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Daily Torpor and Energy Expenditure in *Sminthopsis macroura*: Interactions between Food and Water Availability and Temperature

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ABSTRACT

Endothermy allows maintenance of a constant internal thermal milieu for optimal physiological functions but results in high energy expenditure and water loss. Since torpor can reduce both expenditure of energy and loss of water and thus reduces food and water requirements, we determined how different food and water regimes affect torpor occurrence and patterns in the dasyurid marsupial *Sminthopsis macroura* at ambient temperatures of 18°C (well below the thermoneutral zone) and 28°C (close to the thermoneutral zone). At 18°C, torpor was more frequent and more pronounced than at 28°C. Withdrawal of food reduced the average daily metabolic rate by 20%; withdrawal of water alone had little effect. The average daily metabolic rate of individuals displaying torpor was 20% lower than that of individuals remaining normothermic. At 28°C, the average daily metabolic rate under food restriction was 85% of that with food available ad lib. However, this reduction of average daily metabolic rate at 28°C seems due not to the use of torpor but mainly to a reduction of the resting metabolic rate. The results suggest that at low temperature, torpor is used to adjust energy expenditure to availability of food, whereas at high temperature, reductions of resting metabolic rate are employed.

Introduction

Endothermic thermoregulation of small mammals requires high metabolic rates. This is especially true at low ambient temperatures (T_a's), since high heat production is needed to compensate for a large amount of heat loss. The increased heat production requires an increased respiratory rate, which results in increased water loss. In addition, normothermic animals with higher body temperatures (T_b's) lose more water to the environment owing to higher water vapour pressure (Fisher and Manery 1967). Since during torpor T_b and metabolic rate are lowered, both pulmonary and vapour pressure–related evaporatory water loss, in addition to energy expenditure, are substantially reduced (Fisher and Manery 1967). Therefore, torpor can be regarded as an avenue for an animal to extend its survival time on its available energy and water reserves (Thomas and Cloutier 1992). Although it has been well documented that many small mammals exhibit torpor when their food supply is restricted, there is little information on torpor in response to water deprivation (MacMillen 1972; Buffenstein 1985). Moreover, little is known about how T_a and food and water availability interact in influencing torpor and energy conservation in small mammals. This information is important for understanding the energetic strategies of small mammals under harsh environmental conditions.

The stripe-faced dunnart, *Sminthopsis macroura* (Dasyuridae), is a mouse-sized nocturnal insectivorous marsupial. It is widespread in arid and semiarid areas in central Australia characterized by pronounced daily and seasonal temperature fluctuations and highly variable rainfall. Consequently, the animal is frequently faced with periods of food and water shortage (Morton 1982). Little is known about the biology of the species in the field, but in the laboratory daily torpor has been reported over a range of T_a's (Geiser and Baudinette 1985).

In this study, we investigated the effects of food and/or water withdrawal on torpor frequency, torpor pattern, and energy expenditure of *S. macroura* at a low T_a well below the thermoneutral zone and a high T_a close to the thermoneutral zone. We also determined how torpor influences average daily metabolic rate and the change of body mass of the animals under different food and water regimes.

Material and Methods

Twelve adult male *Sminthopsis macroura* (body mass 22.5 ± 2.4 g) were obtained from a breeding colony at La Trobe University, Melbourne. Animals were maintained individually in cages (30 × 22 × 14 cm) containing sawdust, shredded paper, and nest boxes at the University of New England in Armidale. They were fed daily with a mixture of macerated cat food pellets and canned dog food and supplied with calcium and vitamins. The water content of the food was approximately 68%. Drinking water was provided. The photoperiod throughout the experiment was 12L : 12D (lights on 0600–1800). All experi-

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ments were conducted between March 10 and November 4, 1993 (i.e., Australian winter and spring). *N* indicates the number of animals and *n* the total number of measurements.

After acclimation to a T_a of 22° ± 1°C for 6 wk, animals were separated into two groups of six individuals with matched body mass. The animals in the first group were exposed to a sequence of T_a's, lasting for about 6 wk each, of 18° ± 1°C, 22° ± 1°C, and 28° ± 1°C. To account for a possible seasonal influence, the individuals in the second group were exposed for the same period, but the T_a sequence was 28° ± 1°C, 22° ± 1°C, and 18° ± 1°C.

At both 18° and 28°C, all animals from both groups were twice subjected to the same series of experimental treatments lasting for 24 h each: food and drinking water available ad lib., food available ad lib. and drinking water withheld, food withheld and drinking water available ad lib., food and drinking water withheld, and dry food available ad lib. and drinking water withheld (where the food had been dried at 50°C for 24 h). Between every two treatments, animals had access to food and drinking water ad lib. for 1 or 2 d until more than 95% of the original body weight was reached. Body mass change, eye surface temperature, and/or T_b were measured at 0900 hours after every treatment.

Average daily metabolic rates in response to different food and water regimes were determined at T_a's of 18° and 28°C in three individuals from each group (i.e., a total of six animals at each T_a). Average daily metabolic rates were monitored continuously for 7 d under different food and water regimes. New regimes of food and water were introduced at 1200 hours each day, and the animals were weighed.

Eye surface temperature was measured to the nearest 1.0°C by placing the sensor of an infrared digital thermometer (Omega, OS-600, Stamford) about 2 cm above the eye. Rectal measurements of T_b (Omega, HH-21 thermocouple thermometer, to the nearest 0.1°C) were taken together with readings of the eye surface temperature, on several occasions, to determine whether the surface temperature reliably predicts T_b. Eye surface temperature was linearly related to T_b measured rectally at T_a's of 18°C ($r^2 = 0.98$, $P < 0.001$, $N = 11$, $n = 21$) and 28°C ($r^2 = 0.95$, $P < 0.001$, $N = 11$, $n = 21$; Fig. 1).

For the determination of average daily metabolic rate, animals were placed into 2-L respiratory chambers fitted with a small plastic nest box. The chambers were placed in a temperature-controlled cabinet (± 0.5°C). Four channels, three animal channels and one reference channel, were scanned with solenoid valves. Each channel was read for 3 min (i.e., outside air and rate of oxygen consumption [$\dot{V}\text{O}_2$] of each individual were measured every 12 min). The flow rate (about 300 mL min^{-1}) of dry air through the respiratory chamber was monitored with a mass flowmeter (Omega, FMA-5606). The oxygen content of air leaving the respiratory chamber and air in the reference chamber was consecutively measured with a single-chamber oxygen analyser (Ametek Applied Electrochemistry S-3A/1, Pittsburgh) fitted with a high-resolution output board (80335SE). Analyser output from the flowmeter and the oxygen analyser were interfaced to a personal computer via a 12-bit analog/digital card.

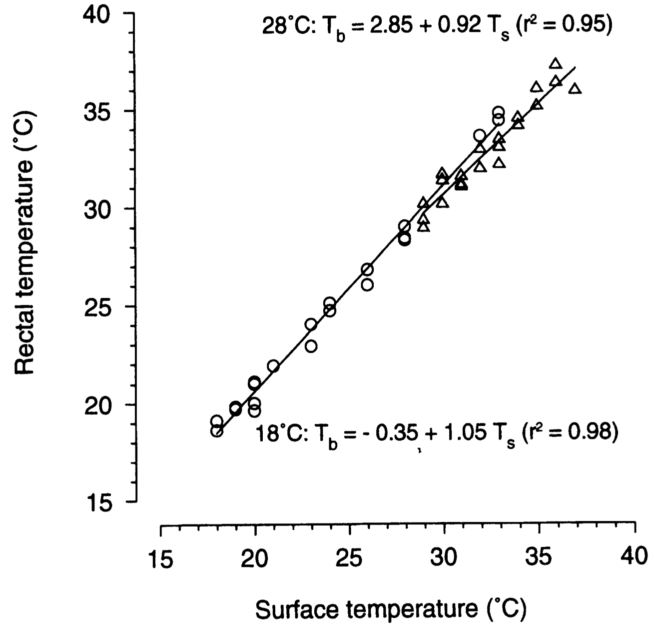

Figure 1. The relationship between eye surface temperature (T_s) and the rectal temperature (T_b) of *Sminthopsis macroura* at T_a's of 18°C (*circles,* $N = 11$, $n = 21$) and 28°C (*triangles,* $N = 11$, $n = 21$). T_b and T_s are linearly related at T_a's of 18° and 28°C ($P < 0.01$).

Animals were considered torpid when the eye surface temperature was less than 30°C at a T_a of 18°C and less than 31°C at a T_a of 28°C, which is equivalent to T_b's of less than 31°C (see Fig. 1). When only metabolic rate measurements were available, animals were considered torpid when their metabolic rates fell below 75% of the resting metabolic rate at the same T_a. Torpor frequency was determined for each individual, and percentage of torpor was calculated from the individual mean.

Resting metabolic rate was determined from the mean of the three lowest consecutive $\dot{V}\text{O}_2$ values (i.e., over 36 min) of normothermic individuals obtained in the afternoon before 1700 hours. The metabolic rate during torpor was determined from the mean of the three lowest consecutive $\dot{V}\text{O}_2$ values in a torpor bout. The average daily metabolic rate was determined as the average of all mass-specific $\dot{V}\text{O}_2$'s taken at 12-min intervals over 24 h. A linear change of body mass during 1-d measurement was assumed to calculate the mass-specific $\dot{V}\text{O}_2$.

Body mass change overnight was determined as the change in body mass in milligrams per gram of initial mass. Food intake was determined as the dry mass of food consumed in milligrams per gram of body mass. Results are presented as mean ± 1 standard deviation. Torpor frequencies under different experimental treatments were examined by means of chi-square analysis. The impact of the various food and water

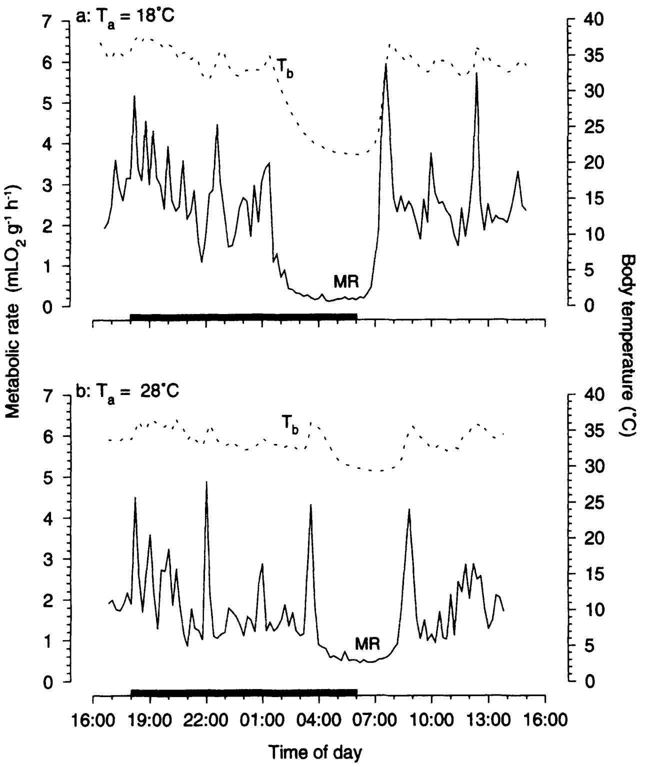

Figure 2. Fluctuations of metabolic rate (MR) and body temperature (T_b) of a *Sminthopsis macroura* at T_a's of 18° (*a*) and 28°C (*b*). Food and water were not available. The dark bar indicates the dark phase.

regimes on eye surface temperature and average daily metabolic rate were analysed by ANOVA. Pairwise comparisons were made with Tukey's test. Change of body mass was analysed by three-way ANOVA, and a posteriori comparisons of means were carried on food and water regimes. Food intake was examined by two-way ANOVA. Differences in average daily metabolic rate between animals entering torpor and those remaining normothermic were examined with Student's *t*-test. Linear regressions were fitted by the least squares method.

Results

Torpor Patterns and Frequency

Sminthopsis macroura displayed torpor at T_a's of 18° and 28°C (Fig. 2). After lights-out, animals were active and had an elevated metabolic rate. Torpor began during the dark phase and was characterized by a substantial drop in both metabolic rate and body temperature. Torpor was terminated by spontaneous arousal usually before midday (Fig. 2).

Torpor frequency was affected by T_a (Fig. 3). When food and water were freely available, the frequency of spontaneous torpor was 63.6% ± 14.1% ($N = 12$, $n = 22$) at a T_a of 18°C and 33.3% ± 13.6% ($N = 12$, $n = 24$) at a T_a of 28°C. Torpor frequency differed between 18° and 28°C under all food and water regimes ($P < 0.05$, χ^2-test; Fig. 3). Although torpor frequency appeared to be somewhat elevated when food was withheld, it was not significantly affected by the different food and water regimes at either 18° or 28°C ($P > 0.05$, χ^2-test).

Eye Surface Temperature

The eye surface temperature during torpor at T_a of 18°C was influenced by the various food and water regimes ($P < 0.001$, ANOVA; Fig. 4*a*). When food and water were available, the average eye surface temperature during torpor was 26.7° ± 3.1°C ($N = 9$, $n = 14$). When both food and water were withheld, the eye surface temperature decreased to 22.9° ± 3.3°C ($N = 11$, $n = 18$). When only dry food was available and water was withheld, the eye surface temperature was 24.6° ± 2.6°C ($N = 11$, $n = 18$). However, withdrawing drinking water while food was available resulted in an eye surface temperature of 28.2° ± 0.7°C ($N = 9$, $n = 14$), which was not significantly different from that with food and water available ad lib.

At a T_a of 28°C, the eye surface temperature of individuals that showed spontaneous torpor was 30.1° ± 0.6°C ($N = 6$, $n = 8$) when food and water were available, and the different food and water regimes did not cause a change in eye surface temperature during torpor ($P > 0.05$, ANOVA; Fig. 4*b*).

The different food and water regimes also did not significantly affect the eye surface temperature of individuals remaining normothermic at both air temperatures ($P > 0.05$,

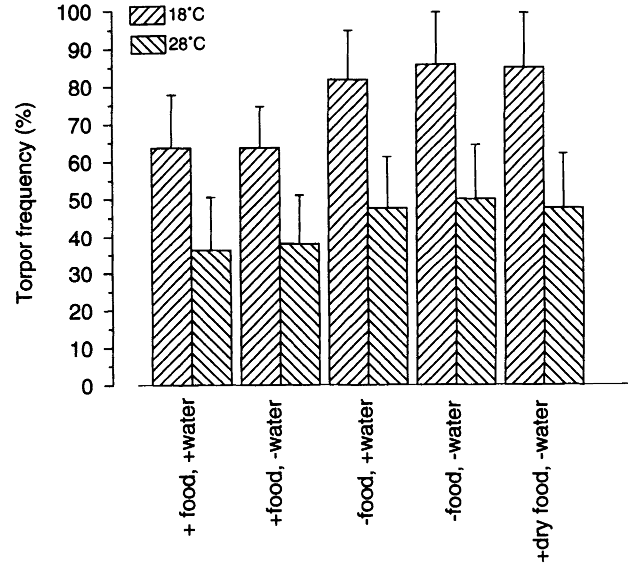

Figure 3. Torpor frequency of *Sminthopsis macroura* under different food and water regimes at T_a's of 18°C and 28°C. The error bars represent the standard deviations. Torpor was more frequent at 18°C than at 28°C ($P < 0.05$, χ^2-test).

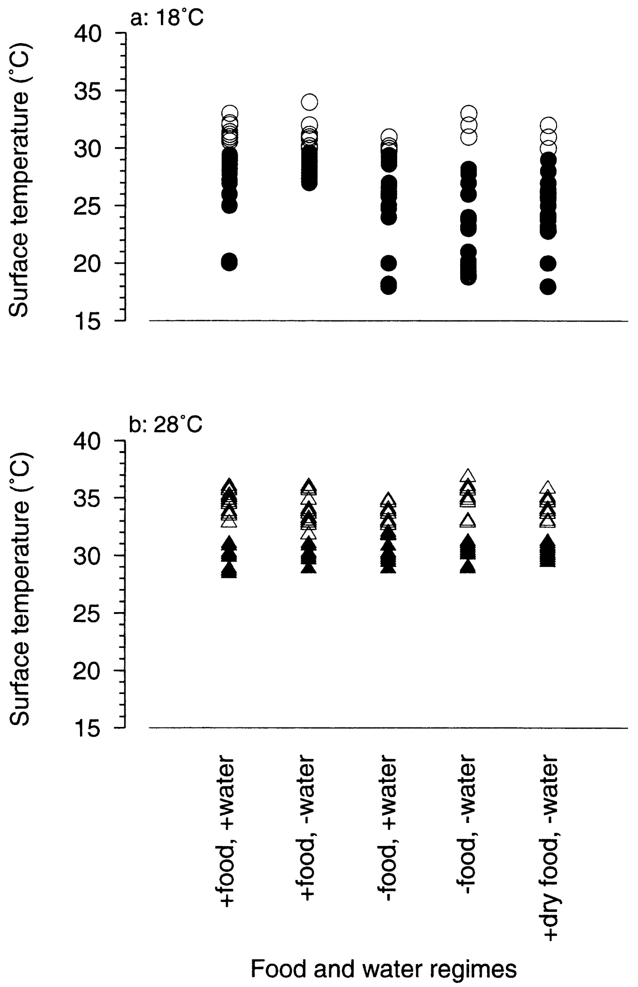

Figure 4. Eye surface temperature of *Sminthopsis macroura* under different food and water regimes at T_a's of 18°C (*a*) and 28°C (*b*). Eye surface temperature was measured at 0900 hours after each 24-h treatment. Solid symbols represent torpid individuals and open symbols normothermic individuals. Significant differences are given in the text.

ANOVA; Fig. 4*a, b*). The average eye surface temperature was 31.8° ± 0.9°C ($N = 7$, $n = 26$) at a T_a of 18°C and 34.3° ± 1.1°C ($N = 9$, $n = 58$) at a T_a of 28°C, which reflects rectal temperatures of 32.4°C and 34.4°C, respectively (see Fig. 1).

Body Mass and Food Intake

The T_a, use of torpor, and food and water regimes all had independent, but not interactive, effects on body mass. Animals at 18°C lost more body mass than at 28°C ($P < 0.05$, three-way ANOVA; Table 1). Body mass reduction was significantly smaller for individuals that entered torpor than those that remained normothermic ($P < 0.001$, three-way ANOVA; Table 1). Body mass change overnight varied profoundly among various food and water regimes at both temperatures, irrespective of torpor ($P < 0.001$, three-way ANOVA). When food and water were available, body mass remained stable or increased slightly. While withdrawal of drinking water had little effect on body mass change, the withdrawal of both food and water and the withdrawal of water when dry food was available resulted in a substantial body mass loss. Body mass loss was intermediate when drinking water was available and food was withheld (Table 1).

Food intake was influenced by both T_a and the food and water regimes ($P < 0.001$, two-way ANOVA). When both food and water were freely available, animals consumed 119.2 ± 15.0 mg g^{-1} ($N = 11$, $n = 20$) at 18°C and 70.0 ± 16.1 mg g^{-1} at 28°C ($N = 11$, $n = 18$). Food intake increased to 200.2 ± 18.4 mg g^{-1} at 18°C and 145.4 ± 20.6 mg g^{-1} at 28°C when water was withheld. However, no dry food was consumed when water was withheld.

Average Daily Metabolic Rate

The average daily metabolic rate was affected by different food and water regimes at both a T_a of 18°C ($P < 0.005$, ANOVA; Fig. 5*a*) and a T_a of 28°C ($P < 0.01$, ANOVA; Fig. 5*b*). The average daily metabolic rate was significantly lower when both food and water were withheld or when only water was available than when food was available with or without drinking water.

The average daily metabolic rate was also significantly affected by T_a. At a T_a of 18°C the average daily metabolic rate was higher than that at 28°C for both individuals displaying torpor and remaining normothermic ($P < 0.01$, *t*-test). At a T_a of 18°C, the average daily metabolic rate of individuals that entered daily torpor (3.15 ± 0.44 mL g^{-1} h^{-1}, $N = 6$, $n = 27$) was about 80% of those that remained normothermic (3.80 ± 0.69 mL g^{-1} h^{-1}, $N = 6$, $n = 15$; $P < 0.01$, *t*-test). In contrast, at a T_a of 28°C, the average daily metabolic rate did not differ significantly between individuals displaying daily torpor (2.26 ± 0.59 mL g^{-1} h^{-1}, $N = 6$, $n = 23$) and those remaining normothermic (2.46 ± 0.24 mL g^{-1} h^{-1}, $N = 6$, $n = 19$; $P > 0.05$, *t*-test).

Discussion

Effect of Environmental Temperature on Torpor and Energy Expenditure

Our study shows that both energy expenditure and the use of torpor in *Sminthopsis macroura* are strongly affected by T_a. At a T_a of 18°C (well below the thermoneutral zone), the average daily metabolic rate of individuals that remained normothermic was much (about 55%) higher than that of the animals at 28°C (close to the thermoneutral zone) since a larger amount of energy is required for thermoregulation. Consequently, at the low T_a *S. macroura* displayed torpor more frequently, especially under food restriction, most likely owing to the depletion

Table 1: Changes in body mass of *Sminthopsis macroura* after 24 h under different food and water regimes

Treatments	Animals Displaying Torpor 18°C	Animals Displaying Torpor 28°C	Animals Remaining Normothermic 18°C	Animals Remaining Normothermic 28°C
Food and water available:				
Change in body mass (mg g^{-1})	18.6 ± 30.1	28.3 ± 43.6	5.9 ± 29.0	7.4 ± 32.1
Body mass (g)	22.0 ± 2.7	21.1 ± 1.6	22.4 ± 1.7	20.0 ± 1.9
Observations	14	8	8	14
Food available, water withheld:				
Change in body mass (mg g^{-1})	19.1 ± 23.2	16.3 ± 30.7	−14.1 ± 25.3	2.7 ± 23.7
Body mass (g)	22.6 ± 2.5	22.5 ± 2.5	24.1 ± 3.6	22.4 ± 2.7
Observations	14	8	8	13
Food withheld, water available:				
Change in body mass (mg g^{-1})	−91.9 ± 14.4	−58.2 ± 20.2	−105.3 ± 28.1	−78.7 ± 23.3
Body mass (g)	23.2 ± 3.0	23.5 ± 2.9	23.8 ± 3.0	23.6 ± 4.9
Observations	17	10	4	11
Food and water withheld:				
Change in body mass (mg g^{-1})	−117.9 ± 35.6	−126.3 ± 23.6	−156.7 ± 14.1	−143.4 ± 27.1
Body mass (g)	21.1 ± 2.6	22.2 ± 1.3	22.8 ± 1.9	22.9 ± 1.4
Observations	18	11	3	10
Dry food available, water withheld:				
Change in body mass (mg g^{-1})	−135.0 ± 22.9	−122.5 ± 14.2	−162.7 ± 14.5	−143.4 ± 33.2
Body mass (g)	21.9 ± 3.2	22.4 ± 2.4	21.9 ± 2.6	22.1 ± 2.8
Observations	18	10	3	11

Note. Values are presented as mean ± SD. Negative signs indicate a decrease. The T_a, use of torpor, and treatment affected the change in body mass independently ($P < 0.05$, three-way ANOVA).

of stored energy reserves below a threshold (Dawson 1989; Hiebert 1990).

As in some other small mammals (Holloway and Geiser 1995), daily torpor at a low T_a reduced daily energy expenditure in *S. macroura*. However, the reduced average daily metabolic rate (decreased by 20% in animals at a T_a of 18°C) was still significantly higher than that at 28°C, demonstrating that daily torpor does not completely compensate for the energetic costs of thermoregulation in the cold.

Although torpor in *S. macroura* at the high T_a was less frequent than at the low T_a, it did occur even when food and water were freely available. At the high T_a, torpor did not significantly reduce daily energy expenditure, apparently because the difference between the metabolic rate during torpor and the resting metabolic rate was too small and torpor bouts were too short to make a significant impact. However, in its desert environment, even during summer when daytime T_a's are high, animals are exposed to low T_a's at night and therefore are able to significantly reduce metabolic rate during torpor. The use of torpor at relatively high T_a's also may reflect the lack of insects during dry, hot summers. This strongly suggests that the use of torpor in *S. macroura* at the high T_a forms part of a daily routine and reflects a long-term adaptation to its environment. Some other species also use torpor routinely without the need for an energy deficit, while short-term stresses only enhance the depth or frequency of torpor (Hudson 1973).

Effect of Food Availability on Energy Expenditure

Energy consumption in a daily heterotherm is the sum of metabolic rate during activity and rest and, if the animal displays torpor, the total metabolic rate during a torpor cycle. In *S. macroura*, at T_a's of 18° and 28°C, the average daily metabolic rate (ADMR) of individuals that remained normothermic was closely related to the resting metabolic rate (RMR; ADMR = 1.16 + 1.01 RMR, $r^2 = 0.88$, $P < 0.01$, $N = 6$, $n = 15$ at 18°C; ADMR = 1.44 + 0.55 RMR, $r^2 = 0.29$, $P < 0.05$, $N = 6$, $n = 19$ at 28°C). In individuals that displayed torpor, the average daily metabolic rate not only was related to the resting metabolic rate (ADMR = 2.03 + 0.41 RMR, $r^2 = 0.17$, $P < 0.05$, $N = 6$, $n = 27$ at 18°C; ADMR = 0.55 + 0.85 RMR, $r^2 = 0.69$, $P < 0.01$, $N = 6$, $n = 23$ at 28°C) but also was a function of the metabolic rate during torpor (TMR; ADMR = 2.70 + 0.34 TMR, $r^2 = 0.37$, $P < 0.01$, $N = 6$, $n = 27$ at 18°C; ADMR = 1.42 + 1.06 TMR, $r^2 = 0.36$, $P < 0.01$, $N = 6$, $n = 23$ at 28°C). Moreover, the metabolic rate during torpor and the resting metabolic rate were positively correlated (TMR = −1.13 + 0.87 RMR, $r^2 = 0.20$, $P < 0.05$, $N = 6$,

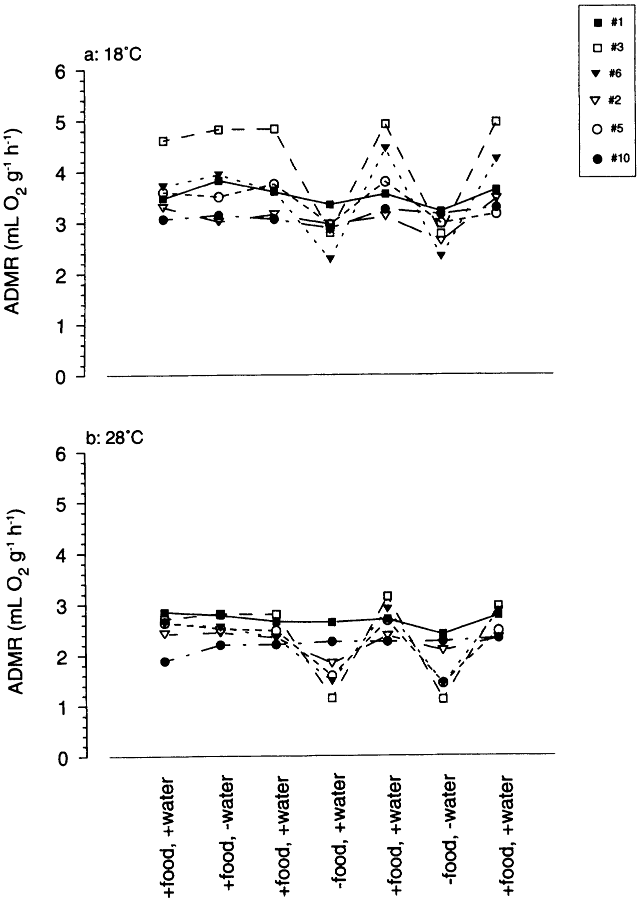

Figure 5. The average daily metabolic rate (ADMR) of *Sminthopsis macroura* under different food and water regimes at T_a's of 18°C (*a*) and 28°C (*b*). The average daily metabolic rate was measured continuously for 7 d. Data from different individuals are shown by different symbols.

$n = 27$ at 18°C; TMR $= -0.02 + 0.40$ RMR, $r^2 = 0.47$, $P < 0.01$, $N = 6$, $n = 23$ at 28°C). This shows that an individual that has a low resting metabolic rate also tends to have a low metabolic rate during torpor and that a low average daily metabolic rate is due to a combined contribution of several variables, including low metabolic rate during torpor and a low resting metabolic rate. These findings suggest that *S. macroura* can conserve energy by decreasing energetic costs during all physiological states, as is known to be the case for other species (Ruf and Heldmaier 1992; Sheafor and Snyder 1996).

While the reduction of average daily metabolic rate was caused by a reduced energy expenditure during all physiological states, the relative contribution differed between low and high T_a's. At the low T_a the resting metabolic rate was not affected by the different food and water regimes ($P > 0.05$, ANOVA); the energy savings due to food withdrawal were caused mainly by enhanced torpor, as has also been shown for a hibernating rodent (Brown and Bartholomew 1969). The reduced T_b (about 4°C in *S. macroura*) results in a lower metabolic rate (Song et al. 1995), and that in turn prolongs torpor bouts (Geiser et al. 1990).

In contrast, at a T_a of 28°C, torpor did not result in significant energy savings. However, food and water regimes influenced the resting metabolic rate ($P < 0.01$, ANOVA) in the same way as they affected average daily metabolic rate. This suggests that at high T_a's, energy conservation was achieved mainly by a reduction of resting metabolic rate due to a lower T_b during normothermia and perhaps also due to the lack of regulatory diet-induced thermogenesis.

Effect of Water on Torpor and Energy Expenditure

Although torpor and energy expenditure were affected by food availability, depriving the animals of drinking water had little effect on the above variables of *S. macroura* at either low or high T_a's. This suggests that freely available drinking water is less important than food availability for induction of torpor in this species, which is adapted to an arid environment. However, when water was withheld, the animal compensated by consuming a larger amount of moist food. In the field, *S. macroura* is nocturnal and avoids exposure to high T_a's and extreme dryness and thus water loss by hiding under logs or rocks (Morton 1982). Since desert species including *Sminthopsis* are known to have very effective kidneys (Brooker and Withers 1994), they have low water turnover rates (Kennedy and Macfarlane 1971) and are able to survive on water from food and metabolic water (Hudson and Bartholomew 1964; MacMillen 1972). Thus, short-term removal of drinking water is probably not a physiological stress for *S. macroura*.

This interpretation may not appear to be supported by our observation that the availability of dry food resulted in deeper and more frequent torpor when water was withheld. However, it is likely that this result was not due to lack of water but due to a reduction of food intake because thirsty animals are known to dislike dry food (Hudson 1973), and *S. macroura* consumed none of it. Moreover, it is known that low environmental humidity can induce torpidity in small heterothermic endotherms because of a decline of food consumption (Hudson and Bartholomew 1964).

We conclude that thermoregulation and energy expenditure of *S. macroura* are strongly affected by food availability but little influenced by restriction of drinking water. Reduction of energy expenditure due to food shortage at low and high T_a's is achieved by different physiological responses. In the cold, energy conservation is achieved by employing torpor, whereas in a warm environment a reduction of resting metabolic rate is used to save energy.

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