

The key to winter survival: daily torpor in a small arid-zone marsupial

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Abstract Mammalian hibernation, which lasts on average for about 6 months, can reduce energy expenditure by >90% in comparison to active individuals. In contrast, the widely held view is that daily torpor reduces energy expenditure usually by about 30%, is employed for a few hours every few days, and often occurs only under acute energetic stress. This interpretation is largely based on laboratory studies, whereas knowledge on daily torpor in the field is scant. We used temperature telemetry to quantify thermal biology and activity patterns of a small arid-zone marsupial, the stripe-faced dunnart *Sminthopsis macroura* (16.9 g), in the wild and to test the hypothesis that daily torpor is a crucial survival strategy of this species in winter. All individuals entered torpor daily with the exception of a single male that remained normothermic for a single day (torpor on 212 of 213 observation days, 99.5%). Torpor was employed at air temperatures (T_a) ranging from approximately -1°C to 36°C . Dunnarts usually entered torpor during the night and aroused at midday with the daily increase of T_a . Torpor was on average about twice as long (mean 11.0 ± 4.7 h, $n=8$) than in captivity. Animals employed sun basking during rewarming, reduced foraging time significantly, and occasionally omitted activity for several days in sequence. Consequently, we estimate that daily torpor in this species can reduce daily energy

expenditure by up to 90%. Our study shows that for wild stripe-faced dunnarts daily torpor is an essential mechanism for overcoming energetic challenges during winter and that torpor data obtained in the laboratory can substantially underestimate the ecological significance of daily torpor in the wild.

Keywords Arid-zone Australia · Daily torpor · Energy expenditure

Introduction

The diversity of small insectivorous marsupials of the family Dasyuridae in the Australian arid zone is high (Dickman 2003) despite the low primary productivity of this vast area that covers about half of the continent's landmass. More than half of the family's species live entirely or partially in the arid zone and it has been suggested that in the insectivorous dasyurids the ability to enter daily torpor is an important adaptation to survive in this resource-poor environments (Geiser 2004). As daily torpor, characterized by reductions in body temperature (T_b) and metabolic rate for several hours, lowers daily energy and water requirements (Ruf and Heldmaier 1992; Holloway and Geiser 1995; Carey et al. 2003; Cooper et al. 2005; Gutman et al. 2006), it may be crucial for survival and reproduction of small insectivorous mammals in the arid zone.

The assumption that the use of daily torpor is a significant survival strategy employed by arid-zone dasyurids in the wild is to a large extent based on laboratory investigations. Predominant among these is work on the stripe-faced dunnart, *Sminthopsis macroura* (body mass ~ 20 g), which is by far the best-studied species of the family with regard to thermal biology (Godfrey 1968; Geiser

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and Baudinette 1987; Song et al. 1995; Lovegrove et al. 1999; Geiser 2004). This species enters torpor frequently in the laboratory even when food is freely available (spontaneous torpor) and thermal conditions are mild (Geiser and Baudinette 1987). As there is no obvious requirement for employment of torpor when food is plentiful and without a thermal challenge, it has been suggested that the use of spontaneous torpor in the laboratory may reflect the requirement to deal with low or fluctuating availability of food in their natural habitat. Daily torpor may be part of the normal daily routine of the species perhaps to reduce energy expenditure and thus foraging and food requirements (Geiser and Baudinette 1987; Song et al. 1995; Körtner and Geiser 2000a). However, this hypothesis has never been tested in the wild and knowledge about other aspects of the ecology and biology of *S. macroura* in the field is scarce (Morton and Dickman 2008).

As laboratory conditions differ from those experienced by wild animals and hence torpor expression is often less pronounced in captivity (Geiser et al. 2000), the purpose of our study was to quantify the thermal biology and torpor patterns of *S. macroura* in relation to its activity in the field. We especially aimed to obtain long-term data on individuals in winter to gain a better understanding about how important daily torpor is for energy conservation and how torpor and foraging are interrelated.

Material and methods

The study was conducted in Astrebla Downs National Park, southwestern Queensland (24° 10' S, 140° 34' E) during the Austral winter (June to August 2007). The park is situated ~120 m above sea level and is characterized by plains of virtually vegetation-free gibber (ironstone pebbles) and cracking clay soils that after rain support ephemeral Mitchell grass (*Astrebla* spp.). During the time of our study, aboveground vegetation was restricted to some of the larger drainage lines whereas most of the Mitchell grass plains were bare ground. Due to the flatness of the terrain and lack of substantial vegetation cover, strong winds prevail throughout most of the year. Drought is the norm for this region and the environmental conditions experienced by the animals during this study were by no means exceptional.

We used established pitfall-trap lines to trap dunnarts. Each of nine trap lines consisted of six vertically buried storm-water pipes (diameter 15 cm, depth 60 cm) that were spaced 4–5 m apart and were linked with a fine wire-mesh drift fence. Distance between pitfall lines was >1 km.

Core T_b was measured in eight dunnarts (six males, two females) with implanted temperature-sensitive radio transmitters (1.9 g; Sirtrack, Havelock, New Zealand). Depending

on food intake, body mass can vary by 5 g/day in this species without obvious effects on locomotion, suggesting that 1.9-g transmitters do not unduly interfere with foraging ability. Before implantation, transmitters were coated with inert wax and calibrated over a temperature range of 9–40°C to the nearest 0.1°C against a mercury thermometer traceable to a national standard. Sterilized transmitters were implanted intraperitoneally under general oxygen/isoflurane anesthesia; ventral incisions were sutured, and a topical anesthetic (Ban Itch, Apex Laboratories Pty. Ltd., Sommersby, NSW, Australia) and Leuko Spray Bandage (BSN medical (Aust) Pty. Ltd., Clayton, Vic, Australia) were applied. After surgery, animals were orally administered with liquid Children's Panadol (Ermington, NSW, Australia), were held for the following night and day while being provided with kangaroo mince *ad libitum* supplemented with freshly caught locusts and were released at the site of capture on the following evening.

Measurements were performed during two field trips (1 to 30 June and 11 July to 15 August 2007). Tagged individuals were radio-tracked to their burrows daily, beginning before sunrise. For each animal, a portable data logging system measuring the interval between two transmitter pulses every 10 min was placed close to the burrow (Körtner and Geiser 1998). Loggers had to be relocated if the animal had moved to a different burrow and consequently, not all torpor entries but almost all arousals were recorded. Data were downloaded to a computer after several days. Interval data were converted to T_b values using the transmitter calibration curves. Activity outside the burrow was inferred from the absence of interval data from the logger trace (reception distance was about 10 m). Torpor entry and arousal were defined by T_b falling below and rising above 30°C, respectively, and torpor bout duration was calculated from the time that T_b remained below 30°C (Körtner and Geiser 2000b).

Air temperature (T_a) was measured ~1 m aboveground in the shade with a temperature logger at 30-min intervals to the nearest 0.06°C (Hydrochron i-Buttons, Maxim Integrated Products, Sunnyvale, CA, USA).

Energy expenditure values were calculated by combining timing, T_b , and T_a records from this study with published metabolic rate measurements at similar T_a s (body mass 25 g, normothermia at T_a =16°C 1.68 kJ/h, normothermia with radiant heat source 0.46 kJ/h, torpor 0.19 kJ/h, active arousal 1.51 kJ, passive arousal 0.24 kJ; Geiser and Drury 2003; Geiser et al. 2004). The energy content of body fat was estimated to be 39.2 kJ/g (Withers 1992). A linear mixed-effects model accounting for the repeated measure design (R 2.7.0) was used to describe the relationship between T_a and bout length as well as T_a and minimum T_b during torpor. All other statistical tests were performed in Minitab V13.1 (Minitab Inc.). Significance

was assumed at a 5% level. Data are presented as the mean \pm 1SD (mean of the mean of individuals); n denotes the number of individuals and N the number of measurements.

Results

During the time of our study, T_a ranged from an absolute minimum of -0.9°C to a maximum of 35.5°C (Fig. 1). The mean daily T_a s were: $14.4 \pm 3.8^\circ\text{C}$ (average), $5.9 \pm 3.6^\circ\text{C}$ (minimum), and $24.5 \pm 5.1^\circ\text{C}$ (maximum).

The occurrence of torpor in the eight adult *S. macroura* (capture body mass of 16.9 ± 1.3 g) was high. Only one individual male (Sm2) did not enter torpor on a single day (5 June) during the study (Fig. 2), when T_a ranged from 12.3°C to 22.5°C . Thus, in the time between June and August (austral winter), torpor occurred on 212 of 213 (99.5%, $n=8$) of observation days. Torpor was observed on days when T_a minima were around 0°C but also occurred when the maximum daily T_a ranged from 30°C to 35°C .

On average, torpor entry occurred around midnight, with T_b falling from $37.6 \pm 0.6^\circ\text{C}$ ($n=8$) during activity to well below 30°C during torpor. Arousal usually occurred in the late morning when T_a had increased significantly and one individual was observed twice to bask in the sun during rewarming with a minimum T_b of 19.3°C . Four individuals occasionally displayed a second short (<2.5 h) torpor bout in the afternoon. Mean night–morning torpor bout duration was 9.0 ± 3.2 h ($n=6$, $N=77$) in males and 17.0 h ($n=2$, $N=38$) in females, but, in both sexes, torpor bout duration increased significantly with decreasing average night T_a (male: bout length[h] = $-0.65T_a[^\circ\text{C}] + 15.95$, $P < 0.001$; female: bout length[h] = $-0.65T_a[^\circ\text{C}] + 24.11$, $P < 0.001$; Fig. 3a). The model revealed a significant difference of

the intercept of the two regressions ($F_{1,104} = 155.6$, $P < 0.001$) but not of the slope ($F_{1,104} = 0.3$, $P = 0.59$). The model was modified accordingly by removing the interaction term between T_a and sex and, hence, at all T_a s, night–morning torpor bouts were on average 8 h longer in females than in males ($F_{1,6} = 16.2$, $P = 0.007$). The minimum T_b reached during torpor was also affected by T_a but without a difference between sexes ($T_{b\text{min}}[^\circ\text{C}] = 0.23T_a[^\circ\text{C}] + 15.67$, $R^2 = 0.09$, $P < 0.001$; Fig. 3b). The individually recorded T_b minima for all individuals was $12.3 \pm 2.2^\circ\text{C}$ ($n=8$) and the lowest recorded T_b was 11.3°C in a female (Sm4).

The extensive use of torpor in this species in the wild is illustrated for a female (Sm4) in Fig. 4. This individual displayed long bouts of torpor daily and over the illustrated time period had only very brief normothermic periods during midday. Timing of these normothermic periods during the hottest part of the day and the fact that her transmitter always remained within logger range suggest that no foraging occurred over five successive days and nights. During the entire 5.1 days (first torpor entry to final arousal), the female was normothermic for only 16.7% out of 122.5 h and torpid for the rest. During the July–August measurement, this individual remained inactive on 15 out of 36 days and torpor bouts were also exceptionally long. For example, on 15–16 July, the female remained torpid ($T_b \sim 16^\circ\text{C}$) for 25.9 h. On this occasion, the animal entered torpor in the late afternoon of 15 July, remained torpid throughout the night and the next overcast and cool day, partially aroused to 26°C at 15:00, re-entered torpor to 23°C , and fully aroused at sunset to commence activity.

Discussion

Our study shows that torpor forms an integral part of the daily life cycle of free-ranging *S. macroura* during winter. Both males and females used daily torpor everyday with only a single exception, and, on average, dunnarts remained torpid for about half the day. Although torpor was longer than a full day on one occasion, torpor bout duration remained well below the maximum of several weeks observed in hibernators (Geiser 2007; Bieber and Ruf 2009). Nevertheless, the long torpor bouts were accompanied by only short periods of activity and it appears that the low energy and water requirements during torpor allows the species to substantially reduce winter foraging or even omit foraging for a few days if this is required. Such multi-day fasting in small mammals is usually only associated with hibernation and obviously for much longer periods (months) than observed here (French 1985; Geiser and Ruf 1995). However, the omission of foraging for a few days is evidently compatible with the torpor patterns of some daily heterotherms despite the frequent arousals.

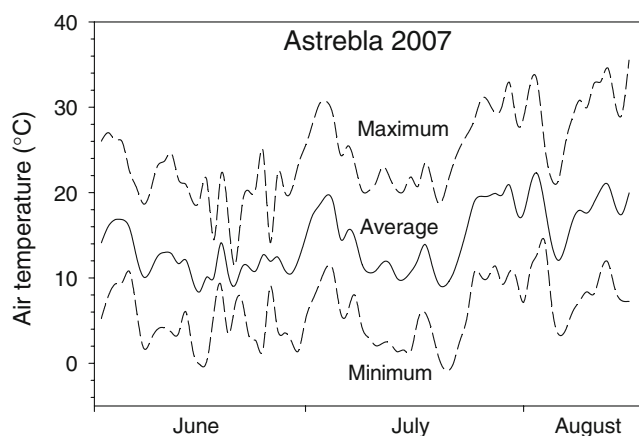
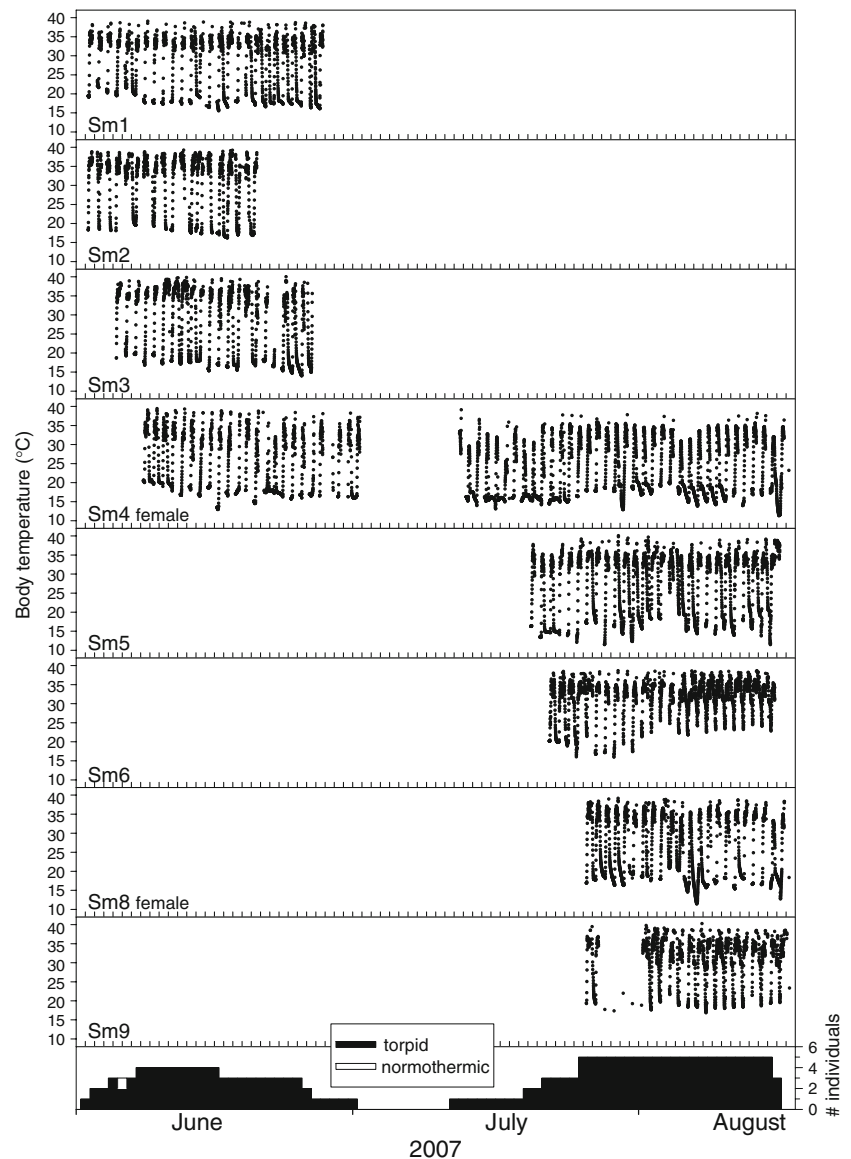


Fig. 1 Traces of daily averages, maxima, and minima of air temperature (T_a) for June to August 2007 at Astrebla Downs National Park

Fig. 2 Complete traces of body temperature (T_b) records for all eight stripe-faced dunnarts radio-tracked (females are labeled, all others are males). The *stacked bar graph* at the *bottom* of the figure illustrates the number of animals monitored at any given day. The number of them that entered torpor is shown in *black* whereas those that stayed normothermic in *white*. Some data are missing for Sm9 in late July/early August



Dunnarts adjusted torpor use according to T_a and torpor bouts were longer and deeper on cold nights. Females remained torpid longer than males at any given T_a . It appeared therefore that the females reduced energy expenditure further than males. Gender-related differences in torpor use of free-ranging dasyurids have been reported previously for the related mulgara (*Dasyercus blythi*) and fat-tailed pseudantechinus (*Pseudantechinus macdonnellensis*) and might be related to energy reallocation between different phases of the prolonged reproductive cycle of dasyurid marsupials (Geiser 2004; Körtner et al. 2008) that often commences in winter (McAllan 2003). Although both females showed no signs of imminent reproduction when trapped initially, we were unable to re-trap these individuals and it remained therefore unclear whether reproduction commenced during the measuring periods.

Torpor in our study occurred over a wide range of T_a from daily minima of $<0^{\circ}\text{C}$ to a daily maximum of 35.5°C . These observations are similar to those made on four free-ranging individuals of the related *S. crassicaudata*, which entered torpor frequently in autumn and winter, albeit at lower T_a (-2.4°C to 24.6°C ; Warnecke et al. 2008). The torpor occurrence of almost 100% observed here was well above that observed for spontaneous torpor (food provided) of captive individuals in winter (30%) but similar to induced torpor (food withheld; Geiser and Baudinette 1987; Song et al. 1995). This suggests that, in the wild, food availability in winter is low and animals use torpor to deal with this energy shortage. This interpretation is also supported by the relatively low body mass (16.9 g) of free-ranging individuals in our study, which was well below that of the species commonly measured in captivity (~ 25 g;

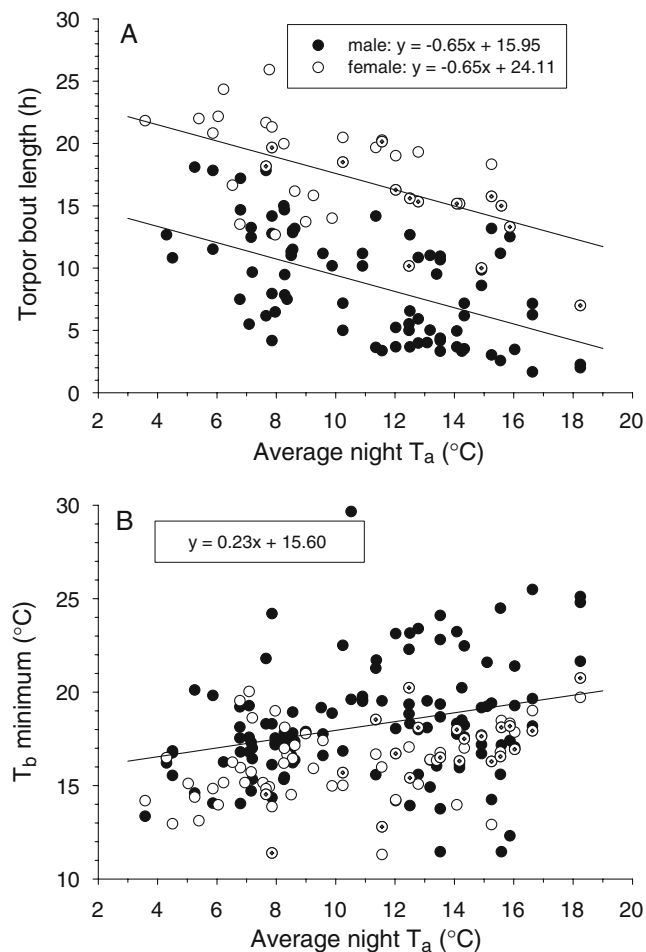


Fig. 3 Torpor bout length (a) and minimum T_b during torpor (b) as a function of average night ambient temperature (T_a). For bout length, the intercept but not the slope of the regressions differ significantly between males and females. No gender difference was found for the minimum T_b during torpor and data were pooled for the regression. As the female dataset comprised only two individuals, the symbols for these are individually identified

Geiser and Baudinette 1987; Song et al. 1995) and shows that in the wild dunnarts carry little body fat stores. A correlation between low body mass and frequent torpor use has been previously demonstrated in small dasyurids (Morton 1978; Holloway and Geiser 1996).

The mean minimum T_b measured during torpor (17.7°C, present study) was only slightly lower than that of captive individuals in winter (18.4°C, Geiser and Baudinette 1987). However, the duration of torpor bouts measured here in the wild (11 h) was on average about twice that in the laboratory (6 h; food deprived, $T_a \sim 16^\circ\text{C}$) and consequently reduced energy requirements well below that often calculated for daily heterotherms measured at constant T_a in captivity. Compared to the measured average daily energy expenditure in captivity of 48 kJ/day (25g) for a normothermic *S. macroura* (Geiser and Drury 2003; Geiser et al.

2004), a similar-sized wild dunnart showing torpor and activity patterns similar to the female (Sm4) shown in Fig. 4 (torpor 18.9 h, rest 3.4 h, arousal 1.7 h) would have reduced daily energy requirements to only 11.8 kJ/day (equivalent to 0.3 g of body fat, a 75% reduction in energy turnover), provided the animal remained underground during normothermia and arousals were achieved exclusively by endogenous heat production. Venturing to the surface and being exposed to solar radiation during arousal and normothermia would have reduced daily energy expenditure further to 5.5 kJ/day (equivalent to 0.14 g of body fat, a 89% reduction in energy turnover; Geiser and Drury 2003). Both calculated values for daily energy expenditure are below the basal metabolic rate of this species (13.1 kJ/day, Geiser and Baudinette 1987). Consequently, daily torpor *per se* plus the ensuing reduction in foraging requirements (Ruf et al. 1991; present study), the daily T_a cycle, and the access to solar radiation can reduce energy expenditure well below estimates based on previous laboratory measurements (Ruf and Heldmaier 1992; Holloway and Geiser 1995).

Our study demonstrates that work on daily heterotherms, which has been conducted almost entirely in the laboratory, needs to be verified by field investigations. The most frequently studied species in this regard, such as the Siberian hamster (*Phodopus sungorus*; Ruf and Heldmaier 1992; Stamper et al. 1999; Hiebert et al. 2000) or mice *Peromyscus* spp. and *Mus musculus* (Lynch et al. 1978; Swoap et al. 2007), have been investigated with regard to many clearly important functional questions. However, as almost nothing is known about the torpor use of these species in the field, it seems paramount that they are examined in the wild to ensure that laboratory data can be interpreted in an ecologically meaningful way.

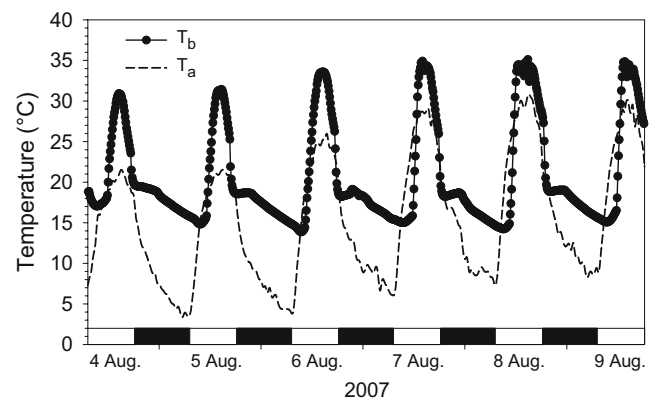


Fig. 4 Example of a body temperature (T_b) trace for one female (Sm4) and air temperature (T_a) over a 6-day period. This individual aroused daily, remained normothermic for only a short period around midday, and was inactive for over 5 days. Dark and light bars at the bottom of the graph indicate night and day

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