

Torpor and basking in a small arid zone marsupial

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Abstract The high energetic cost associated with endothermic rewarming from torpor is widely seen as a major disadvantage of torpor. We tested the hypothesis that small arid zone marsupials, which have limited access to energy in the form of food but ample access to solar radiation, employ basking to facilitate arousal from torpor and reduce the costs of rewarming. We investigated torpor patterns and basking behaviour in free-ranging fat-tailed dunnarts *Sminthopsis crassicaudata* (10 g) in autumn and winter using small, internal temperature-sensitive transmitters. Torpid animals emerged from their resting sites in cracking soil at ~1000 h with body temperatures as low as 14.6°C and positioned themselves in the sun throughout the rewarming process. On average, torpor duration in autumn was shorter, and basking was less pronounced in autumn than in winter. These are the first observations of basking during rewarming in *S. crassicaudata* and only the second direct evidence of basking in a torpid mammal for the reduction of energetic costs during arousal from torpor and normothermia. Our findings suggest that although overlooked in the past, basking may be widely distributed amongst heterothermic mammals. Therefore, the energetic benefits from torpor use in wild animals may currently be underestimated.

Introduction

Torpor is a state of controlled reduction in body temperature (T_b) and metabolic rate (MR) used by many mammals

and birds (Wang 1989). Torpor is most common in small mammals, which have to cope with a substantial loss of body heat to the environment because of their large surface area to volume ratio and consequently appropriate thermal strategies such as torpor are pivotal for their survival. Torpid individuals may reduce their MR by more than 90% compared to that during normothermia and thus have the potential to substantially reduce energy expenditure (Wang 1989). The high energetic cost of endothermic arousal, however, is viewed to be one of the disadvantages associated with daily torpor because it can limit the overall daily energy savings to only 20–50% (Wang 1989). Apparently to lower arousal costs and thus enhance energy savings, several mammals and birds employ passive rewarming (Geiser et al. 2004). Experimental evidence shows that small mammals are capable of raising their T_b passively with an increase in ambient temperature (T_a) without the need of a substantial increase in MR that is required for active, endothermic arousals at low T_a (Schmid 1996; Lovegrove et al. 1998). This reduction in rewarming costs is even more extreme in animals with access to radiant heat, which are able to maintain energy requirements below basal MR (BMR) throughout most of the rewarming process (Geiser and Drury 2003). These substantial reductions in energy expenditure achieved by rewarming passively in the laboratory suggest that wild animals could profit from and may also take advantage of external heat sources.

This assumption is supported by observations on wild animals, which seem to select resting sites that warm passively during the day to minimize energy expenditure (Körtner and Geiser 1999; Dausmann et al. 2005; Turbill 2006; Willis 2006). Furthermore, small mammals have been observed basking probably for thermal comfort during the normothermic phase (Bartholomew and Rainy 1971;

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Frey 1991; Schwaibold and Pillay 2006; Brown and Downs 2007), and activity patterns and pelt properties have been used by others to imply that basking may be employed (Read 1989; Cooper et al. 2003). Nevertheless, direct evidence that small mammals expose themselves to radiant heat during rewarming from torpor is currently only available for a single species from the Australian arid zone, the fat-tailed antechinus (*Pseudantechinus macdonnellensis*; Geiser et al. 2002).

Although food and water resources are scant in the Australian arid zone, this inland region is characterised by ample access to solar radiation. It also harbours most small insectivorous marsupials of the family Dasyuridae perhaps because of their extensive use of torpor (Geiser 2004). It has been proposed that the large number of daily heterotherms in the southern hemisphere in general may reflect the need to deal with unpredictable climatic conditions as in the Australian arid zone, but access to the sun for passive rewarming may also be of critical importance (Lovegrove 2000; Geiser and Drury 2003). To further test this hypothesis, we investigated torpor patterns in a small free-ranging dasyurid marsupial, the fat-tailed dunnart *Sminthopsis crassicaudata*, in inland Australia. Our specific aim was to determine whether the species uses radiant heat to minimise rewarming costs and thus maximise the energetic benefits of torpor.

Materials and methods

We examined torpor and behaviour of dunnarts at Kinchega National Park, western New South Wales, Australia (32°30'S, 142°20'E) in winter (May to July) 2006 and autumn (March/April) 2007. Dunnarts feed mainly on insects and spiders and are considered to be strictly nocturnal (Morton 1995). We caught dunnarts in floodplains using both box and pitfall traps. Nine animals were used for radio tracking, five in winter (body mass, 10.0±1.3 g, all males) and four in autumn (body mass, 10.9±2.19, three males and one female). Animals were transported to a field laboratory, kept under natural photoperiod at $T_a=20^\circ\text{C}$, fed daily with insects and a mixture of dried and canned pet food; water was provided ad libitum. In the arid zones, dunnarts inhabit soil cracks and quickly shed external transmitters in these small spaces. Therefore, we surgically implanted small temperature-sensitive transmitters (Holohil BD-2TH) intraperitoneally, under isoflurane/oxygen anaesthesia in a field laboratory. Before implantation, waxed transmitters (0.9 g) were calibrated to the nearest 0.1°C in a water bath from 10 to 40°C using a mercury thermometer traceable to a national standard. Animals were kept until fully recovered from surgery (<48 h) and released at their point of capture. Signal detection range of the internal transmitters was <20 m

because of the unavoidably small size of internal transmitters (14×5.5 mm with loop antenna), so five animals were never detected after release. Dunnarts may travel considerable distances (maximum 2,647 m/night, mean 412.5 m/night; Haythornthwaite and Dickman 2006), so these individuals likely left the study area. Consequently, data presented in this paper are limited to four male dunnarts (two winter, two autumn), which we were able to record for several days, starting >5 days after surgery. For T_b measurements, we located animals using manual receivers and then recorded pulse intervals every 10 min via receiver/data loggers (for details, see Körtner and Geiser 1998). Due to a short detection range, loggers had to be moved when dunnarts changed location and data collection was not always continuous. Additionally, we manually recorded T_b several times during the day using a receiver (Telonics CR-4) and a stopwatch based on transmitter-specific calibration curves (as in Dausmann et al. 2005). We observed the soil crack entrances using binoculars in the mornings after we found animals torpid the previous night and continued behavioural observations throughout the day if animals were visible. The T_a data were obtained from a Bureau of Meteorology weather station located 11 km from the study site. We also measured temperature at the site in a soil crack 0.25 m under the surface (T_{soil}), and on the surface of the ground in the shade (T_{surface}) to the nearest 0.5°C using data loggers (DS 1921G Thermochron iButtons). Numeric values are reported as means±SD for the number of individuals 'n'; 'N' is the number of measurements. Statistical tests were not performed because of the small sample size.

Results

Winter

Ambient conditions in winter were characterised by cold nights and mostly sunny, mild days; mean daily minimum T_a was 3.6±3.5°C (range -2.4 to 12°C), and mean daily maximum T_a was 17.7±2.7°C (range 12.8 to 25.8°C). Soil cracks provided buffered conditions with a mean T_{soil} of 13.6±1.9°C (daily minimum T_{soil} 12.9±2.0°C, range 9.5 to 17.5°C; daily maximum T_{soil} 14.2±1.8°C, range 11.5 to 18.0°C), while T_{surface} was much more variable with a mean of 9.0±5.9°C (daily minimum T_{surface} 3.1±3.0°C, range -2.5°C to 9.0°C; daily maximum T_{surface} 19.5±5.0°C, range 11.5 to 28.0°C). The daily fluctuation in T_{soil} was 0.5 to 3.0°C compared to 5.5 to 28.5°C for T_{surface} .

We recorded 15 complete torpor bouts. Most bouts lasted for about two-thirds of a day (17.1±2.2 h; $n=1$, $N=10$), whereas a few lasted only for 2.2±1.3 h ($n=2$, $N=5$). On two additional occasions, we were unable to determine the onset of torpor because dunnarts were out of logger/

receiver range when they entered torpor but were found later while already torpid, and thus, we cannot present bout duration. The mean minimum T_b during the long torpor bouts (>5.5 h duration) was $13.2 \pm 1.4^\circ\text{C}$ ($n=1, N=10$) and $21.0 \pm 4.6^\circ\text{C}$ during the short bouts (<5.5 h duration; $n=2, N=5$) and the individual minimum T_b was 10.8°C .

The mean time when T_b in torpid individuals began to rise was $1029 \text{ h} \pm 27 \text{ min}$ ($n=2, N=15$, excluding two afternoon bouts), 3.0 h after sunrise (0728 hours ± 7 min). On three occasions, we observed dunnarts emerging from the crevice and positioning themselves in the sun before T_b began to rise (Fig. 1); the lowest T_b we observed in a dunnart basking during rewarming was 14.6°C . On six occasions, dunnarts were found basking within the arousal phase, after T_b had risen to values between 15.3 and 31.6°C . Only on a single occasion was a dunnart not detected basking before it had reached its normothermic T_b level. Altogether, we observed dunnarts basking on 10 out of 17 arousals; however, basking animals were difficult to detect due to their small body size and selection of sites that minimized visibility and provided protection from wind.

The mean minimum T_b at the beginning of arousals was $16.4 \pm 2.4^\circ\text{C}$ and increased to $32.4 \pm 0.2^\circ\text{C}$ within 66 ± 6.3 min with a mean arousal rate of $0.27 \pm 0.01^\circ\text{C}/\text{min}$ ($n=2, N=17$). The fastest overall arousal rate ($0.39^\circ\text{C}/\text{min}$) and the fastest maximum arousal rate over 10 min ($0.65^\circ\text{C}/\text{min}$) were measured on a sunny day, while the dunnart was observed basking. On the two cloudy days, rewarming rates were lower (fastest overall arousal rate $0.29^\circ\text{C}/\text{min}$, maximum arousal rate $0.45^\circ\text{C}/\text{min}$).

On average, dunnarts had reached a normothermic T_b level by $1118 \text{ hours} \pm 7 \text{ min}$ ($n=2, N=15$; two afternoon bouts not included). On every day when dunnarts were

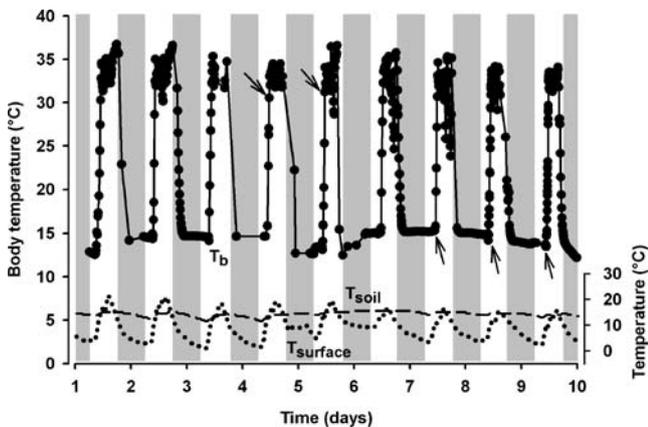


Fig. 1 Body temperature (T_b , circles with solid line) of a free-ranging fat-tailed dunnart *Sminthopsis crassicaudata* over 9 consecutive days in winter (May/June 2006) with the temperature measured 0.25 m deep in a soil crack (T_{soil} , dashed line) and on the surface (T_{surface} , dotted line). The arrows indicate when dunnarts were observed basking: On days 4 and 5, we found the dunnart basking during the arousal phase; on days 7, 8 and 9, we saw it when first emerging from the crevice at the minimum T_b . Grey bars indicate the scotophase

observed basking in the morning, they stayed in the sun during normothermia for the entire time of observation, which varied each day. When clouds covered the sun, T_b fell instantly (Fig. 2) and the dunnart returned into the crevice, but emerged immediately when the sun reappeared.

Dunnarts typically showed long torpor bouts and short activity periods. On a representative day (Fig. 3), individuals would employ a long torpor bout, bask during arousal, followed by several hours of normothermia, leave the soil crack to forage (no T_b data due to low detection range) as early as 1530 hours and enter torpor again around 1730 hours.

Autumn

During autumn, ambient conditions were milder than in winter; mean daily minimum T_a was $6.7 \pm 2.7^\circ\text{C}$ (range 2.4 to 11.6°C), and mean daily maximum T_a was $20.3 \pm 3.0^\circ\text{C}$ (range 14.2 to 24.6°C). T_{soil} was $21.7 \pm 1.2^\circ\text{C}$ (daily minimum T_{soil} $20.9 \pm 0.9^\circ\text{C}$, range 18.5 to 22.5°C ; daily maximum T_{soil} $22.7 \pm 1.2^\circ\text{C}$, range 20.0 to 25.0°C), and T_{surface} $19.7 \pm 4.8^\circ\text{C}$ (daily minimum T_{surface} $13.8 \pm 2.8^\circ\text{C}$, range 7.5 to 21.0°C ; daily maximum T_{surface} $19.5 \pm 5.0^\circ\text{C}$, range 11.5 to 28.0°C). The daily fluctuation in T_{soil} was 0.5 to 2.5°C compared to 5.0 to 23.0°C for T_{surface} .

We recorded ten long torpor bouts (10.9 ± 1.3 h, mean minimum $T_b = 17.7 \pm 2.7^\circ\text{C}$, $n=2, N=10$, individual minimum $T_b = 13.6^\circ\text{C}$), five short bouts (4.6 ± 0.2 h, mean

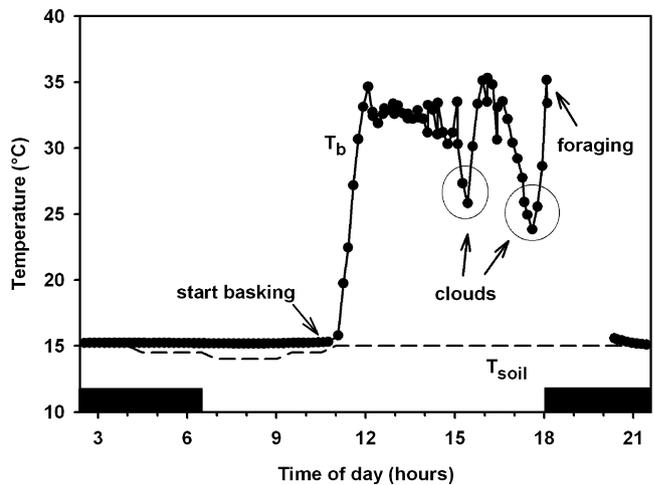


Fig. 2 Body temperature (T_b , circles with solid line) of a free-ranging fat-tailed dunnart *Sminthopsis crassicaudata* with the temperature measured 0.25 m deep in a soil crack (T_{soil} , dashed line). We observed the dunnart moving out of its crevice at 1026 hours with a T_b of 15.2°C and basking in the sun until 1650 hours. From that time (and also briefly between 1445 and 1505 hours), clouds covered the sun and the dunnart retreated into the hole, where it remained until 1750 hours. It then emerged and started to forage on the ground for approximately 90 min, before it returned to the same crevice and entered torpor before 2000 hours. Data presented are details of day 7 from Fig. 1. The black bars indicate the scotophase

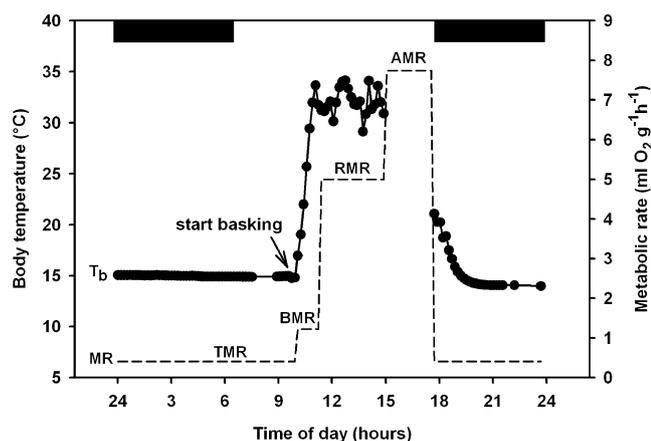


Fig. 3 Body temperature (T_b , circles with solid line) and calculated metabolic rate (MR, dashed line), based on MR data from the literature (see “Discussion”), of a free-ranging fat-tailed dunnart *Sminthopsis crassicaudata*. The dunnart was observed basking from 0945 to 1200 hours, when observations ended, as indicated by the arrow. TMR torpid MR; BMR basal MR; RMR resting MR; AMR active MR. Note that MR stays on BMR-level during the arousal phase, resulting from the observed basking behaviour that reduced the calculated daily energy expenditure by 25% compared to endothermic arousal (see “Discussion” for details). The black bars indicate the scotophase

minimum $T_b = 23.5 \pm 0.5^\circ\text{C}$, $n=2$, $N=5$) and 15 additional arousals from torpor bouts without information on torpor entry. Arousals began at 0956 hours ± 21 min ($n=2$, $N=30$), 3.1 hours after sunrise (0653 hours ± 8 min), and we recorded basking behaviour during nine of these arousals ($T_b = 23.9 \pm 0.9^\circ\text{C}$). On two occasions, we could only detect the dunnart basking at the end of the arousal phase with a normothermic T_b of $34.8 \pm 1.3^\circ\text{C}$. In contrast to winter, when afternoon basking was common, dunnarts in autumn were not seen on the surface about 15 min after they reached their normothermic T_b . Moreover, basking dunnarts in autumn only exposed their head or parts of their back to the sun, whereas in winter usually the whole body was exposed.

Arousal rates were slower in autumn than in winter with a mean of $0.16 \pm 0.04^\circ\text{C}/\text{min}$ (T_b increased from 21.2 ± 1.8 to $34.6 \pm 0.3^\circ\text{C}$ in 98 ± 0.4 min, $n=2$, $N=30$). The fastest overall arousal rate ($0.33^\circ\text{C}/\text{min}$) and maximum arousal rate over 10 min ($0.7^\circ\text{C}/\text{min}$) were measured in a basking dunnart, and arousals on cloudy days were slower (fastest overall arousal rate $0.12^\circ\text{C}/\text{min}$ and maximum arousal rate $0.23^\circ\text{C}/\text{min}$). Dunnarts reached their normothermic T_b at 1122 hours ± 6 min ($n=2$, $N=30$).

Discussion

Our study shows that dunnarts use radiant heat during rewarming from torpor. The T_b when basking commenced was considerably lower than that of the only other mammal

known to bask during arousal (19.3°C ; Geiser et al. 2002). The minimum T_b measured here (10.8°C) is the lowest value, and the maximum torpor bout length (22.6 h) is amongst the longest observed for dasyurid marsupials to date.

Recent evidence has shown that the choice of nesting sites affects thermo-energetics in small mammals. Free-ranging lemurs (*Cheirogaleus medius*) exhibited different torpor patterns according to the quality of insulation provided by their nesting sites (Dausmann et al. 2005) and elephant shrews (*Elephantulus myurus*) resting under rocks with poor thermal insulation in the wild showed that arousals from torpor are closely correlated with T_a (Mzilikazi et al. 2002). Additionally, tree-roosting bats (*Nyctophilus gouldi* and *Lasiurus cinereus*) select roosts with the minimal insulation likely to optimise passive rewarming (Turbill 2006; Willis 2006). However, unlike these poorly insulated nest sites, soil cracks provide a stable microclimate. Consequently, it appears that dunnarts minimise daily energy expenditure by using the combination of a resting site with a stable microclimate near their minimum T_b (see Figs. 1, 2), and thus, minimum MR during torpor, together with the use of radiant heat to decrease energetic costs of rewarming.

Importantly, the basking behaviour described here differs from most other recorded passive rewarming processes (e.g. Dausmann et al. 2005; Turbill 2006) because it involved the act of moving from the resting site to the entrance of the soil crack order to encounter solar radiation while torpid. We observed animals emerging from their crevices with T_b s as low as 14.6°C , which, to our knowledge, is by far the lowest core T_b recorded for any mammal with active movements. The next lowest core T_b s at which active movements were observed are 22.6°C for the fat-tailed antechinus (*P. macdonnellensis*; Geiser et al. 2002) and 23°C for the echidna (*Tachyglossus aculeatus*; Brice et al. 2002), although peripheral temperatures around 20°C during activity have been recorded for large ungulates (Arnold et al. 2004). Dunnarts seem to be able to climb considerable vertical distances with T_b s around 15°C and, although animals moved slowly while emerging, they were nevertheless able to retreat quickly inside the crevice when frightened. We observed dunnarts basking on about 60% of arousals in winter when, on average, torpor bouts were longer, and on about 30% in autumn; however, we assume that basking occurred on additional occasions when we were unable to see the animals. The similar daily T_b pattern on all days (Fig. 1) supports this assumption.

In winter, dunnarts were observed using radiant heat not only to rewarm from torpor but also to maintain their normothermic T_b . They stayed on the surface during the day with minimal visible protection, so it appears that the energetic advantages of radiant heat, even during normothermia, may outweigh the risk of predation. Similar

observations have been made on free-ranging rock hyraxes (*Procapra capensis*), where basking behaviour was used to conserve energy during normothermia (Brown and Downs 2007). Based on a study of captive normothermic stripe-faced dunnarts (*Sminthopsis macroura*) exposed to decreasing T_a with and without access to radiant heat (Geiser and Drury 2003), we can predict that basking dunnarts in the wild should be able to keep their resting MR (RMR) near BMR even at low T_a s. Although basking during normothermia was not observed during autumn, we found that the transmitter signal strength remained reasonably strong during the day, and we therefore assume that dunnarts stayed close to the surface after basking. Therefore, it appears that during autumn, they may be able to minimise the risk of predation by staying under the surface while still gaining enough external heat in the warm top soil layer to maintain their normothermic T_b despite reduced thermoregulatory costs.

We estimated the energy savings fat-tailed dunnarts gained from basking based on metabolic data collection from captive individuals. Initial passive rewarming from torpor caused by increasing T_a resulted in a reduction of energy expenditure to ~64% of active arousals in two small mammals; however, endothermic rewarming was initiated at a T_a of ~25°C (Schmid 1996; Lovegrove et al. 1998). In contrast, stripe-faced dunnarts at low T_a provided with radiant heat did not initiate endogenous heating during the entire arousal phase and thus reduced arousal costs to 15% of that during active arousal (Geiser and Drury 2003). Thus, it is likely the free-ranging dunnarts in our study gained similar energy savings by using radiant heat during the arousal phase. In addition to possible energetic benefits, the faster arousal rate caused by basking may also be advantageous for survival.

To estimate overall energy savings for a free-ranging dunnart (10 g) during winter conditions, we calculated the daily energy expenditure using MR data from captive animals measured at $T_a=12^\circ\text{C}$, which is similar to mean T_{soil} (MR during torpor, $\text{TMR}=0.41\pm 0.01$ ml $\text{O}_2/\text{g h}$; normothermic $\text{RMR}=5.0\pm 0.04$ ml $\text{O}_2/\text{g h}$; active MR, $\text{AMR}=7.74\pm 0.19$ ml $\text{O}_2/\text{g h}$; MR during the arousal phase, $\text{MR}_{\text{ar}}=8.51$ ml $\text{O}_2/\text{g h}$; Holloway and Geiser 1995), and BMR (1.22 ml $\text{O}_2/\text{g h}$; Geiser and Baudinette 1987). During passive arousal and normothermic basking, the MR was assumed to be BMR (see Geiser and Drury 2003). Based on a typical daily pattern (Fig. 3), the average daily metabolic rate (ADMR) in winter would be:

$$(\text{TMR}\cdot 15\text{h})+(\text{BMR}\cdot 3\text{h})+(\text{RMR}\cdot 4\text{h})+(\text{AMR}\cdot 2\text{h}) = 9.1 \text{ kJ/d}$$

(assuming 20.1 J/ml O_2). Endothermic arousal increased ADMR to:

$$(\text{TMR}\cdot 15\text{h})+(\text{MR}_{\text{ar}}\cdot 1\text{h})+(\text{RMR}\cdot 6\text{h})+(\text{AMR}\cdot 2\text{h}) = 12.1 \text{ kJ/d.}$$

Assuming a torpor bout of 2 h duration only, the ADMR would further be increased to 24.1 kJ/d, and the ADMR for a strictly normothermic animal would be 25.2 kJ/d. To perform the same calculations for dunnart in autumn, we used MR data for dunnarts measured at 18°C (see Holloway and Geiser 1995), which is close to the mean T_{soil} value during that period. On a typical day during autumn (9.5 h torpor bout followed by passive arousal, 8 h of rest and a 5.5 h activity period), the ADMR would be 14.9 kJ/d, which would be increased to 16.3 kJ/d by an active arousal and to 21.4 kJ/d by strict normothermia.

These calculated values are much lower than the field metabolic rate (FMR) of dunnarts (68.7 kJ/d) measured in southeastern Australia (Nagy et al. 1988). This is probably due to much longer activity periods spent foraging through most of the night displayed by individuals at that particular site and the only occasional use of torpor at that time of year (Morton 1978, Nagy et al. 1988). In contrast, dunnarts in our study showed very short activity periods, especially in winter, of often less than 2 h, which together with long, frequent torpor bouts and basking, will influence energy expenditure substantially.

Based on our calculations, dunnarts in winter conditions saved 25% of their daily energy expenditure by passive arousal followed by 2 h of normothermic basking, compared to the same day with no basking behaviour. The ADMR of a basking dunnart, as estimated here, is decreased by 64% when compared to the ADMR of a normothermic individual and is decreased by 82% in comparison to FMR. Theoretical savings in autumn were less, due to higher T_a values and shorter torpor bouts, with 9% reduction comparing basking/non-basking individuals, 30% comparing heterothermic/normothermic individuals and 78% when comparing our calculated values with FMR. Accordingly, the energy savings gained by employing torpor and basking provide a substantial reduction in energy expenditure, especially in harsh winter conditions, which means less time is required for foraging. Consequently, torpor and basking are likely to be pivotal for survival in this small, arid-zone marsupial.

Our study adds a second mammalian species known to actively seek radiant heat for passive arousal from torpor. We provide further direct evidence that basking is a frequently exercised thermoregulatory behaviour in small marsupials, used to reduce energetic costs of arousal from torpor. We predict that basking behaviour is widely employed among mammals and that the energetic benefits of torpor in the wild may currently be underestimated.

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References

- Arnold W, Ruf T, Reimoser S, Tataruch F, Onderschecka K, Schober F (2004) Nocturnal hypometabolism as an overwintering strategy of red deer (*Cervus elaphus*). *Am J Physiol Regul Integr Comp Physiol* 286:R174–R181
- Bartholomew GA, Rainy M (1971) Regulation of body temperature in the rock hyrax, *Heterohyrax brucei*. *J Mammal* 52:81–95
- Brice PH, Grigg GC, Beard LA, Donovan JA (2002) Patterns of activity and inactivity in echidnas (*Tachyglossus aculeatus*) free-ranging in a hot dry climate: correlates with ambient temperature, time of day and season. *Aust J Zool* 50:461–475
- Brown KJ, Downs CT (2007) Basking behaviour in the rock hyrax (*Procavia capensis*) during winter. *Afr Zool* 42(1):70–79
- Cooper CE, Walsberg GE, Withers PC (2003) Biophysical properties of the pelt of a diurnal marsupial, the numbat (*Myrmecobius fasciatus*), and its role in the thermoregulation. *J Exp Biol* 206:2771–2777
- Dausmann K, Glos J, Ganzhorn JU, Heldmaier G (2005) Hibernation in the tropics: lessons from a primate. *J Comp Physiol B* 175:147–155
- Frey H (1991) Energetic significance of torpor and other energy-conserving mechanisms in free-living *Sminthopsis crassicaudata* (Marsupialia: Dasyuridae). *Aust J Zool* 39:689–708
- Geiser F (2004) The role of torpor in the life of Australian arid zone mammals. *Aust Mammal* 26:125–134
- Geiser F, Baudinette RV (1987) Seasonality of torpor and thermoregulation in three dasyurid marsupials. *J Comp Physiol B* 157:335–344
- Geiser F, Drury RL (2003) Radiant heat affects thermoregulation and energy expenditure during rewarming from torpor. *J Comp Physiol B* 173:55–60
- Geiser F, Goodship N, Pavey CR (2002) Was basking important in the evolution of mammalian endothermy? *Naturwissenschaften* 89:412–414
- Geiser F, Drury RL, Körtner G, Turbill C, Pavey CR, Brigham RM (2004) Passive rewarming from torpor in mammals and birds: Energetic, ecological and evolutionary implications. In: Barnes BM, Carey HV (eds) *Life in the cold: 12th International Hibernation Symposium*. University of Alaska, Fairbanks, pp 51–62
- Haythornthwaite AS, Dickman CR (2006) Long-distance movements by a small carnivorous marsupial: how *Sminthopsis youngsoni* (Marsupialia: Dasyuridae) uses habitat in an Australian sandridge desert. *J Zool* 270:543–549
- Holloway JC, Geiser F (1995) Influence of torpor on daily energy expenditure of the dasyurid marsupial *Sminthopsis crassicaudata*. *Comp Biochem Physiol A* 112:59–66
- Körtner G, Geiser F (1998) Ecology of hibernation in the marsupial mountain pygmy-possum (*Burramys parvus*). *Oecologia* 113:170–178
- Körtner G, Geiser F (1999) Roosting behaviour of the tawny frogmouth (*Podargus strigoides*). *J Zool* 248:501–507
- Lovegrove BG (2000) Daily heterothermy in mammals: coping with unpredictable environments. In: Heldmaier G, Klingenspor M (eds) *Life in the cold. 11th International Hibernation Symposium*. Springer, Berlin, pp 29–40
- Lovegrove BG, Körtner G, Geiser F (1998) The energetic cost of arousal from torpor in the marsupial *Sminthopsis macroura*: benefits of summer ambient temperature cycles. *J Comp Physiol B* 169:11–18
- Morton SR (1978) Torpor and nest-sharing in free-living *Sminthopsis crassicaudata* (Marsupialia) and *Mus musculus* (Rodentia). *J Mammal* 59:569–575
- Morton SR (1995) Fat-tailed dunnart *Sminthopsis crassicaudata* (Gould, 1844). In: Strahan R (ed) *The mammals of Australia*. Reed Books, Sydney, pp 129–131
- Mzilikazi N, Lovegrove B, Ribble D (2002) Exogenous passive heating during torpor arousal in free-ranging rock elephant shrews, *Elephantulus myurus*. *Oecologia* 133:307–314
- Nagy KA, Lee AK, Martin RW, Fleming MR (1988) Field metabolic rate and food requirements of a small dasyurid marsupial, *Sminthopsis crassicaudata*. *Aust J Zool* 36:293–299
- Read DG (1989) Microhabitat separation and diel activity patterns of *Planigale gilesi* and *P. tenuirostris* (Marsupialia: Dasyuridae). *Aust Mammal* 12:45–53
- Schmid J (1996) Oxygen consumption and torpor in mouse lemurs (*Microcebus murinus* and *M. myoxinus*): Preliminary results of a study in western Madagascar. In: Geiser F, Hulbert AJ, Nicol SC (eds) *Adaptations to the cold: the Tenth International Hibernation Symposium*. University of New England Press, Armidale, pp 47–54
- Schwaibold U, Pillay N (2006) Behavioral strategies of the African ice rat *Otomys sloggetti robertsi* in the cold. *Physiol Behav* 88:567–574
- Turbill C (2006) Roosting and thermoregulatory behaviour of male Gould's long-eared bats, *Nyctophilus gouldi*: energetic benefits of thermally unstable tree roosts. *Aust J Zool* 54:57–60
- Wang LCH (1989) Ecological, physiological, and biochemical aspects of torpor in mammals and birds. In: Wang LCH (ed) *Advances in comparative and environmental physiology*. Springer, Berlin, pp 361–401
- Willis CKR (2006) Energetics, thermal biology, and torpor in Australian bats. In: Zubaid A, McCracken CF, Kunz TH (eds) *Functional and evolutionary ecology of bats*. Oxford University Press, New York, pp 38–55