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The energetic cost of arousal from torpor in the marsupial *Sminthopsis macroura* : benefits of summer ambient temperature cycles

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Abstract The costs of arousal from induced torpor were measured in the striped-faced dunnart (*Sminthopsis macroura*; ca. 25 g) under two experimental ambient temperature cycles. The sinusoidal-type temperature cycles were designed to evaluate the effects of passive, ambient temperature heating during arousal from torpor in these insectivorous marsupials. It was hypothesised that diel ambient temperature cycles may offer significant energy savings during arousal in animals that employ daily torpor in summer as a response to unpredictable food availability. The cost of arousal in animals in which passive, exogenous heating occurred was significantly lower than that in animals not exposed to an ambient temperature cycle. The total cost of all three phases of torpor (entry, maintenance and arousal) was almost halved when animals were exposed to an ambient heating cycle from 15 °C to 25 °C over a 24-h period. In all animals, irrespective of the experimental ambient temperature cycle employed, the minimum torpor body temperature was 17–18 °C. The body temperature (T_b) of animals exposed to exogenous heating increased from the torpor T_b minimum to a mean value of 22.59 °C before endogenous heat production commenced. This relatively small increase in T_b of ca. 5 °C through 'free' passive heating was sufficient to account for the significant ca. three-fold decrease in the cost of arousal and may represent an important energetic aid to free-ranging animals.

Key words *Sminthopsis macroura* · Marsupial · Torpor · Arousal · Unpredictable environments

Abbreviations T_a ambient temperature · T_b body temperature

Introduction

The evolution of the physiological capacity for torpor and hibernation is thought to be associated with the attendant reduction of the daily energy expenditure of small mammals during periods of energy shortage (Lyman et al. 1982; Heldmaier 1989). Indeed, many employ spontaneous and induced daily torpor in response to cold and food deprivation (Hudson and Scott 1979; Lyman et al. 1982; Heldmaier 1989; Geiser 1994; Geiser and Ruf 1995). The proportion of the normothermic daily energy expenditure that can be saved through daily torpor is dependent primarily upon four factors: (1) body size, (2) the depth of torpor, i.e. the minimum torpor body temperature, (3) the duration of torpor bouts, and (4) ambient temperature (T_a) (Ruf and Heldmaier 1992; Geiser and Ruf 1995). The depth and duration of torpor also provide two of several physiological measures that distinguish between daily torpor and hibernation in small mammals (Geiser and Ruf 1995).

Despite the high cost of arousal from torpor, small mammals have been shown to conserve a component of the obligatory normothermic daily energy expenditure after employing even the shortest possible torpor bouts, i.e. entry followed by immediate arousal (Schmidt-Nielsen 1983). Thus, although the cost of arousal may comprise as much as 75% of the total energy expended during a torpor bout (Tucker 1965), energy is conserved relative to normothermic metabolism nevertheless.

To date, the majority of laboratory studies on induced and spontaneous daily torpor have measured the energetics of torpor in winter-acclimated Nearctic and Palaearctic small mammals and birds (Lyman et al. 1982). During the course of data measurement, the animals are maintained at a constant T_a , usually at 5 °C or 18 °C. More recently, however, an increasing number of

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studies have investigated the incidence and characteristics of winter and summer torpor in Afrotropical (Ellison and Skinner 1991, 1992; Schmid 1996; Webb and Skinner 1996; Lovegrove and Raman 1998), Australasian (Geiser 1994; Holloway and Geiser 1996) and Neotropical (Bozinovic and Rosenmann 1988; Bozinovic and Marquet 1991) small mammals. Several observations and implications of these studies differ distinctly from those on Holarctic small mammals.

Firstly, torpor tends to be employed as readily under conditions of summer acclimation (long-day photoperiods) as it is under short-day winter conditions (Geiser and Baudinette 1985; Holloway and Geiser 1996; Webb and Skinner 1996; Lovegrove and Raman 1998). In this respect, several authors have argued that the evolution of summer torpor may optimise fitness in small non-Holarctic mammals inhabiting regions of unpredictable summer resource availability (Geiser 1994; Lovegrove 1996; Lovegrove and Raman 1998). Unpredictable resources are generally associated with below-average monsoon rainfall and droughts generated by the El Niño Southern Oscillations in the Afrotropical, Australian, Indomalayan and Neotropical zoogeographical zones (Ropelewski and Halpert 1987; Seleshi and Demaree 1995; Stone et al. 1996). By contrast, adaptive heterothermy in Holarctic mammals has been associated primarily with predictable, harsh cold winters (Heldmaier and Steinlechner 1981; Lyman et al. 1982; Heldmaier et al. 1990; Ruf et al. 1993).

Secondly, there is some evidence to suggest that the marked diel cycles of ambient temperature associated with summer may assist arousal from torpor through passive heating in free-ranging small mammals. Ortmann et al. (1996) and Schmid (1996) have measured body temperature (T_b) and oxygen consumption patterns during torpor under natural ambient temperature cycles in mouse lemurs (*Microcebus* sp.) housed in outdoor enclosures in Madagascar. Their data revealed two distinct phases of oxygen consumption and body temperature during arousal in these small primates. Exogenous, passive heating by the increasing T_a of the early photophase was followed by endogenous heat production once a T_b of ca. 25 °C was attained.

In terms of our current understanding of the costs and benefits of daily torpor, there are several fundamental questions we could ask concerning the abiotic conditions associated with summer torpor. First, is the two-phase heating process of arousal identified by Ortmann et al. (1996) and Schmid (1996) a common feature of arousal from summer torpor in nocturnal small mammals? Second, if so, what are the energetic benefits of assisted arousal by passive heating? In this study we address these questions by investigating the costs of entry, maintenance and arousal from daily torpor, under various experimental T_a cycles, in the small insectivorous marsupial *Sminthopsis macroura* (striped-faced dunnart). The stripe-faced dunnart occurs throughout the arid and semi-arid regions of central and western Australia (Strahan 1991).

Materials and methods

Eight adult male *S. macroura* were obtained from a captive breeding program at the University of Melbourne in October 1997. The animals were housed in a constant environment room at a T_a of 22 °C on a 12:12 L:D photoperiod regime. They were fed a daily diet of tinned dog food and macerated cat food pellets ad libitum, supplemented with live mealworms. Water was provided ad libitum.

Following a 3-week adjustment period, temperature-sensitive telemeters (Minimitter type XM) were surgically implanted into the intraperitoneal cavity of the animals under inhalation anaesthesia (Isoflurane in oxygen; 3–4% induction, 1–2% maintenance). The telemeters were calibrated in a water bath at temperatures ranging from 5 °C to 45 °C using a mercury thermometer (0.05 °C).

Experimental design and protocol

During metabolic measurements, the animals were transferred to a temperature cabinet consisting of a converted upright freezer. The temperature inside the cabinet was monitored continuously with a temperature transducer and compared with a setpoint temperature calculated by a personal computer from the algorithm of the experimental temperature cycle. Two sinusoidal-type temperature cycles were used with the maximum T_a coincident with 1700 hours real time (Fig. 1). A 'full-sinusoidal cycle' with a wavelength of 24 h and an amplitude of 10 °C cycled between a minimum of 15 °C and a maximum of 25 °C (Fig. 1a). A 'half-sinusoidal cycle' involved the minimum T_a being maintained at the minimum, once attained at 0500 hours (Fig. 1b). Since our interest was focused primarily on the costs associated with arousal, the two T_a cycles had similar entry-phase profiles, and differed only in respect of the arousal phase. A computer-controlled feedback mechanism was used to control the cabinet temperature by control switching of a 100 W ceramic infrared element (Elstein, Germany) whenever T_a decreased below the time-specific set-point temperature. The cabinet was fitted with a fan to circulate air and minimise and disrupt thermal layering in the cabinet. The cabinet temperature did not vary by more than ca. 0.5 °C from the set-point temperature. A 12:12 L:D photoperiod was maintained in the cabinet at all times.

The animals were maintained in the temperature cabinet in conventional, plastic rodent cages covered with wire mesh lids. Animals not involved in metabolic rate measurement were fed each

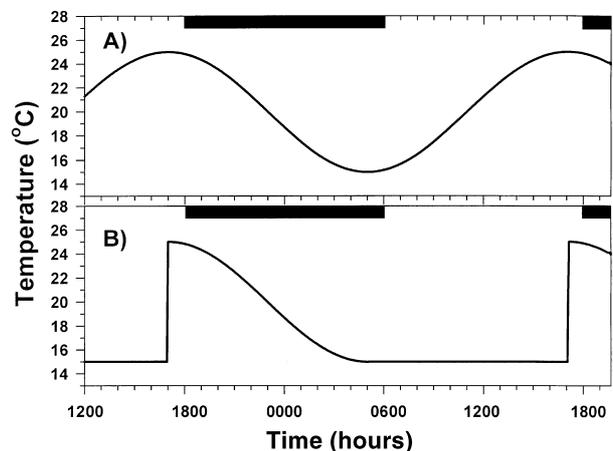


Fig. 1A, B The two experimental ambient temperature (T_a) cycles comprising: (A) a 'full-sinusoidal' cycle (period = 24 h, amplitude = 10 °C, maximum = 25 °C, minimum = 15 °C) and (B) a 'half-sinusoidal' cycle in which the minimum (T_a = 15 °C) is maintained for 12 h from 0500 hours to 1700 hours

day at the same time (ca. 1600 hours). During this feeding period, two experimental animals were placed in respirometers (500 ml) also housed in the temperature cabinet. These experimental animals were not fed prior to being placed in the respirometers. The T_b of all animals, whether they were housed in the respirometers or not, was measured continuously every 6 min for the full 28 days of the data measurement period by the method described in Holloway and Geiser (1995, 1996). Again, all animals, whether they were housed in the respirometer or not, were exposed to the same temperature and photoperiod regime within the temperature cabinet.

The animals were maintained on the full-sinusoidal cycle for 1 week prior to data measurement. Thereafter, two animals were placed in the respirometers every 24 h for oxygen consumption measurement. Repeat measurements were made for each animal at 4-day intervals. After 8 days on the full-sinusoidal cycle, repeat measurements for each animal were also made on the half-sinusoidal cycle. Oxygen consumption and T_b were measured every 3 min and 6 min, respectively, by the methods outlined in Holloway and Geiser (1995, 1996).

Data analysis

A torpor bout is typically comprised of three phases; entry, maintenance and arousal (Schmidt-Nielsen 1983). In order to determine the onset and end of each phase in the torpor cycle, we used the objective method of Yeager and Ultsch (1989) to determine points of deviation or 'inflection' from steady-state physiological measures. The method repeatedly seeks the minimum of the residual sums of squares of two least-squares linear regressions fitted to each side of potential inflexion points. We used this method to determine for the oxygen consumption data: (a) the point of entry into torpor from normothermic values, (b) the onset of the period of sustained torpor, i.e. the maintenance period, (c) the onset of the arousal from torpor, and (d) the end of the peak heat production phase associated with arousal. The total energy expenditure of each phase was calculated by integrating total metabolic rate (ml O_2 /h) over the time period of the torpor phase. Integrated values were converted to units of energy equivalence (kJ) with the factor 20.083 kJ/l O_2 (Schmidt-Nielsen 1983). For each animal, only one of the two replicate torpor bouts at each experimental temperature was chosen for analysis. We subjectively chose the 'best' bout as that in which the depressed metabolic state during the maintenance phase remained more-or-less constant for the longest period of time. The replicates allowed us to discard data for torpor bouts in which partial arousal and re-entry occurred.

Single factor analysis of variance (ANOVA) was used to test for differences in physiological measures between the main experimental factor, i.e. full- and half-sinusoidal temperature cycles. Unless otherwise stated, all mean values reported represent the mean \pm 1 SD.

Results

Body mass

The mean body mass of the animals prior to the commencement of data measurement on the full-sinusoidal cycle (26.33 ± 2.77 g; $n = 8$) was not significantly different to that at the start of data measurements on the half-sinusoidal cycle, 26.03 ± 2.27 g (ANOVA; $F_{1,29} = 0.069$, $P > 0.05$).

On the full-sinusoidal cycle, the body mass of the animals decreased by 3.54 ± 0.58 g during the 24 h food-deprivation measurement cycle. This decrease was, on average, $13.54 \pm 1.85\%$ lower than the body mass at

the start of each measurement period. Similarly, the mean mass loss on the half-sinusoidal cycle was 3.65 ± 0.60 g, an average of $14.17 \pm 2.33\%$ lower than the body mass at the start of the food-deprivation data measurement cycle.

General observations on torpor

Of the eight animals used in the study, six entered a period of sustained torpor lasting longer than 8 h each time that torpor was induced by food deprivation. Generally, the animals entered torpor only when food was withheld. However, animal no. 14 also entered torpor spontaneously on three occasions during the acclimation period (Fig. 2). Animal no. 17 did not enter torpor at all during six separate attempts to induce torpor (Fig. 3). The torpor patterns in animal no. 09 were characterised by consecutive short torpor bouts lasting several hours only. The data from the latter two animals were discarded from all analyses.

The mean minimum T_b during torpor under a full-sinusoidal temperature cycle (17.74 ± 1.29 °C, $n = 5$) was not significantly different (ANOVA; $F_{1,8} = 1.071$, $P > 0.05$) to that under a half-sinusoidal temperature cycle (17.16 ± 0.87 °C, $n = 5$).

The real time of entry into induced torpor ranged from 2030 hours to 0554 hours with a strong median time of entry at 0506 hours (Fig. 4). The mean time of entry was 0318 hours \pm 162 min. The real times by

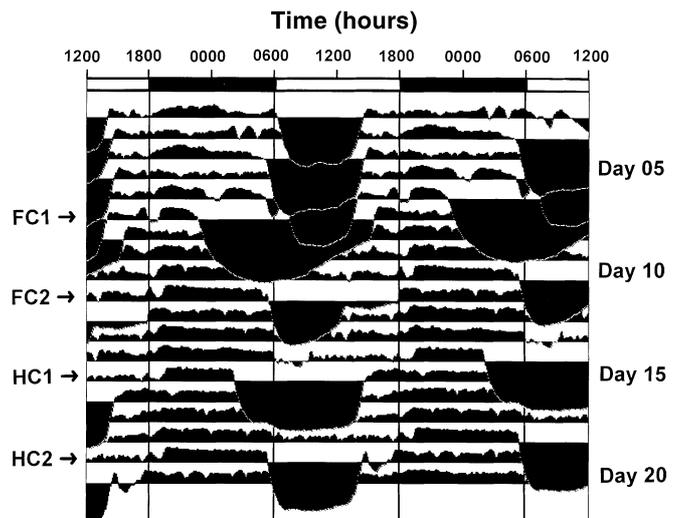


Fig. 2 The body temperature (T_b) of animal no. 14 measured over a 20-day period. The data are double-plotted for easy visual examination. The dark horizontal bars indicate the hours of the scotophase. The scale of T_b ranges from 33 °C to 39 °C in each plot of each day. Torpor bouts are indicated as T_b s less than 33 °C. Food deprivation occurred under the full-sinusoidal temperature cycles (replicates FC1 and FC2) and the half-sinusoidal cycle (replicates HC1 and HC2) where indicated for the respective days. Torpor bouts not associated with food deprivation represent spontaneous torpor bouts

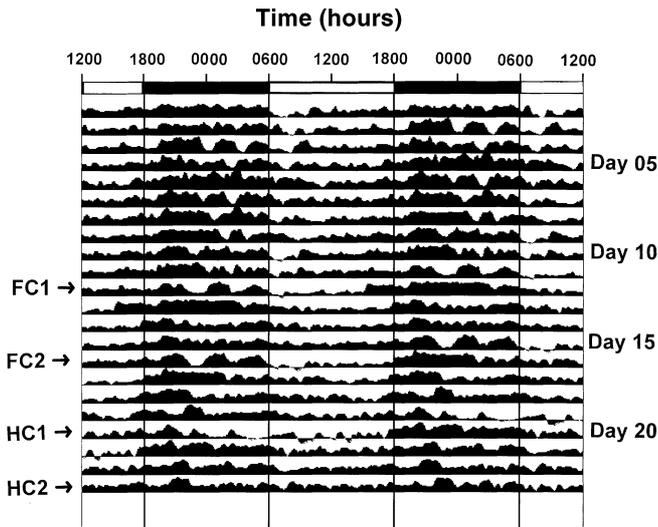


Fig. 3 The T_b of animal no. 17 measured over a 24-day period. The data are double-plotted for easy visual examination. The dark horizontal bars indicate the hours of the scotophase. The scale of T_b ranges from 33 °C to 39 °C in each plot of each day. Food deprivation occurred under the full-sinusoidal temperature cycles (replicates FC1 and FC2) and the half-sinusoidal cycle (replicates HC1 and HC2) where indicated for the respective days. Torpor could not be induced in this animal

which full arousal had occurred were less variable than those for entry into torpor (Fig. 4). Arousal times ranged from 1236 hours to 1548 hours, again with a strong median time at 1412 hours which was, in this instance, closer to the mean real time of 1415 hours \pm 51 min (Fig. 4).

After attaining a minimum torpor T_b , the mean heating rate of animals under a full-sinusoidal cycle (0.018 ± 0.006 °C/min) was approximately double that under the half-sinusoidal cycle (0.009 ± 0.004 °C/min; Fig. 5). The heating rates were not significantly different, however, albeit barely so (ANOVA; $F_{1,8} = 5.97$, $P = 0.0503$). During this period, the rate of oxygen consumption increased marginally under both T_a cycles, but remained low nevertheless (Fig. 5). However, once endogenous heat production commenced, the heating rate of the body increased at a rate proportional to that of heat production (Fig. 5). The mean T_b corresponding with the inflexion point of oxygen consumption at the onset of endogenous heat production was 22.59 ± 0.99 °C under a full-sinusoidal cycle, significantly higher (ANOVA; $F_{1,8} = 14.486$, $P < 0.05$) than that under a half-sinusoidal cycle ($T_b = 19.74 \pm 1.12$ °C). The difference between these two mean T_b s can be attributed to the higher heating rate of animals under a full-sinusoidal cycle.

Following the onset of heat production, the mean heating rate increased several-fold to 0.147 ± 0.036 °C/min and 0.188 ± 0.041 °C/min, under a full- and half-sinusoidal cycle, respectively. These latter heating rates were not significantly different (ANOVA; $F_{1,8} = 2.171$, $P > 0.05$).

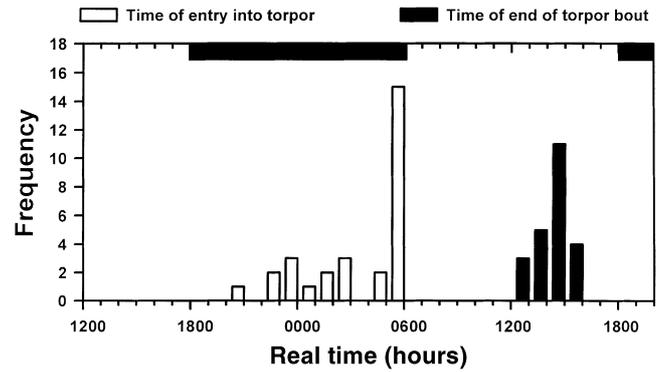


Fig. 4 The real times of entry and full arousal from torpor in *Sminthopsis macroura*. The bins represent hourly intervals. The dark horizontal bars indicate the scotophase. The total number of entry and arousal data points do not correspond because of a few telemeter reception problems

Bout length

The mean bout lengths for six torpor bouts under the full- and half-sinusoidal cycles were 503.0 ± 81.6 min and 654.0 ± 160.5 min, respectively (Fig. 6). These total times were not significantly different (ANOVA; $F_{1,10} = 4.22$, $P > 0.05$). Similarly, the total times for entry and maintenance of torpor (Fig. 6) did not differ significantly between the full- and half-sinusoidal cycles (ANOVA; $F_{1,10} = 3.00$, $P > 0.05$ and $F_{1,10} = 1.11$, $P > 0.05$, respectively). However, the mean arousal time during the full-sinusoidal cycle, 81.0 ± 24.2 min,

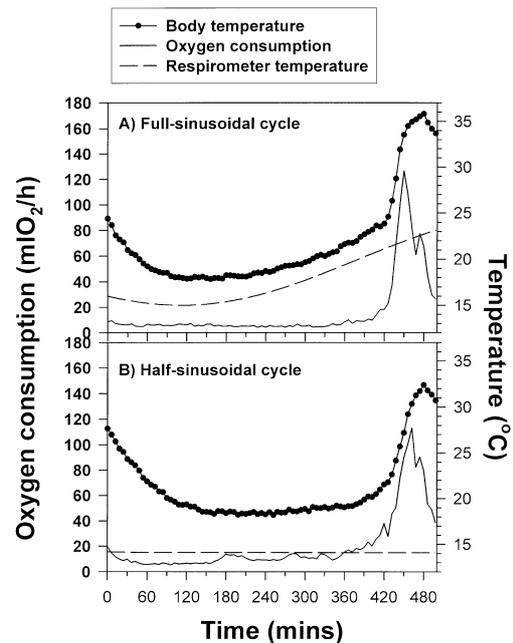


Fig. 5A, B The T_b and oxygen consumption of animal no. 14 during arousal from torpor under: **A** a full-sinusoidal T_a cycle, and **B** the half-sinusoidal T_a cycle. For all animals, the mean T_b s at the oxygen consumption inflexion point associated with the onset of endogenous heat production were 22.6 °C and 19.7 °C under the full- and half-sinusoidal temperature cycles, respectively

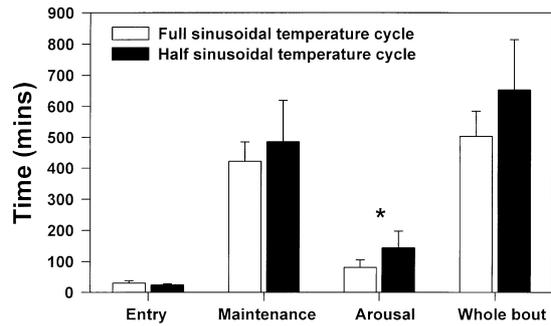


Fig. 6 The mean \pm SD time spent in torpor (whole bout), as well as the mean times spent in the various phases of torpor; entry, maintenance and arousal, in *S. macroura* under the full- and half-sinusoidal T_a cycles. The asterisk (*) indicates a significant difference between the two experimental temperature cycles

was significantly shorter (ANOVA; $F_{1,10} = 6.87$, $P < 0.05$) than that during the half-sinusoidal cycle, 144.0 ± 53.7 min (Fig. 6).

Energy expenditure

The total energy expenditure calculated between the full- and half-sinusoidal cycles did not differ for torpor entry (ANOVA; $F_{1,10} = 0.121$, $P > 0.05$) and maintenance (ANOVA; $F_{1,10} = 2.00$, $P > 0.05$; Fig. 7). During torpor maintenance, the mean energy expenditure during the half-sinusoidal cycle (2807.7 ± 1495.6 kJ) was nevertheless 34% higher than that calculated for the full-sinusoidal cycle (1850.7 ± 714.9 kJ). On the other hand, the mean cost of arousal in the half-sinusoidal cycle (3732.5 ± 1867.1 kJ) was significantly 2.76 times higher (ANOVA; $F_{1,10} = 8.96$, $P < 0.05$) than that under a full-sinusoidal cycle (1350.0 ± 561.2 kJ; Fig. 7). Consequently, the mean energy expenditure for the whole torpor bout (i.e. entry + maintenance + arousal) was also significantly higher (ANOVA; $F_{1,10} = 7.26$, $P < 0.05$) under the

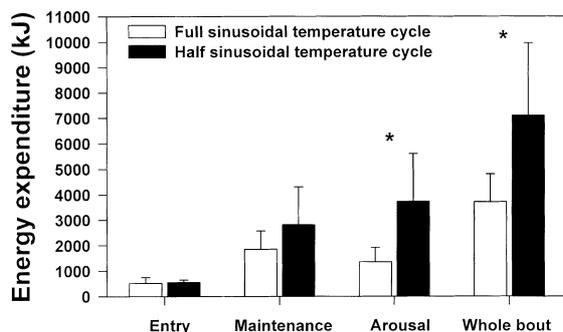


Fig. 7 The mean \pm SD energy expenditure of torpor (whole bout), as well as the mean energy expenditure of the various phases of torpor; entry, maintenance and arousal, in *S. macroura* under the full- and half-sinusoidal T_a cycles. The asterisk (*) indicates a significant difference between the two experimental temperature cycles

half-sinusoidal cycle (7092.3 ± 2870.6 kJ), compared with that under the full-sinusoidal cycle (3719.0 ± 1080.0 kJ; Fig. 7). On average, the cost of arousal represented 36.55% of the total energy expenditure of the torpor bout under the full-sinusoidal cycle compared with 51.86% under the half-sinusoidal cycle.

Discussion

S. macroura show intraspecific variation in the propensity for induced and spontaneous daily torpor that has been reported in several small mammals (Elliott et al. 1987; Tannenbaum and Pivorun 1987; Kirsch et al. 1991; Ruf et al. 1991). Animals that are readily induced to enter daily torpor have been termed 'torpor-prone', whereas those that do not enter torpor and those that are extremely reluctant to enter torpor are termed 'torpor-resistant' (Ruf and Heldmaier 1992). Ruf and Heldmaier (1992) have suggested that the "...striking variability of torpor depth and duration in the Djungarian hamster *Phodopus sungorus* results from individually different solutions to the problem of counteracting demands for a maximal reduction of energy uptake and a minimal loss of alertness, activity, and energy uptake". Lovegrove and Raman (1998) have also shown strong gender differences in the propensity for torpor in Afro-tropical pouched mice (*Saccostomus campestris*). They argue that the torpor resistance of summer-acclimated male pouched mice (80–100 g) under food and/or cold stress may be associated with the increased probability of obtaining matings with non-torpid females during the summer breeding season.

Although *S. macroura* readily enter torpor during summer or under long-day conditions (Geiser and Baudinette 1987), this study and other studies (Geiser et al. 1984; Holloway and Geiser 1995, 1996) confirm that male *Sminthopsis* sp. readily enter torpor. Hence, it is likely that torpor resistance may be restricted to a small percentage of the male *S. macroura* population, rather than to all males sensu the larger pouched mice. Presumably, the small body mass of *Sminthopsis* (ca. 25 g) and its attendant high mass-specific energy demands necessitates more widespread intra-gender employment of torpor.

The torpor-prone animals in this study displayed a circadian rhythm of T_b (Fig. 3) and oxygen consumption consistent with the metabolic circadian rhythms of nocturnal small mammals (Aschoff 1970, 1982, 1983; Aschoff et al. 1982; Kenagy and Vleck 1982). Nevertheless, torpor bouts were not restricted to the rest-phase (photophase) – they commenced throughout most of the mid- and late-scotophase.

An experimental sinusoidal temperature cycle with an amplitude of 10 °C, cycling between a minimum of 15 °C and a maximum of 25 °C, significantly reduced the cost of arousal from torpor in *S. macroura*. This temperature cycle was designed to simulate, in the simplest, theoretical sense, a natural T_a cycle. During the heating phase of the T_a cycle, torpid animals were heated

passively. Body temperatures increased from a mean minimum torpor T_b of 17.74 °C to an average of 22.59 °C (an increase of 4.85 °C) at little or no energetic cost to the animal.

Although the influence of passive heating accounted for exogenous heating of the body temperature of only ca. 5 °C, the associated energetic savings of arousal and hence total energy savings are considerable. In short, the cost of arousal was reduced from 52% to 37% of the total energy expenditure of the torpor bout, nearly halving the total energy expenditure of the torpor bout. Hence T_a cycles coincident with the photophase can profoundly optimise the energetic advantages of daily summer torpor in small mammals, even under T_a cycles with relatively small temperature amplitudes. Laboratory studies that measure the cost of torpor under conditions of constant temperature may therefore be significantly underestimating the energetic benefits of daily summer torpor in free-ranging mammals.

To some extent, the relative mean times that animals spent in each phase of the torpor bout (Fig. 6) will influence the total energy expenditure of each phase (Fig. 7). In this study, animals under a half-sinusoidal ambient temperature cycle did indeed spend a longer mean time in the maintenance and arousal phases. However, the times were significantly different between the two experimental temperature treatments for the arousal phase only. A longer arousal time is to be expected under a half-sinusoidal cycle because the animals need to reheat from the minimum torpor T_b (17.74 °C). Animals under a full cycle, on the other hand, need to be reheated from 22.59 °C only, owing to prior exogenous passive heating.

Despite assisted arousal by passive heating under a full-sinusoidal cycle, there was no difference in the time of the day at which full arousal under the respective temperature-cycle treatments occurred. Theoretically, the T_b could have been elevated even higher through passive heating, perhaps to 1–2 °C higher than 25 °C, had endogenous heat production not commenced when it did. However, since circadian rhythms of endogenous heat production associated with arousal are closely synchronised with photoperiod (Aschoff et al. 1974; Aschoff 1983, 1986), maximum passive heating should occur only when the peak of any T_a cycle is attained several hours prior to the onset of the scotophase. In this study, the peak T_a occurred at 1700 hours, 1 h prior to the lights-off time.

The potential daily energy savings which free-ranging animals could accrue from cycles of T_a should depend not only on the amplitude of the cycle and its phase relationship with the natural photoperiod, but also upon the extent of thermal buffering of refugia. For example, Lovegrove and Knight-Eloff (1988) have shown that the peak soil (burrow) temperatures occur later in the day the deeper the burrow, i.e. the more attenuated the magnitude of 24-h temperature oscillations. Their data, measured in the Kalahari Desert at various soil depths in a sandy habitat, showed that the maximum soil tem-

perature at a soil depth of 5 cm occurred at ca. 1500 hours and 1630 hours in mid-winter and mid-summer, respectively. However, at 10 cm soil depth, the peak soil temperature was reached about 3 h later, at ca. 1800 hours, whereas at 30 cm depth, the peak occurred during the scotophase at ca. midnight.

Assuming that these data are fairly typical in general of thermal profiles in thermally-buffered refugia, such as those of *S. macroura* in cavities under rocks and logs and cracks in the soil (Strahan 1991), we may expect nocturnal mammals that employ summer torpor to be fairly specific in their choice of refugia. The latter may be particularly pertinent during periods of energy stress. Clearly, minimum thermal buffering has the advantage that animals can benefit from maximum heating by the T_a cycle during the early and mid-photophase, before endogenous heat production occurs several hours prior to the scotophase. The disadvantage is that animals may be aroused too early in the photophase and be exposed to unnecessary risks of predation if they leave their refugia. In addition, as also discussed by Schmid (1996), minimal thermal buffering and good thermal insulation may not provide T_a s sufficiently low for animals to attain their most cost-effective minimum torpor body temperature.

Theoretically, free-ranging nocturnal mammals can maximise energy savings if they enter torpor during the early or mid-scotophase because the low T_a associated with the mid- to late scotophase permits the T_b of small mammals to approach or attain their theoretical minimum torpor T_b . In this study we did not manipulate the timing of the peak temperature of the sinusoidal cycle with respect to the real time of the day. This option is, however, clearly a useful future experimental procedure. For example, a peak T_a cycle synchronised with the mid-photophase (ca. 1200 hours) should theoretically avoid the heating effects of the endogenous onset of heat production determined, for example, by the animal's pacemaker clock. The avoidance of experimental T_a cycles with an acrophase close to the endogenous onset of heat production will thus permit a clearer separation of the relative importance of endogenous and exogenous heating effects.

An examination of torpor entry times relative to arousal times may provide some insight into the physiological capacity of *S. macroura* to optimise energy savings during torpor. Our study and previous studies (Geiser and Baudinette 1985; Holloway and Geiser 1996) have shown that *Sminthopsis* sp. are capable of entering torpor at any time during the scotophase. Hence, the active-phase does not inhibit the physiological or mechanistic capacity for torpor.

Few data on daily torpor patterns have been measured in free-ranging mammals under natural T_a cycles. However, Ortmann et al. (1996) and Schmid (1996) have measured torpor patterns during winter in mouse lemurs (*Microcebus* sp.) housed in outdoor enclosures on site in Madagascar. These data reveal several interesting points in light of the discussion thus far. Firstly, the animals

entered torpor at all times during the scotophase, but mostly during the late scotophase (Ortmann et al. 1996). Hence, these nocturnal primates clearly possess the capacity to enter torpor during the active phase and maximise energy savings through prolonged torpor bouts. Secondly, arousal from torpor commenced in the absence of endogenous heat production through exogenous, passive T_a heating (Schmid 1996). However, endogenous heat production commenced at ca. 1100 hours after T_b had reached ca. 28–30 °C. Full arousal was achieved by 1300–1400 hours (Ortmann et al. 1996; Schmid 1996).

One interesting implication of these data is the possibility that the onset of heat production may have been triggered by a specific T_b of the lemurs during arousal, rather than by an endogenous heat production rhythm entrained to a photoperiod. In both this study and the lemur study, endogenous heat production commenced when T_b s had reached 23–28 °C. In the case of the mouse lemurs, an onset of heat production at ca. 1100 hours is unlikely to reflect endogenous entrainment to photoperiod. Hence there may exist a threshold T_b at which the stimulation of heat production occurs in the absence of endogenous pacemaker cues. This aspect of passive heating during arousal requires further investigation.

In conclusion, this study investigated the characteristics and costs of arousal from induced daily torpor in the presence of simulated T_a cycles in the small marsupial insectivore *S. macroura*. The objectives of the study were to determine whether small mammals that employ daily torpor during summer in response to unpredictable food availability are aided energetically during arousal from torpor by the marked diel T_a s characteristic of southern hemisphere continents. Using a simple sinusoidal T_a cycle with an amplitude of 10 °C, it was shown that *S. macroura* halved the total cost of torpor through passive T_a heating. These data suggest that conclusions concerning the energetic benefits of torpor drawn from laboratory studies that have measured the energetics of torpor under constant T_a conditions may be underestimating the benefits of torpor in free-ranging small mammals during summer.

It was also argued that these savings might be elevated even further if arousal times are more closely synchronised with the real time at which the maximum T_a is attained (early afternoon). The thermal characteristics of refugia, it was suggested, should determine the degree of synchronisation of arousal times with the T_a cycle. Potential savings through tight synchronisation may, however, be offset by increased risks of predation through early arousal in nocturnal mammals, and perhaps higher refugia temperatures that may not optimise energy savings during torpor. Taken together, these considerations suggest that the behaviour of free-ranging small mammals that employ torpor during summer warrants investigation.

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