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## Radiant heat affects thermoregulation and energy expenditure during rewarming from torpor

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**Abstract** The high expenditure of energy required for endogenous rewarming is one of the widely perceived disadvantages of torpor. However, recent evidence demonstrates that passive rewarming either by the increase of ambient temperature or by basking in the sun appears to be common in heterothermic birds and mammals. As it is presently unknown how radiant heat affects energy expenditure during rewarming from torpor and little is known about how it affects normothermic thermoregulation, we quantified the effects of radiant heat on body temperature and metabolic rate of the small (body mass 25 g) marsupial *Sminthopsis macroura* in the laboratory. Normothermic resting individuals exposed to radiant heat were able to maintain metabolic rates near basal levels (at  $0.91 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ) and a constant body temperature down to an ambient temperature of  $12^\circ\text{C}$ . In contrast, metabolic rates of individuals without access to radiant heat were 4.5-times higher at an ambient temperature of  $12^\circ\text{C}$  and body temperature fell with ambient temperature. During radiant heat-assisted passive rewarming from torpor, animals did not employ shivering but appeared to maximise uptake of radiant heat. Their metabolic rate increased only 3.2-times with a  $15^\circ\text{C}$  rise of body temperature ( $Q_{10}=2.2$ ), as predicted by  $Q_{10}$  effects. In contrast, during active rewarming shivering was intensive and metabolic rates showed an 11.6-times increase. Although body temperature showed a similar absolute change between the beginning and the end of the rewarming process, the overall energetic cost during active rewarming was 6.3-times greater than that during passive, radiant heat-assisted rewarming. Our study demonstrates that energetic models assuming active rewarming from torpor at low ambient temperatures can substantially

over-estimate energetic costs. The low energy expenditure during passive arousal provides an alternative explanation as to why daily torpor is common in sunny regions and suggests that the prevalence of torpor in low latitudes may have been under-estimated in the past.

**Keywords** Arid zone · Thermoenergetics · Marsupial mammal · *Sminthopsis macroura* · Torpor

**Abbreviations** *ADMR* average daily metabolic rate · *BMR* basal metabolic rate · *C* apparent thermal conductance · *MR* metabolic rate · *RMR* resting metabolic rate ·  $T_a$  ambient temperature ·  $T_b$  body temperature · *TMR* torpor metabolic rate

### Introduction

It is widely accepted that torpor in mammals and birds, which is characterised by periodic reductions of body temperature ( $T_b$ ) and metabolic rate (MR), is primarily used for energy conservation (Lyman et al. 1982; Boyer and Barnes 1999). Nevertheless, a major disadvantage from an energetic point of view seems to be the high expenditure of energy that is required for endothermic arousals at the end of a torpor bout. This is especially the case for daily torpor, which usually lasts for up to about 12 h within a 24-h cycle. Although MR may be reduced by 90% or more during daily torpor compared with that in normothermic, resting individuals, daily energy savings through the use of torpor are usually in the order of 50–20% or less because of the high costs of rewarming (Kenagy 1989; Ellison and Skinner 1992; Geiser and Ruf 1995; Holloway and Geiser 1995; Lovegrove et al. 1999). It has been suggested that during short and shallow bouts of torpor, the energetic costs associated with rewarming may outweigh energy savings accrued during torpor and that consequently torpor may be counterproductive (Prothero and Jürgens 1986; Ellison and Skinner 1992).

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Calculations made of energy expenditure during torpor in order to assess its relative advantages and disadvantages have largely been based on data from laboratory studies, usually conducted under constant ambient temperatures ( $T_a$ ). However, recent evidence from field studies in both mammals and birds clearly shows that rewarming in many species can be to a large extent a passive process (Schmid 1996; Brigham et al. 2000; Körtner et al. 2000; Mzilikazi et al. 2002) and that rewarming costs in the laboratory can be reduced considerably by passive rewarming via a rise of  $T_a$  (Lovegrove et al. 1999). Moreover, basking in the sun, which is also likely to reduce the costs of rewarming, has been observed during and after arousal from torpor in free-ranging *Pseudantechinus macdonnellensis*, an insectivorous member of the marsupial family Dasyuridae from central Australia (Geiser et al. 2002). Consequently, energetic costs of rewarming in many species may have been substantially over-estimated in the past.

As the effect of radiant heat on energy costs during rewarming from torpor has not been previously investigated, and little is known about its effect on normothermic thermoregulation, we determined how radiant heat affects the thermal response and energy expenditure in torpid, as well as normothermic, dunnarts, *Sminthopsis macroura*. This small, nocturnal, insectivorous arid-zone marsupial, like *Pseudantechinus*, is also a member of the Dasyuridae and has a high propensity for torpor in the laboratory (Geiser and Baudinette 1987; Hume 1999). Although no field experiments have been conducted to verify that *S. macroura* basks in the wild, it basks in the sun during rewarming from torpor in captivity (F. Geiser and R.L. Drury unpublished observation). Moreover, the species has ample access to solar heat throughout most of the year in its natural habitat and several members of its family use basking extensively (Geiser 2002).

## Material and methods

Six adult *S. macroura* of body mass  $25.2 \pm 1.9$  g and captive-bred at the University of New England in Armidale, were used in the study. Animals were maintained individually in cages (40 cm  $\times$  26 cm  $\times$  16 cm; containing a nest box) under a 12L:12D photoperiod (lights on 06:00–18:00 hours). Cages were cleaned and bedding material changed weekly when animals were weighed. Food, consisting of canned moist dog food (Pal) and macerated dry cat food (Friskies Go-Cat), supplemented with minerals and multi-vitamins (PetVite), was supplied daily ad libitum; water was available ad libitum, and mealworms were provided once per week.

Before measurements began, we implanted temperature-sensitive transmitters (Mini-mitter, Sunriver,  $\pm 0.1$  °C, mass 1.6 g) into the body cavity of the animals under Oxygen/Forthane anaesthesia. Prior to surgery, transmitters were calibrated (to the nearest 0.1 °C) in a water bath against a precision mercury thermometer traceable to a national standard.

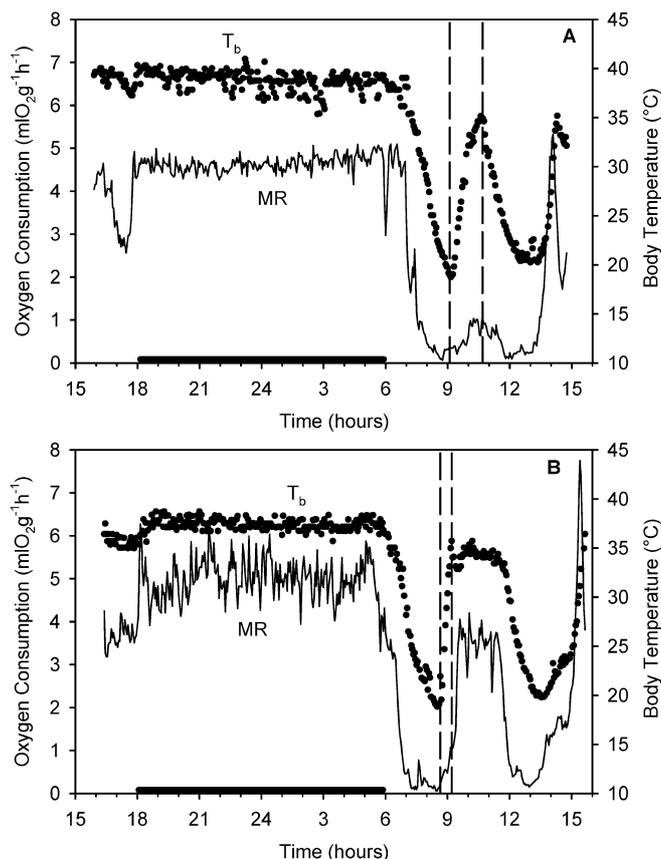
Two types of measurements were performed: (i) during the day, from about 08:00 hours to 17:00 hours to determine the response of  $T_b$  and MR to radiant heat of normothermic, resting individuals, and (ii) overnight, from about 16:00 hours and lasting for 23–24 h; these measurements were conducted to induce torpor and to

determine the response of  $T_b$  and MR to radiant heat in torpid individuals on the following morning (Fig. 1).

Normothermic individuals were exposed to a  $T_a$  that was reduced in steps from about 22 °C to 16 °C to 12 °C, while MR and  $T_b$  were being measured. Each  $T_a$  was maintained for 2–3 h to determine resting MR (RMR) at each  $T_a$ , both with and without radiant heat. Thus, after adjusting  $T_a$ , animals were measured for about 1 h each with and without radiant heat. Experiments on normothermic, resting individuals usually lasted for about 9 h during the rest phase of this nocturnal species.

To determine the response of torpid individuals to radiant heat, the  $T_b$  and MR of each animal was measured over 23–24 h at a  $T_a$  of about 16 °C beginning at about 16:00 hours. These measurements were also used to determine general torpor patterns and torpor use and average daily metabolic rates (ADMIR). Torpor was defined as  $T_b$  falling below 30 °C and torpor bout duration as the time with a  $T_b < 30$  °C (Barclay et al. 2001).

Radiant heat was provided by a heat lamp (Sylvania incandescence 60 W reflector globe, 99% colour rendering index, 2850 K) placed at an angle of 45° and 25 cm away from the glass respirometer. The natural solar radiation on sunny days in winter in Armidale ranges from 100,000 lux to 120,000 lux at 09:00–14:00 hours (when our rewarming measurements were conducted), in comparison to the 5,000 lux generated by the heat lamp at 25 cm distance (Gossen Panlux). The  $T_a$  in the respirometer was maintained by reducing the  $T_a$  in the temperature-controlled cabinet during the time when the lamp was on and closely monitoring



**Fig. 1A–B** Time course of body temperature ( $T_b$ ) and metabolic rate of two individual *Sminthopsis macroura* exposed to  $T_a$  16 °C. At the beginning of passive rewarming body mass was estimated to be 23.7 g (A) and 18.6 g (B). The black bar on the x-axis indicates the dark phase and the broken vertical lines indicate the beginning and end of the passive radiant heat-assisted rewarming phase, when the heat lamp was switched on

the  $T_a$  within the metabolic chamber. Behaviour of animals was observed via a small Perspex-covered hole in the temperature-controlled cabinet.

MR was measured as rate of oxygen consumption using open-flow respirometry. Animals were placed into 0.75-l glass respirometry chambers (flow rate  $450 \text{ ml min}^{-1}$ ) within a temperature-controlled cabinet ( $\pm 0.5^\circ\text{C}$ ) under a 12L:12D photoperiod. Food and water were not available during the measurements. Animals were weighed before and after each MR measurement period and a linear decrease of body mass was assumed for calculation of mass-specific MR. A dual-channel oxygen analyser (Ametek Applied Electrochemistry S-3A/II, Pittsburgh) was used, but only one channel was read to ensure no disturbance would occur (i.e. one individual was measured at a time). The millivolt output from this channel was recorded every 3 min. A fresh air sample, taken from outside the building by solenoid valves every 15 min, was used to calculate the differential with air from the animal channel. The flow-rate of dry air passing through the respirometry chamber was controlled with rotameters (7908, Aarlborg, New York) and measured with mass flowmeters (FMA-5606, Omega, Stamford). For both RMR and MR during torpor (TMR), at least three to four consecutive readings (i.e. over at least 9–12 min) when MR was stable and minimal were averaged and these were assumed to represent steady-state values. These means were used for further calculations. Energetic costs of rewarming with and without radiant heat were calculated by integrating the MR readings from the beginning to the end of the rewarming process when  $T_b$  had reached  $\sim 35^\circ\text{C}$ . For calculation of ADMR, measurements were integrated over the entire 23–24 h, excluding the 1st h to exclude the initial high MR due to handling. Alternatively, ADMR were also calculated after passive rewarming assuming: (i) animals were resting and exposed to radiant heat for the entire post-arousal period, and (ii) animals were resting without radiant heat at  $T_a 16^\circ\text{C}$ . Oxygen consumption values were converted to joules assuming  $20.083 \text{ J ml O}_2^{-1}$ . Calculation of MR was performed according to Eqn. 3a from Withers (1977) assuming an RQ of 0.85. Apparent thermal conductance (C) was calculated using the standard equation:  $C = \text{MR}/(T_b - T_a)$ .

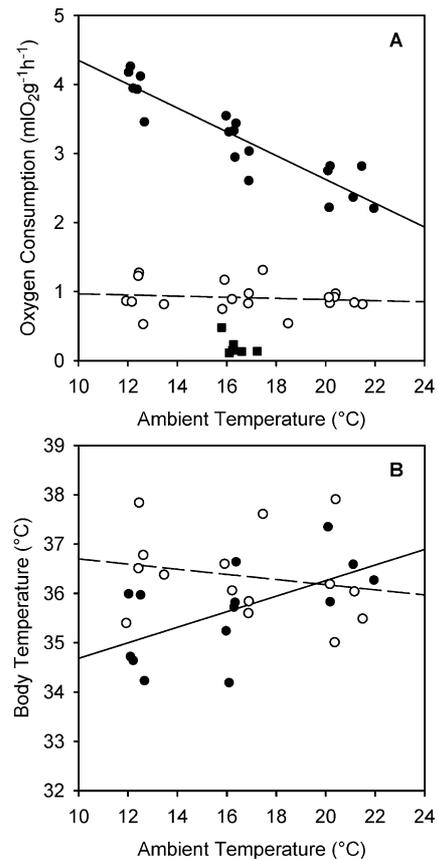
The  $T_b$  of individuals and the  $T_a$  were measured every 3 min at the time MR was determined and the mean values were calculated as described for MR. The transmitter signal from each individual was received by a ferrite rod antenna connected to a receiver and was transformed to a square-wave signal after subtraction of background noise. The  $T_a$  in the respirometry chamber was measured by a thermocouple that was inserted 1 cm into the chamber to the nearest  $0.1^\circ\text{C}$  and recorded with a digital thermometer (Omega DP116). Output from the flowmeter, oxygen analyser, receiver and digital thermometer were interfaced to a personal computer using an A/D 14-bit converter card.

Numerical values are presented as mean  $\pm$  1SD for  $n$  number of individuals.  $N$  represents the number of measurements. Paired  $t$ -tests were used to determine differences between physiological variables. Linear regressions were fitted using the method of least squares and differences between regressions were determined using ANCOVA.

## Results

### Normothermia

Radiant heat had a pronounced effect on the RMR of normothermic *S. macroura*. The RMR of normothermic individuals without exposure to radiant heat increased with decreasing  $T_a$  ( $r^2 = 0.84$ ; slope  $-0.17$ ;  $C = 0.17 \pm 0.01 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ ) between a  $T_a$  of  $22^\circ\text{C}$  and  $12^\circ\text{C}$  (Fig. 2A). In contrast, when radiant heat was provided, MR over the same  $T_a$  range was almost constant



**Fig. 2A–B** Metabolic rates (MR) (A) measured as oxygen consumption, and  $T_b$  (B) as a function of  $T_a$  in normothermic, resting *S. macroura* without (filled circles) and with (unfilled circles) access to radiant heat. The minimum MR of torpid individuals (filled squares) are shown for comparison. The equations were:  $\text{MR} = 6.07 - 0.17 T_a$ ,  $r^2 = 0.84$ ,  $P < 0.001$  (without radiant heat);  $\text{MR} = 1.05 - 0.008 T_a$ ,  $r^2 = 0.02$ ,  $P > 0.5$  (with radiant heat);  $T_b = 33.11 + 0.16 T_a$ ,  $r^2 = 0.37$ ,  $P < 0.025$  (without radiant heat);  $T_b = 37.22 - 0.05 T_a$ ,  $r^2 = 0.04$ ,  $P > 0.4$  (with radiant heat)

( $r^2 = 0.02$ ; slope  $-0.008$ ,  $C = 0.05 \pm 0.01 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ ) and the average RMR ( $0.91 \pm 0.21 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ;  $n = 6$ ,  $N = 18$ ) over the entire  $T_a$  range was essentially identical to the BMR of this species ( $0.89 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ; Song et al. 1995). The response of  $T_b$  to a reduction of  $T_a$  also differed between individuals with and without radiant heat (Fig. 2B). Whereas  $T_b$  rose with  $T_a$  in individuals without radiant heat ( $r^2 = 0.37$ ; slope  $+0.16$ ) it was almost constant in individuals exposed to radiant heat ( $r^2 = 0.04$ ; slope  $-0.05$ ) and the slope of the two equations differed significantly ( $P < 0.05$ ). However, the overall mean  $T_b$  of normothermic individuals was similar with ( $T_b = 36.4 \pm 0.9^\circ\text{C}$ ) and without ( $T_b = 35.7 \pm 0.9^\circ\text{C}$ ) radiant heat.

### Torpor and arousal

Torpor usually commenced in the second part of the night or early morning (Fig. 1). When animals approached or had reached steady state torpor, usually by 09:00 hours, the heat lamp was switched on, the re-

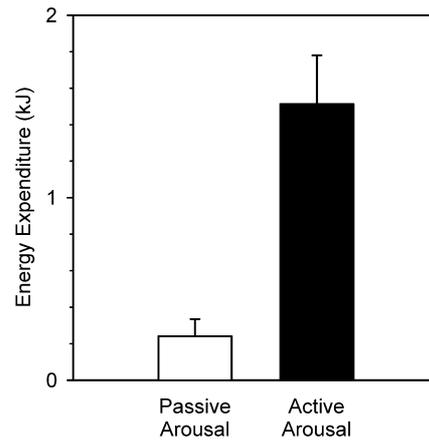
sponse of MR and  $T_b$  was measured and the animal was observed at regular intervals. Although  $T_a$  increased marginally by  $2.5 \pm 0.9$  °C from the beginning to the end of the passive, radiant heat-assisted rewarming process,  $T_b$  increased from an average minimum of  $20.6 \pm 2.6$  °C, over  $46 \pm 22$  min by  $0.36 \pm 0.11$  °C min<sup>-1</sup> to an average  $T_b$  of  $35.6 \pm 0.4$  °C, after which the heat lamp was switched off. In contrast to  $T_b$ , the MR increased only 3.2-times; from  $0.37 \pm 0.18$  ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup> to  $1.19 \pm 0.27$  ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>, and the average  $Q_{10}$  between the beginning and end of the passive rewarming process was 2.2. Thus, for 81% of the passive rewarming time animals were able to maintain MR below basal levels. Throughout the rewarming process no shivering was observed. All individuals basked in the radiant heat and stretched out with their back or side facing the heat lamp, apparently to maximise heat uptake.

On most occasions ( $n=6$ ,  $N=6$  out of  $N=8$  observations), animals re-entered a second bout of torpor  $1.43 \pm 0.05$  h after the heat lamp was switched off and remained in this torpor bout for an average of  $2.5 \pm 0.03$  h. Arousal from the second bout of torpor without radiant heat was achieved with endogenous heat production and a large MR peak (Fig. 1) and thus differed substantially from the largely passive rewarming process described above. The minimum  $T_b$  at the beginning of active arousal was  $21.5 \pm 2.0$  °C and increased to  $34.9 \pm 1.5$  °C over  $78 \pm 30$  min at a rate of  $0.18 \pm 0.04$  °C min<sup>-1</sup> while the  $T_a$  increased by  $0.6 \pm 0.2$  °C. The MR showed an enormous (11.6-times) increase from  $0.50 \pm 0.38$  ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup> to  $5.82 \pm 1.19$  ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup> over the same time period and the  $Q_{10}$  calculated for comparison with the passive rewarming process was 6.2 (recognising that the value is artificially high because it compares two physiologically different states, i.e. thermo-conforming with thermo-regulating individuals, rather than providing a measure of a direct temperature effect on MR). Paired  $t$ -tests revealed that the  $T_b$  did not differ at the beginning and end of the passive and active arousal processes, nor did the TMR at the beginning of the passive and active arousal processes. However, the maximum MR at the end of arousal and the rate of rewarming differed significantly ( $P < 0.025$ ) between active and passive rewarming.

The overall cost of rewarming was  $0.241 \pm 0.094$  kJ during radiant energy-assisted rewarming in comparison to the 6.3-times greater ( $P < 0.001$ ) cost of rewarming ( $1.513 \pm 0.267$  kJ) during active arousal (Fig. 3). The average minimum C during torpor was  $0.03 \pm 0.01$  ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup> °C<sup>-1</sup> and increased to  $0.06 \pm 0.01$  ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup> °C<sup>-1</sup> during passive rewarming and  $0.29 \pm 0.03$  ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup> °C<sup>-1</sup> during active rewarming.

## Discussion

Our study shows that radiant heat substantially affects energy expenditure during arousal from torpor. It suggests that calculations estimating energy expenditure



**Fig. 3** Total energy expenditure during radiant heat-assisted passive, and active rewarming of *S. macroura*

during torpor using laboratory data measured under constant  $T_a$  are likely to be overestimates of energy expenditure in the wild. Moreover, our study provides a plausible explanation for the common use of daily torpor in sunny regions.

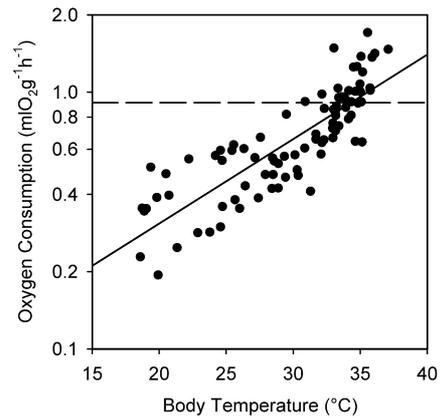
Our study is the first to investigate in detail the effect of radiant heat on rewarming from torpor. Observations on *Pseudantechinus macdonnellensis* in the field showed that dasyurids are capable of coordinated movements at  $T_b$  of about 20 °C (Geiser et al. 2002), similar to the  $T_b$  at which our passive rewarming process in *S. macroura* began. In previous studies it was shown that a rise of  $T_a$  can reduce costs of rewarming to about 36% of that during active rewarming at constant  $T_a$  (Lovegrove et al. 1999), but in most of the observed cases, active rewarming, as indicated by a steep rise in MR, was activated after  $T_b$  had reached about 25 °C (Schmid 1996; Lovegrove et al. 1999). In contrast, in the present study, torpid *S. macroura* did not initiate active rewarming throughout exposure to radiant heat and arousal costs were consequently reduced to about 15% of those required for active rewarming at constant  $T_a$ . Somewhat surprisingly, the average arousal cost of passive rewarming was also only about 70% of BMR, whereas during active arousal the average energy expenditure was 340% of BMR. As MR during passive rewarming remained below basal levels for most of the arousal process, essentially any form of torpor, no matter how short, would result in a reduction in energy expenditure, provided there was access to sufficient external heat, when compared to RMR at most  $T_a$ .

It is interesting that after passive rewarming and normothermic periods of just over 80 min, most animals re-entered torpor a second time to arouse again actively before the next activity period. This is a pattern that seems to be common in the field in both birds and mammals and is in contrast to most laboratory studies under constant  $T_a$  with only a single bout per day (Brigham et al. 2000; Geiser et al. 2000; Turbill et al. 2002). Although the second torpor bout was short and may appear counterproductive because of the high re-

warming costs, it nevertheless saved energy as reflected by the overall daily energy expenditure and afternoon energy expenditure during and after the second torpor bout. Despite the short torpor bout duration and the high rewarming MR peak, energy expenditure from the beginning of the second torpor bout to the end of MR measurements at about 15:00 hours was on average  $1.94 \pm 0.58 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ , which is 60% of that if the animals would have been resting at  $T_a$  16 °C for the same time period. Moreover, ADMR for animals undergoing one active and one passive arousal was on average  $40 \text{ kJ day}^{-1}$ . Assuming that the animals had access to radiant heat throughout the afternoon after the passive arousal, ADMR would have been reduced by about 13% to  $35 \text{ kJ day}^{-1}$ . In contrast, if the animals were using RMR at  $T_a$  16 °C for the rest of the afternoon, ADMR would have increased by about 8% to  $43.1 \text{ kJ day}^{-1}$ . Thus, although the cost of active arousal in the afternoon torpor bout was 6.3 times that of passive rewarming, and the bouts lasted for only 2.5 h, daily energy expenditure was still reduced in comparison to that required for RMR over the time period the second torpor bout was employed.

While our observations may be especially important for daily heterotherms, evidence is emerging that hibernators (species capable of prolonged bouts of torpor lasting for several days or weeks) may also commonly use external heat for periodic rewarming. For example, hibernating fat-tailed lemurs (*Cheirogaleus medius*) in Madagascar show predictable daily changes of  $T_b$  rising more or less with  $T_a$  from about 20 to 30 °C with parallel changes in MR (Dausmann et al. 2000). The daily, largely passive change in  $T_b$  may be the reason why this species can hibernate for up to 7 months, although its MR is on average about 10-times that predicted for a hibernator at  $T_b < 10$  °C (Geiser and Ruf 1995), apparently because it is freed from the requirement for energy-expensive active arousals. These costly arousals are characteristic for most other hibernators and account for most of the energy used during the hibernation season (Boyer and Barnes 1999). Radiation also appears to be employed by poorwills (*Phalaenoptilus nuttallii*) in Arizona (Brigham et al. 2002). Prolonged bouts in poorwills are often used in winter when the species is dormant for most of the time, although partial passive rewarming by sun and  $T_a$  is used every day. Furthermore, torpid Australian tree roosting bats that are capable of hibernation show daily cycles of  $T_b$  which closely follow the change of  $T_a$ , and usually arouse after  $T_b$  has been substantially raised by external heat (Turbill et al. 2002). Even young alpine marmots (*Marmota marmota*) that hibernate in deep burrows at more or less constant low  $T_a$  use external heat to reduce costs of rewarming, although in this case the heat is provided by the parents (Arnold 1993).

The relationship between  $T_b$  and MR during torpor has received considerable attention. Often illogical calculations of  $Q_{10}$  comparing different physiological states rather than the effects of temperature on rates have led



**Fig. 4** Metabolic rates measured as oxygen consumption of thermo-conforming *S. macroura* as a function of  $T_b$  during passive, radiant heat-assisted rewarming. The vertical broken line represents the average MR of normothermic, resting individuals exposed to radiant heat. The best fit was achieved after log-transformation of the y-axis and the equation was:  $\log_{10} \text{ TMR} = -1.17 + 0.033 T_b$ ,  $r^2 = 0.70$ ,  $P < 0.001$

to some confusion (Wang and Lee 2000). Our study provides clear evidence that MR during passive rewarming, when animals did not switch between physiological states and maintained a low  $C$ , is a function of  $T_b$  (Fig. 4). The logarithm of MR was a function of  $T_b$  ( $r^2 = 0.70$ ) and the slope calculated from the regression corresponds to a  $Q_{10}$  of 2.3, which is almost identical to the  $Q_{10}$  of 2.2 calculated from the average minima and maxima of MR and  $T_b$  during passive rewarming. Thus, our results support the view that MR during daily torpor in thermo-conforming animals is to a large extent determined by  $T_b$  (Geiser 1988).

The effect of radiant heat on resting energy expenditure has been studied previously in the roadrunner (*Geococcyx californicus*), a 300-g bird (Ohmart and Lasiewski 1971). In agreement with our study, roadrunners exposed to radiant heat were able to maintain basal levels of MR between  $T_a$  of 9 °C and 22 °C. However, unlike in the present study, roadrunners did not lower  $T_b$  below 33 °C and consequently the MR of birds in mild, regulated hypothermia with a 5 °C reduction of  $T_b$  were similar to those of normothermic birds during basking with a  $T_b$  of about 38 °C. In contrast, in our study, minimum MR during torpor was about 40% of the BMR because  $T_b$  fell by about 15 °C (Fig. 2).

Lovegrove (2000) proposed that the use of daily torpor is common in areas that experience unpredictable changes in climate. While we agree with this argument, we believe that access to solar radiation is another factor that has to be considered. In Lovegrove's (2000) comparative analysis, daily torpor appears to be especially common in Afrotropical and Australasian regions (33 out of a worldwide total of 56 mammal species), which not only are subject to unpredictable climate, but also receive substantial amounts of solar radiation on many sunny days. We believe that it is the access to sun and/or high daily variations of  $T_a$  within the range of  $T_b$

experienced during torpor that provides a selective edge to many species. Thus, our study challenges the traditional view that torpor should be especially common in cold climates. Because moderate, changing  $T_a$  and basking can substantially reduce arousal costs and because species diversity increases towards the equator in most mammalian taxa, it is likely that the absolute number of heterothermic mammals in relatively warm areas exceeds those living in the cold.

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