing tank for a second 25-min acclimation period after which resting MR$_P$ was measured for 15 min while the animal remained stationary in the respirometry dome. Hence, MR$_P$ was measured between 120 and 135 min after the meal. Previous studies (Rosen and Trites 1997) showed that a 50% increase in MR$_P$ occurred at 120–135 min, while the peak 60% increase in metabolism was observed at 150–180 min. The behavior of the sea lions during the measurement was again scored for activity and agitation levels. Data were only used in the final analyses from trials wherein sea lions had minimal movement and agitation during measurements of both MR$_F$ and MR$_P$ resting metabolism.
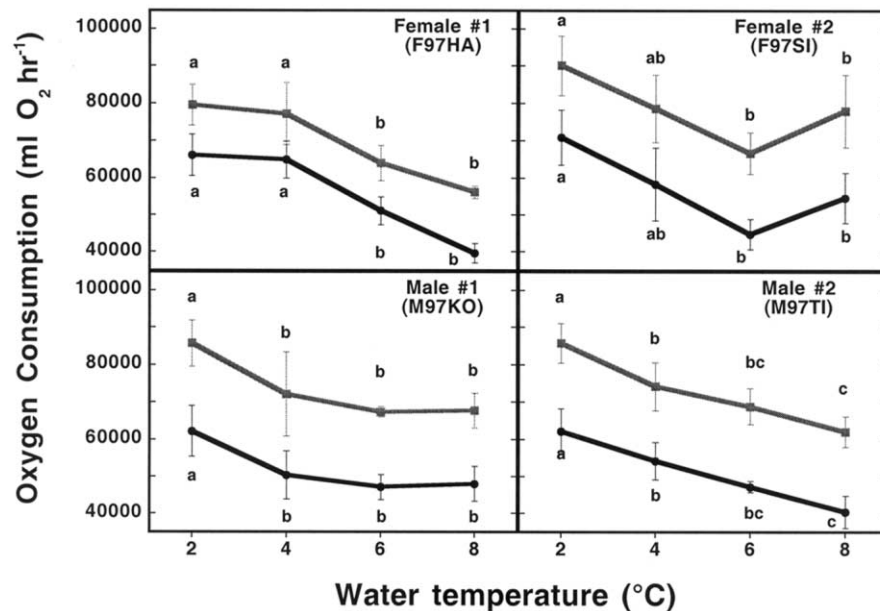
Figure 1. Mean ± SD rate of oxygen consumption at different water temperatures for four juvenile Steller sea lions. The bottom lines (*circles*) represent fasting values, while the top lines (*squares*) represent postprandial values. Letters denote statistical differences between the means (separate for each line) as determined by post hoc comparisons.

Statistical Analysis

HIF is often measured as the total increase in metabolism over the course of digestion. For this study, we defined the parameter HIF as the instantaneous difference in rate of oxygen consumption due to digestion between the MR_F and MR_P measures during the specified measurement period. Hence, HIF was calculated for each individual trial as $HIF = MR_P - MR_F$.

An ANCOVA was performed on the data to detect changes in the MR_F and HIF with water temperature. The potential interaction of body mass was investigated in these analyses because changes in body size may affect both thermoregulatory abilities and HIF. Differences in MR_P and MR_F across water temperatures for each animal were tested using post hoc Tukey comparisons (using temperature as a discontinuous variable). Statistics were performed using S-Plus 2000 with $P = 0.05$.

Results

Our first goal was to determine whether rates of oxygen consumption varied with changes in water temperature. Without an indication that the animals were below their lower critical temperature, there would be no reason to expect thermal substitution to occur. A multiple regression model incorporating water temperature and body mass was run on the data for each animal. This determined whether changes in body mass over the course of the experiments had to be accounted for in the analysis of either HIF or MR_F. We found body mass was not significant in either of the analyses from any of the four sea

lions; therefore, this component was removed from any subsequent models.

ANCOVA was then used on the data from all animals to determine whether MR_F changed with water temperature, using individual sea lions as the covariates. This analysis indicated a significant increase in rates of oxygen consumption with decreasing water temperature ($P < 0.001$ for all individuals; Fig. 1). This indicated that animals had been tested below their lower critical temperature and allowed for potential thermal substitution.

For interest's sake, we tested to see whether a single, simpler model could be used to describe the relationship between MR_F and water temperature. That is, we wanted to see whether a common slope could describe the data from individual sea lions. A test for changes in deviance determined that including individual slopes did not significantly improve the model ($F_{\Delta 3} = 2.04$, $P = 0.18$). This means the slopes from the individual animals were not significantly different from each other; that is, they had a similar thermoregulatory response in metabolism to changes in water temperature.

Our a priori assumption was that MR_F would increase as water temperature decreased. A parallel increase in MR_P was expected if energy from digestion did not offset the increasing thermoregulatory costs of being in colder water. This would be expressed as a lack of change in calculated HIF over a range of water temperatures. Alternately, a decrease in the difference between MR_F and MR_P with decreasing water temperatures would suggest that the heat released from the digestion of food

substitutes for thermoregulation in an animal's energy budget. This would be expressed as a decrease in calculated HIF as water temperature dropped.

An ANCOVA using the data from all animals determined whether calculated HIF changed with water temperature (with the individual sea lion as the covariate). It revealed no significant change in HIF with decreasing water temperature ($t_{63} = 0.22$, $P = 0.83$). This meant that the slope of the MR_P measures was parallel to that of MR_F such that the difference between MR_P and MR_F (i.e., HIF) was constant (Fig. 2). This indicates that no thermal substitution occurred from HIF. Not only did HIF not vary with water temperature, but it was also surprisingly consistent for three of the sea lions (Fig. 2). The average value of HIF for female 1 was much lower than the means exhibited by the other sea lions. We cannot explain this discrepancy—the only apparent outstanding morphological feature of this sea lion was that she was the smallest (although not the thinnest) of the animals tested.

Discussion

Role of HIF in Thermoregulation

The increase in metabolism associated with the work of digestion was recognized as early as 1877 by Bidder and Schmidt (Kleiber 1975) and is known to be related to the ratio of nutrients in the diet (Jobling 1983). Mitchell (1962) proposed that the ideal meal composition should produce the least waste (i.e., minimum HIF). However, Kleiber (1975), seizing on the older concept of *luxuskonsumption*, suggested that the differences in heat production associated with different meals provide an example of "homeostatic waste." HIF thus emanates from two relatively separate processes—"obligatory" and "adaptive" HIF. Obligatory HIF describes the minimal costs associated with the mechanical and biochemical breakdown, assimilation, and processing (including anabolism) of a meal. Adaptive HIF represents the additional heat production associated with consumption in excess of requirements and is a form of controlled energetic dissipation. Evidence supporting the concept of adaptive HIF is still equivocal (Rothwell and Stock 1983) but has implications for the concept of thermal substitution through HIF.

The question of whether HIF is an obligatory waste product is important for understanding (and accurately calculating) the energy budgets of animals. Rubner (1902) was among the first to hypothesize that the heat generated through digestion could be used to offset thermoregulatory costs. Many articles have made the de facto assumption that this hypothesis is true (and have often been misquoted as having tested this concept) when seeking an ecological or evolutionary context to their own studies of HIF (e.g., Baudinette et al. 1986; Markussen et al. 1994; Janes and Chappell 1995; Hawkins et al. 1997).

There are a number of theoretical reasons to expect a bioenergetic interaction. The principle of energy conservation as
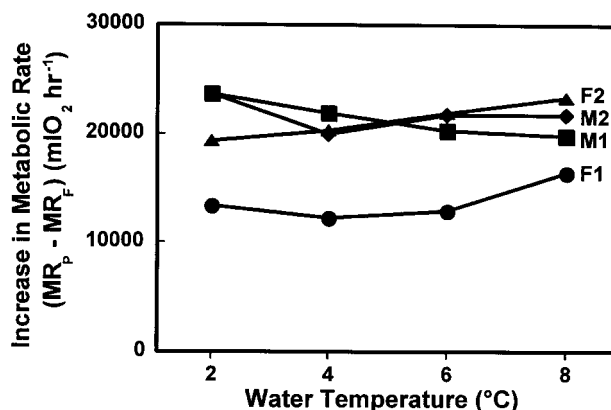
an evolutionary pressure suggests that selection should favor those animals that can most efficiently use their energy intake. There is also a striking physiological similarity between HIF and nonshivering thermogenesis (Rothwell and Stock 1983). Hyperphagic rats, for example, show enhanced thermogenic responses to noradrenalin, supporting the hypothesis that cold exposure and overeating not only use the same thermogenic mechanisms but may also be interactive (Rothwell and Stock 1979). In addition, while cold exposure increases food intake, fasting completely abolishes nonshivering thermogenesis (Rothwell and Stock 1983).

Conversely, there are also a number of theoretical reasons why HIF should not substitute for thermoregulation costs. Principally, mammals already possess a suite of physiological and behavioral mechanisms to limit heat loss effectively (MacArthur 1989). In marine mammals, the primary avenue appears to be through peripheral vasoconstriction (which would also likely curtail the rate of digestion), combined with distinct insulating, hypodermal blubber layers. Alternate adaptations are apparent in aquatic species such as mink and muskrats that actively forage for brief bouts in cold water before retreating to a more moderate clime to consume and digest their meals (MacArthur 1979; Williams 1986). Any thermal benefit from digestion would thus come from a potential buildup of heat before entering the water (MacArthur and Campbell 1994). These animals appear to use digestion to offset the effects of a later thermal challenge by creating a thermal buffer to protect core temperatures in a manner that does not affect total metabolism (MacArthur and Campbell 1994). Obviously, many aquatic mammals do not, or cannot, use a strategy of minimized thermal exposure. However, MacArthur (1989) questioned whether the reliance on HIF for thermoregulation is efficient in light of alternate behavioral and physiological ad-

Figure 2. Mean ± SD difference between paired fasted and postprandial rate of oxygen consumption values for each of the four Steller sea lions. HIF = heat increment of feeding; RMR = resting metabolic rate; F1 = female 1; F2 = female 2; M1 = male 1; M2 = male 2.

aptations that are specifically aimed at maintaining thermo-neutrality and coping with thermal demands.

Another reason to question the efficacy of thermal substitution is the observation that the main determinate of the scope of HIF is the rate of protein turnover (Jobling 1983). As noted by Schieltz and Murphy (1997), this rate (and therefore the potential contribution of HIF to thermoregulation) is relatively independent of thermoregulatory challenge.

Experimental Results

The MR_F and MR_P of the sea lions in this study displayed a similar increase with decreasing water temperatures below their thermoneutral zone (Fig. 2). The constant increase in MR_P is indicative of a lack of thermal substitution or compensation for thermoregulation by HIF. In contrast, a decrease in the difference between MR_F and MR_P with decreasing temperatures would have indicated that a portion of HIF was being used to offset thermoregulatory demands.

Our results are contrary to expectations for a homeotherm living in a thermally challenging environment. Using HIF to offset thermoregulatory costs seems like a reasonable strategy to maximize the animal's energetic efficiency. Yet, our findings and those of a number of other studies—many with animals that seem least likely to afford any thermal challenge—have found no indication of substitution (Table 1). For example, studies of baby Arctic tern chicks (*Sterna paradisaea*; Klassen et al. 1989), star-nosed moles (*Condylura cristata*; Campbell et al. 2000), and muskrats (*Ondatra zibethicus*) in water (Mac-Arthur and Campbell 1994) found no indication of thermal substitution. Data from Java sparrows (*Padda oryzivora*) also seem to indicate a lack of substitution, contrary to the authors' conclusions (Meienberger and Dauberschmidt 1992).

In contrast to the negative findings of these aforementioned studies, various levels of thermal substitution have been clearly demonstrated in a number of species. Approximately 30% of HIF appeared to be used to offset thermoregulation costs in young golden hamsters (*Mesocricetus auratus*) at low environmental temperatures (Simek 1975) and approached 50% for white-tailed deer fawns (*Odocoileus virginianus*) and kestrels (*Falco tinnunculus*; Masman et al. 1988; Jenson et al. 1999). Chappell et al. (1997) further reported that house wren chicks (*Troglodytes aedon*) can exhibit almost complete substitution under adverse thermal conditions. These studies all measured the interaction between thermoregulation and digestion through changes in total energy production, as we also did in this study.

An alternate hypothesis of the energetic interaction between digestion and thermoregulation suggests that HIF may decrease thermoregulatory costs by helping to maintain core temperatures (irrespective of changes in total metabolism). Several studies have investigated the combined effects of digestion and environmental temperature on body temperature (in various guises). Angolan free-tailed bats (*Mops condylurus*; Maloney et al. 1999) and sea otters (*Enhydra lutris*; Costa and Kooyman 1984) have both demonstrated an increased ability to maintain body temperature when fed versus fasted. In sea otters, the time they spent being active decreased during the course of digestion, while body temperature remained constant. This indicates that the animals increasingly used HIF to maintain postprandial body temperature in place of thermic activity. Using a different experimental approach, pigeons (*Columba livia*) have been shown to decrease shivering thermogenesis significantly during digestion in the dark phase. Their strategy of delayed digestion may maximize the substitution effects of HIF during the most thermally challenging period (Rashotte et al. 1999). These examples demonstrating substitution by HIF should not be confused with those studies in which the muscular cost of foraging was primarily responsible for offsetting thermal costs (e.g.,

Table 1: Summary of studies investigating substitution of thermal costs by the heat increment of feeding measured through changes in energy production

Species	Maximum Substitution	Mass	Age	Food Type and Quantity	Environment	Source
Steller sea lions	None	75–159 kg	Juveniles	17% protein, 2 kg	2°–8°C water	This study
Muskrat	None	780–1,100 g	Adult	8% protein, 270–300 g	18.5°C water	MacArthur and Campbell 1994
Star-nosed moles	None	52–67 g	Unknown	60% protein, 3.5 or 10 g	9°–24°C air	Campbell et al. 2000
Arctic terns	None	12–109 g	Chicks	Fish, unknown	0°–37°C air	Klassen et al. 1989
White-tailed deer	48%	31–43 kg	Fawns	5% protein, unknown	−20°–5°C air	Jenson et al. 1999
House wren	"Significant" substitution	>8 g	Chicks	Crickets, 3%–10% body mass	22°C air	Chappell et al. 1997
Golden hamster	30%	?	Young	82% protein, unknown	10°–30°C air	Simek 1975
Kestrel	50%	?	Adult?	Unknown, 35 g	−12°–31°C air	Masman et al. 1988

Note. Details are given on the degree of thermal substitution, the size and age classes studied, the quantity and type of food used in the trials (particularly dry weight protein content), the range of experimental temperatures, and the medium in which the animals were tested.

MacArthur and Campbell 1994; de Leeuw et al. 1998; Campbell et al. 2000).

However, studies of the effect of HIF on maintaining body temperature have also yielded mixed results. Among boiler chickens, for example, HIF appears to have a constant elevating effect on body temperature regardless of ambient temperature (Koh and MacLeod 1999), while the net rate of body cooling in water for muskrats was actually higher in fed versus fasted animals (MacArthur and Campbell 1994). Still, future studies of thermal substitution should try to include measures of core body temperatures.

Differentiating Disparate Results

Why some studies indicate thermal substitution while others do not is unclear. One possible explanation is that the differences are due to integral physiological differences between study animals relating to taxonomy, ecology, or developmental stage. Another is that the inconsistent results are due to differences in experimental design.

The field of comparative physiology suggests that there should be causal differences between those species that demonstrated substitution and those that did not. However, there appear to be no clear divisions according to taxonomic (avian or mammalian), ecological (aquatic or terrestrial), or developmental (age or class) characteristics (Table 1). This lack of an identifiable pattern may be partially attributable to the low number of species studied so far. This paucity of data also precludes certain potentially important comparisons, such as the reaction of diurnal versus nocturnal species and how thermoregulatory mechanisms change with age.

A common (and usually invalid) criticism leveled at studies that do not find substitution is that the thermal challenge was insufficient to evoke this mechanism. In this study, the sea lions exhibited a 45% average increase in metabolic rate across the experimental temperatures, indicating a significant thermal cost (Fig. 1). Similar increases in metabolism were reported in most of the studies that reported minimal or no substitution. Therefore, a lack of significant thermal challenge does not appear to explain the differences in the observed thermogenic responses. Still, there is the slight possibility that although sufficient time was allowed to induce a thermal challenge (as evident through increasing metabolism), it was somehow insufficient to enact thermal substitution.

Conversely, it is worth recognizing that the differences observed in postprandial metabolic responses to thermoregulatory demands may not, in fact, always reflect whether thermal substitution is occurring. As previously noted, most studies assume that a decrease in the difference between MR_F and MR_P with decreasing temperatures indicates that HIF is being used to offset thermoregulatory costs. However, suspending digestive processes during thermal challenges would result in a lack of postprandial increase in metabolism that is empirically indis-tinguishable from thermal substitution (as in MacArthur and Campbell 1994). This study limited the potential of false indications of thermal substitution by allowing initial digestion to occur in a thermal-neutral environment. However, Steller sea lions foraging at sea for days or weeks at a time clearly cannot suspend digestive processes to facilitate thermoregulatory vasoconstriction. Still, future studies of thermal substitution should monitor blood flow and other physiological indicators of digestive activity to support metabolic evidence of thermal substitution.

A more interesting course of investigation results from the proposal that these discrepancies in experimental results are attributable to differences in experimental design (vs. experimental error per se). By assuming a consistency among homeotherms in basic bioenergetic pathways, such studies would aim to determine the circumstances and mechanisms needed to display thermal substitution in a particular animal rather than dividing fauna into those that "do" and those that "do not." For example, given the different types of food used in the various studies and the relationship between the extent of HIF and food composition, the degree of thermal substitution might be related to the degree or source of HIF. However, there is no clear pattern among studies published to date between the occurrence of substitution and type (e.g., protein or energy content) or quantity of food (Table 1). Nor is there a differentiating pattern among factors that might be related to the degree of thermal demands, such as the range of ambient temperatures (particularly in reference to thermoneutral zones), testing medium (air or water), or body mass.

Summary

The results of this study indicate that Steller sea lions do not substitute the heat generated through HIF to offset thermoregulatory costs under the testing conditions we used. Further research is needed to understand the disparity in results observed from various studies to date. One approach is to investigate potential ecological or physiological parameters that dictate why some species do and do not demonstrate thermal substitution. Another is to explore whether particular physiological and environmental circumstances dictate whether a particular animal employs thermal substitution.

Acknowledgments

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