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ORIGINAL PAPER

The energetics of basking behaviour and torpor in a small marsupial exposed to simulated natural conditions

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Abstract Limited information is available on basking behaviour in torpid mammals and its energetic consequences. We investigated the effects of physiological and behavioural strategies on the energetics of the fat-tailed dunnart (*Sminthopsis crassicaudata*). Metabolic rate and body temperature during torpor, basking and rest were measured over 24 h in response to simulated environmental conditions: (a) constant ambient temperature (T_a) of 15°C, (b) constant T_a of 15°C with access to a radiant heat lamp, (c) a T_a cycle (range 15–31°C), and (d) a T_a cycle with access to a radiant heat lamp. When a radiant heat source was provided, all dunnarts ($n = 16$) basked during all measurements, which resulted in energy savings of up to 74% during rest. Overall, torpor was used on 59% of measurements with a maximum duration of 16.2 h and reductions in metabolic rate of 90% compared to normothermic values. Torpid dunnarts actively moved from a shaded area to position themselves under the heat lamp with body temperatures as low as 17.5°C and thereby reduced rewarming costs by 66%. We demonstrated, for the first time in the laboratory, that torpid animals actively move to a heat source to bask, and that this behaviour results in considerable energy savings. Our finding supports the view that basking during normothermia and rewarming from torpor substantially reduces energetic requirements, which may be important for the survival of small dasyurids living on limited resources in the Australian arid zone.

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Abbreviations

ADMR	Average daily metabolic rate
AMR	Active metabolic rate
MR	Metabolic rate
MR_{ar}	Metabolic rate during arousal from torpor
RMR	Resting metabolic rate
T_a	Ambient temperature
T_b	Body temperature
TMR	Metabolic rate during torpor

Introduction

Small mammals inhabiting central Australia face extreme environmental conditions due to large daily and seasonal ambient temperature (T_a) variation and an unpredictable supply of food and water (Morton 1980). It is therefore important for these species to use resources with utmost efficiency. The use of torpor, which is characterised by significant reductions in body temperature (T_b) and metabolic rate (MR) is an efficient energy saving mechanism (Lyman et al. 1982). Many mammalian species inhabiting arid zones are heterothermic (i.e. employ torpor) and their survival in harsh conditions is likely to be favoured by their ability to enter torpor (Geiser 2004). While arid environments often offer limited energy resources in the form of food, they generally provide ample access to radiant heat from the sun. Hence, it is not surprising that solar energy is exploited by small mammals to minimise thermoregulatory energy expenditure.

Basking behaviour has been observed for several mammalian species, mainly in the southern hemisphere where solar radiation in many habitats is plentiful. The rock hyrax (*Procavia capensis*) in South Africa, for example, uses basking behaviour as an energy saving mechanism during normothermia (Brown and Downs 2007). Observations of wild striped mice (*Rhabdomys pumilio*) in a desert in southern Africa documented a correlation of activity and sunshine, and a decrease in basking duration with increasing food availability (Schradin et al. 2007). For the small marsupial Giles' planigale (*Planigale gilesi*), an increase in surface activity of captive individuals during winter was interpreted as an indication of basking (Read 1989). While observations on basking behaviour during normothermia are numerous, information on the relationship between basking and torpor is scarce. Direct observations of basking during arousal from torpor are entirely limited to small dasyurid marsupials (Geiser et al. 2002; Pavey and Geiser 2008; Warnecke et al. 2008; Körtner and Geiser 2009). However, a close correlation between T_b and blackbody temperature for elephant shrews (*Elephantulus myurus*) in South Africa strongly suggested that basking during arousal from torpor is employed by this species (Mzilikazi et al. 2002). Currently, there is only one study that has quantified energy savings during radiant heat-assisted arousal from torpor in mammals, which reported savings of up to 85% for stripe-faced dunnarts (*Sminthopsis macroura*), in comparison to entirely endogenous rewarming (Geiser and Drury 2003).

Torpor patterns and arousals are directly affected by an animal's thermal environment, which emphasises the importance of choice of a resting site for its energy requirements. This has been shown for several mammalian species, for example fat-tailed lemurs (*Cheirogaleus medius*), long-eared bats (*Nyctophilus gouldi* and *N. bifax*) and hoary bats (*Lasiurus cinereus*) (Dausmann et al. 2005; Turbill 2006; Willis 2006; Stawski et al. 2009). Data for marsupials are limited, but some information on the influence of rest site selection on torpor patterns is available for arid zone species (Geiser and Pavey 2007; Körtner and Geiser 2009). For the fat-tailed dunnart (*S. crassicaudata)* in arid Australia, the choice of resting sites was dependent on season (Warnecke et al. 2008). During autumn, dunnarts nested in shallow soil cracks with high daily T_a fluctuations, which can positively affect energetic costs (Lovegrove et al. 1999). Conversely in winter, fat-tailed dunnarts selected a stable microclimate in deep soil cracks that provided ideal conditions for long, deep torpor bouts and perhaps reduced the risk of predation (Geiser and Turbill 2009). In addition, they showed seasonal differences in basking behaviour. While prolonged periods of basking during both rewarming from torpor and normothermia were observed in winter, only brief basking periods were documented in autumn (Warnecke et al. 2008). These behaviours were apparently used to minimise energy expenditure. As a result, an appropriate combination of torpor, basking, and choice of resting site was hypothesised to be a key factor for survival for fat-tailed dunnarts in their harsh arid habitat (Warnecke et al. 2008).

Our study aimed to test the hypothesis that basking influences energy expenditure by quantifying behavioural responses and measuring energy expenditure in captive fat-tailed dunnarts exposed to a thermal environment similar to that experienced in the wild. Winter conditions were simulated using a stable T_a of 15°C, which reflects the microclimate in deep soil cracks as selected in winter; autumn conditions were simulated by a T_a cycle that was based on soil temperature data close to the surface, as selected in autumn (Warnecke et al. 2008). In combination with providing or excluding access to a radiant heat source, we were able to investigate the effects of basking behaviour and the choice of microclimate on thermal energetics.

Methods

Fat-tailed dunnarts (henceforth dunnarts) were obtained from a breeding colony at La Trobe University, Melbourne, and kept at the University of New England, Armidale, in individual plastic cages (50 × 32 × 27 cm) under a light regime of 12:12 LD (lights on 06:00–18:00 h) and T_a of 20 ± 2°C. Dunnarts were fed daily between 17:00 and 17:30 h with mealworms and a mixture of canned cat food and water-soaked cat kibble; a combination of fresh minced meat, egg and dog kibble was added twice a week. Water was freely available.

MR was measured for 16 male dunnarts, half of which were equipped with internal temperature-sensitive transmitters (see details below). Dunnarts were exposed to the following four temperatures regimes: (a) constant T_a of 15°C, (b) constant T_a of 15°C with access to radiant heat, (c) a T_a cycle and (d) a T_a cycle with access to radiant heat (Table 1).

Respirometry

MR was measured as the rate of oxygen consumption using open-flow respirometry. Outside air was pumped (Optima A-807) through a drying tube filled with Drierite ($CaSO_4$) to the animal's chamber via a solenoid valve. From the chamber, dried air passed through a mass flow meter (Omega FMA-5606) at a flow rate of 400 ml min^{-1}, from which a sub-sample of 150 ml min^{-1} was analysed for O_2 (FOX Field oxygen analysis system Version 1.01, FXO301-01R, with an in-built pump). The O_2 analyser was connected via a serial port to a computer

Table 1 Four different temperature treatments each dunnart was exposed to over a period of 24 h

Temperature setting		Reason	*n*
(a)	Constant T_a of 15°C	Represents conditions experienced during winter	16
(b)	Constant T_a of 15°C with access to radiant heat	Represents conditions experienced during winter when basking	16
(c)	T_a cycle (range 15–31°C)	Represents conditions experienced during autumn	16
(d)	T_a cycle with access to radiant heat	Represents conditions experienced during autumn when basking	8

and the flow meter readings were interfaced via a 14 bit A/D converter (Data Taker DT100). Values were calculated and stored via a personal computer using a custom-written Visual Basic V6 program (G. Körtner). The system alternated in sequence every 3 min between two animal channels, measuring $\dot{V}O_2$, T_b and T_a, and one reference channel, resulting in 9-min measurement intervals for each channel. The differential between animal and reference channel was used to calculate $\dot{V}O_2$, thereby correcting for a possible drift. For calculations of MR (according to Eqn. 3a, Withers 1977), an RQ of 0.85 was assumed. Prior to measurements, the O_2 analyser was calibrated (Withers 2001) against high-purity compressed Nitrogen (BOC GASES) and a calibration gas ($O_2 = 19.9 \pm 0.03\%$ in Nitrogen, BOC GASES). The flow meter was calibrated using a custom-made bubble meter (Levy 1964).

Each dunnart was placed in a respirometry chamber (volume 480 ml) made from a 20 cm long Perspex pipe sealed with rubber stoppers with air inlet/outlets on either side, which was horizontally positioned on a plastic rack inside a temperature-controlled cabinet (Fig. 1). To absorb urine and faeces, a small piece of paper towel was attached to the bottom of the metabolic chamber in a way that dunnarts were unable to get under it. Half of the chamber (side of incoming air) was covered with black foil to allow dunnarts to actively choose between the sheltered side of the chamber and the uncovered side, where access to radiant heat was temporarily available (Fig. 1; for details see below).

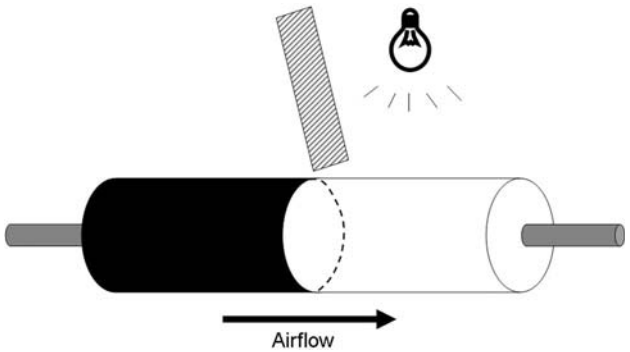

Fig. 1 The respirometry set-up with horizontally placed Perspex metabolic chamber connected with tubes for air inlet and outlet (*grey*). The side of incoming air (*left*, see *black arrow* for direction of airflow) was sheltered with black foil, while the side of outgoing air (*right*) was exposed and temporarily provided access to a radiant heat lamp (*light bulb symbol*). The foil was shaded from the lamp with cardboard (*grey diagonal lines*) to prevent it from heating up. Animals were able to freely move inside the chamber. Not to scale

Measurements commenced at 17:30 h ± 45 min and ended at 16:30 h ± 45 min the following day; food and water were not available. Dunnarts were weighed to the nearest 0.01 g immediately before and after measurements (Sartorius L2200P). A linear rate of mass loss over the 24-h period was assumed in order to calculate mass-specific MR values. Each animal was measured only once for each treatment. MR (ml O_2 g^{-1} h^{-1}) was measured during rest (RMR), activity (AMR), torpor (TMR) and during arousal from torpor (MR_{ar}). The average daily MR (ADMR, ml O_2 g^{-1} day^{-1}) was calculated as integrated MR over the entire measurement period. The missing values for a complete 24-h measurement (between 16:30 and 17:30 h, when equipment was set for the next animal) were replaced by resting values for that individual at the same T_a as this was in the dunnarts' rest phase.

To simulate thermal conditions experienced in the wild, we exposed dunnarts to temperature regimes based on data collected in an arid dunnart habitat in western New South Wales (32°30′S, 142°20′E). We placed iButtons (DS 1921G-F50, Dallas Semiconductor; 0.5°C resolution; 1.0°C accuracy) at different depths in soil cracks of floodplains, where dunnarts were known to rest (Read 1987; Warnecke et al. 2008). During winter (June 2006), the mean T_a measured over 9 days at a depth of 25 cm was 14.4 ± 0.9°C, which is reflected in our selection of a constant T_a of 15°C. During autumn (March 2007), T_a measured over 9 days at a depth of 5 cm was 21.7 ± 5.4°C with large daily fluctuations, which we simulated by a smoothed T_a cycle designed using a custom-written Visual Basic program (G. Körtner). T_a was regulated by a custom-written program Visual Basic V6 (G. Körtner) that measured the temperature within the animal chamber via a thermocouple and regulates T_a via duty-cycling the fridge and a 50 W ceramic heat lamp. Therefore, the system was able to compensate for heat produced by the basking lamp (see below).

Radiant heat access

A SunGlo basking spot lamp (50 W tight beam, ExoTerra; Colour Rendering index of 98, 6,700 K colour temperature) was placed at a 45° angle 20 cm away from the chamber. The light intensity inside the chamber was 3,800 lux (measured with a Gossen Panlux lux meter), which represents <5% of natural sunlight in central Australia (Doube 1975). The lamp was turned on from 09:00 to 14:00 h, approximately the time sunlight reaches soil crack entrances in the field. The covered side of the chamber was shaded with cardboard to prevent the black plastic from heating up. T_a was measured in both the in- and outlet air tubes (Fig. 1) to control for a possible T_a gradient building up inside the chamber due to the heat lamp, and the flow rate of 400 ml min^{-1} ensured a T_a difference of <1°C at all times.

Observations of the respirometry chamber during measurements without disturbing the animal were made using a camera with infra-red LED lights (Swann Secura View, Security Monitoring Kit). Behaviour was recorded between 09:00 and 14:15 h using a VCR (Panasonic NV-MV21) for detailed analyses of basking activities.

Body temperature

Eight dunnarts were equipped with internal temperature-sensitive AM radio-transmitters (XM Mini Mitter, Sunriver). Transmitters were waxed (Paraffin/Elvax) and calibrated to the nearest 0.1°C in a water bath from 10 to 40°C in 5°C-increments using a mercury thermometer traceable to the national standard. Transmitters (1.2 g after waxing) were surgically implanted in the abdominal cavity under sterile conditions using 0.5–4% isoflurane in oxygen for inhalation anaesthesia. Dunnarts were treated with analgesia (Children's Panadol; 1–2 drops on recovery and 2–3 drops mixed in the food) and allowed to recover from surgery for 1 week before measurements commenced. During respirometry measurements, T_b was measured every 9 min using ferrite rod antennas placed under the respirometry chambers multiplexed by a receiver (car radio). The signal was transformed to a square-wave signal after subtraction of background noise. To account for a possible drift in the transmitters' temperature sensitivity, one spare transmitter was waxed, calibrated and kept in a sodium lactate solution (Baxter Viaflex) to simulate body fluid. The above calibration procedure was repeated twice after 4 and 8 weeks (end of study) and the maximum drift over the entire temperature range was <1°C, which was used as an indication that the drift can be neglected.

Data analysis

Data are presented as mean ± standard deviation for '*n*' the number of individuals. '*N*' presents the number of measurements. Differences in '*n*' among measurements reflect problems with signal reception due to electronic interference. Analysis of variance (ANOVA) was used to determine possible effects of the four thermal regimes on ADMR. A post hoc test (Student–Newman–Keul, SNK) was used following significant ANOVA results for pairwise comparisons. Repeated measures ANOVA was used to test for differences in T_b during rest and activity at the different regimes. *T* tests were used to determine a difference in MR between regimes (a) and (b), and in RMR between (b) and (d). Linear regression was used to test for the effect of T_a on RMR, and regressions during basking and non-basking were compared using ANCOVA. All statistical analyses were performed using *statistiXL* version 1.7.

During the T_a cycle, MR during basking and arousal from torpor, as well as RMR and AMR are presented for dunnarts with internal transmitters only to ensure that the correct physiological states were analysed. Also at the T_a cycle, RMR was measured when T_a = 28–31°C during lights on at the end of the measurement, and AMR when T_a = 28–30°C during lights-off at the beginning of measurements.

Results

The mean body mass of dunnarts over all measurements, measured at the start of each measurement, was 19.0 ± 1.6 g (N = 56).

Basking behaviour

Dunnarts always rested in the sheltered side of the chamber when the heat lamp was turned off, independent of the thermal regime. However, when the heat lamp was switched on, all individuals during all measurements moved to the exposed side of the chamber to bask. Basking duration differed between measurement regimes (see below). Energy expenditure was significantly reduced by basking at all temperature regimes (see below).

MR at constant 15°C: regimes (a) and (b)

Regime (a)

Without access to radiant heat at T_a = 15°C the mean RMR was 4.41 ± 0.81 ml O_2 g^{-1} h^{-1} (n = 14); during activity, the AMR was 6.08 ± 0.44 O_2 g^{-1} h^{-1} (n = 16). Torpor was used by 56% of dunnarts with a TMR of 0.42 ± 0.30 O_2 g^{-1} h^{-1} (n = 9) and a mean minimum T_b of 17.8 ± 2.7°C (minimum 15.4°C). Torpor bout duration was 6.7 ± 4.3 h (range 1.6–16.2 h; n = 9), and MR_{ar} was 7.62 ± 1.40 O_2 g^{-1} h^{-1}.

Regime (b)

With access to radiant heat from 09:00 h at $T_a = 15°C$, normothermic dunnarts moved under the heat lamp at 09:27 h ± 41 min and remained there until it was turned off at 14:00 h; this reduced RMR by 74% to 1.15 ± 0.22 ($n = 8$). Torpor was used by 94% of animals with a mean duration of 7.1 ± 3.5 h (range 2.0–12.8 h; $n = 15$) and a mean minimum T_b of 17.5 ± 2.0°C (minimum 15.5°C). Torpid dunnarts moved under the heat lamp at 09:27 h ± 44 min with a mean T_b of 20.2 ± 2.6°C ($n = 7$; minimum 17.5°C), where they aroused largely passively with a MR_{ar} of 2.41 ± 1.23 ml O_2 g^{-1} h^{-1} without the peak of MR_{ar} characteristic for endogenous arousal (Fig. 2, compare a and b). Basking drastically reduced metabolic costs at 15°C, as ADMR ($t_{30} = 2.55$, $P = 0.016$), RMR ($t_{16} = 14.08$, $P < 0.001$) and MR_{ar} ($t_{11} = 6.39$, $P < 0.001$) were significantly lower at 15°C with lamp access than without (Fig. 3).

MR at the T_a cycle: regimes (c) and (d)

Regime (c)

The RMR of dunnarts exposed to the T_a cycle was 1.24 ± 0.21 ml O_2 g^{-1} h^{-1} ($T_a = 28–31°C$) and AMR

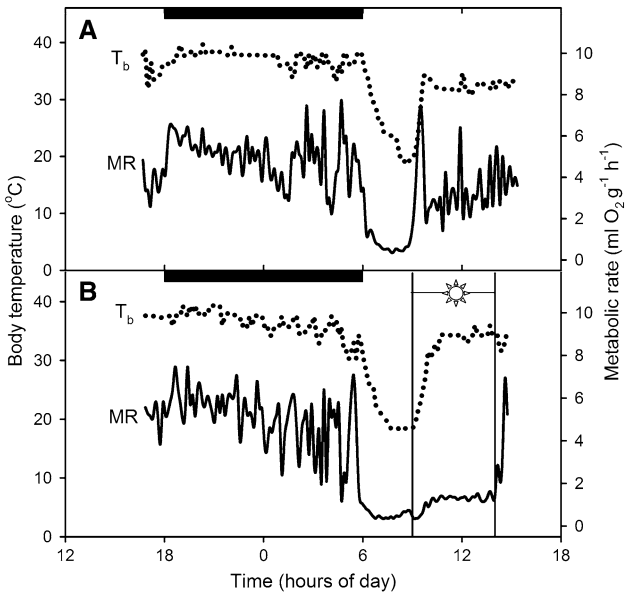

Fig. 2 Body temperature (T_b, *dotted line*) and metabolic rate (*MR*, measured as oxygen consumption, *solid line*) of a heterothermic *S. crassicaudata* at constant T_a of 15°C over 24 h **a** without and **b** with access to a radiant heat lamp. The *vertical lines* in (**b**) with the *sun symbol* indicate the time of lamp access; the dunnart moved under the light immediately after it came on and remained in the uncovered side of the chamber until it was switched off. The *black bars* along the upper *x*-axes indicate the scotophase

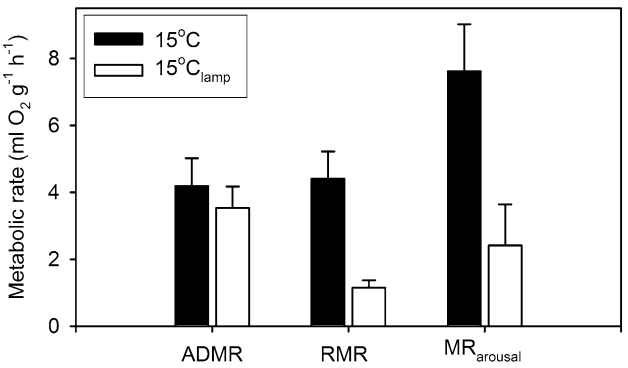

Fig. 3 The effect of basking on the metabolic rate (*MR*, measured as oxygen consumption) of *S. crassicaudata* exposed to a constant temperature of 15°C (*black bars*) and to constant 15°C with access to a radiant heat lamp (15°C_{lamp}, *white bars*). MR was measured over 24 h (ADMR), during rest (RMR) and during torpor arousal ($MR_{arousal}$)

was 3.41 ± 0.52 ml O_2 g^{-1} h^{-1} (at $T_a = 28–30°C$). Torpor was used by 69% of animals with a mean duration of 6.6 ± 2.2 h (range 4.0–10.8 h) and a TMR of 0.34 ± 0.17 O_2 g^{-1} h^{-1} (at $T_a = 15–18°C$; $n = 11$).

Regime (d)

When basking at the T_a cycle, the RMR of normothermic dunnarts remained constant over a wide range of T_as, while during non-basking RMR showed the normal increase with decreasing T_a (Fig. 4). The regression equations were $MR_{non\text{-}basking} = -0.299 \times T_a + 10.59$, $R^2 = 0.84$ ($P < 0.001$), and $MR_{basking} = -0.017 \times T_a + 1.81$, $R^2 = 0.07$ ($P = 0.196$), and the slopes differed significantly ($F_{1,96} = 67.15$, $P < 0.001$, ANCOVA). During torpor, TMR was reduced to 0.35 ± 0.36 ml O_2 g^{-1} h^{-1} and torpor bout duration was 6.3 ± 1.9 h (range 4.5–8.9 h; $n = 4$). Dunnarts showed an initial passive arousal phase with increasing T_a and moved slowly under the lamp at 9:20 h ± 27 min with a T_b of 21.2 ± 4.1°C ($n = 4$), where the arousal was completed. During this radiant heat-assisted rewarming, MR_{ar} did not show the peak characteristic of endogenous arousal (Fig. 5, compare a and b). Normothermic individuals moved under the lamp at 09:21 h ± 20 min ($n = 4$; $T_a = 16.8 ± 0.4°C$). All dunnarts retreated back into the covered side of the chamber at 12:58 h ± 32 min ($n = 8$), while the lamp was still on and T_a was 27.0 ± 1.2°C. The mean RMR during basking was 1.17 ± 0.11 ml O_2 g^{-1} h^{-1} (measured when all individuals had aroused, $T_a = 25.0 ± 0.6°C$).

Importantly, RMR during basking did not differ significantly between 15°C_{lamp} and T_a $cycle_{lamp}$ at $T_a = 25°C$ ($t_{10} = -0.19$, $P = 0.856$), which reveals that a difference in T_a of 10°C did not affect energy expenditure when access to radiant heat was available.

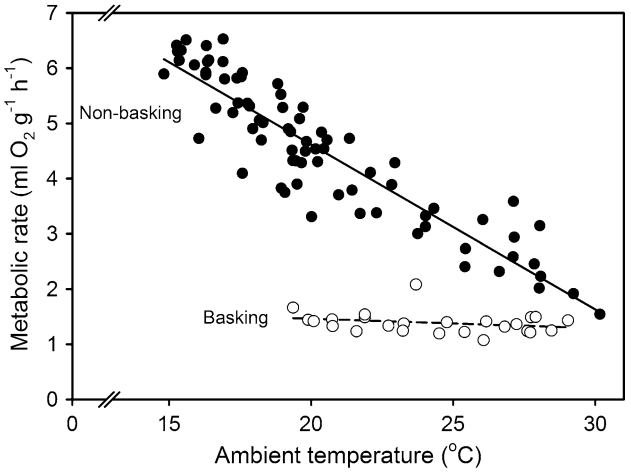

Fig. 4 The effect of ambient temperature on the metabolic rate (measured as oxygen consumption) during non-basking (*closed circles*) and basking (*open circles*) for one individual *S. crassicaudata* exposed to a 24 h temperature cycle with access to a radiant heat source for 4 h (for details see text). Also, for regression details see text

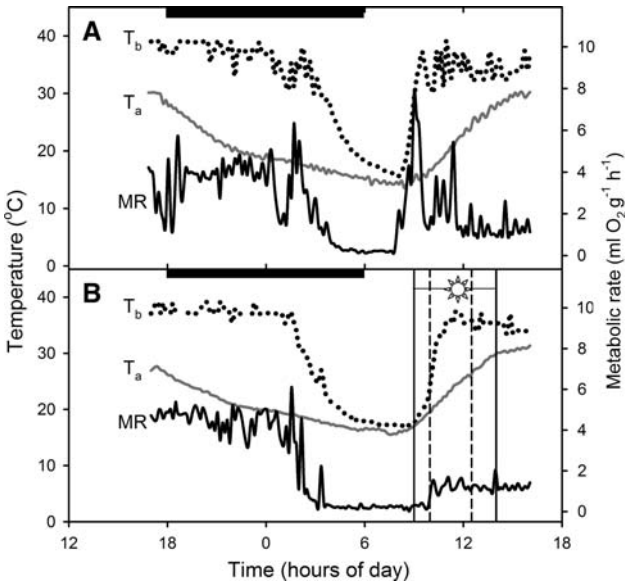

Fig. 5 Body temperature (T_b, *dotted line*) and metabolic rate (*MR*, measured as oxygen consumption, *solid line*) of a *S. crassicaudata* exposed to a temperature cycle (T_a, *grey line*) over 24 h. The same individual was measured **a** without and **b** with access to a radiant heat lamp. The *solid vertical lines* with the *sun symbol* indicate when the lamp was switched on, and the *broken vertical lines* show when the animal was basking. The *black bars* along the upper *x*-axes indicate the scotophase

Body temperature

The mean normothermic T_b during rest was between 34.1 ± 0.8°C (c) and 34.9 ± 1.0°C (d) and during activity between 38.2 ± 0.7°C (c) and 38.9 ± 0.3°C (b), and it was not significantly affected by thermal treatment ($F_{3,28} = 1.87$, $P = 0.159$, repeated measures ANOVA). This means that normothermic resting T_b, unlike MR, was not affected by basking.

ADMR

The mean ADMR significantly differed among the four temperature regimes ($F_{3,52} = 6.09$, $P < 0.001$, ANOVA); it was highest at (a) with 100.7 ± 19.8 ml O_2 g^{-1} day^{-1} ($n = 16$), followed by (b) with 84.8 ± 15.2 ml O_2 g^{-1} day^{-1} ($n = 16$), (c) with 79.4 ± 16.8 ml O_2 g^{-1} day^{-1} ($n = 16$) and (d) with 74.5 ± 13.4 ml O_2 g^{-1} day^{-1} ($n = 8$). Pairwise post hoc comparisons indicated that ADMR under regime (a) was significantly higher than for all other regimes ($P < 0.010$, SNK), but ADMR under regimes (b), (c) and (d) did not differ ($P > 0.374$, SNK).

ADMR varied greatly among measurements, which emphasises the strong effect of both basking and torpor on ADMR, independent of T_a. For example, the maximum individual ADMR (126.2 ml O_2 g^{-1} day^{-1}) was measured for a strictly normothermic animal at 15°C without radiant heat access. In contrast, only 64% of this value was measured for a normothermic individual that basked (82.4 ml O_2 g^{-1} day^{-1}). The use of torpor further increased energy savings; the individual minimum ADMR at 15°C (54.9 ml O_2 g^{-1} day^{-1}) was 44% of the maximum value, and was obtained from an individual that entered a long torpor bout (16.2 h) and basked during arousal from torpor. The lowest individual ADMR overall (48.1 ml O_2 g^{-1} day^{-1}) was only 38% of the maximum ADMR, measured for an individual exposed to the T_a cycle that entered torpor for 8.9 h and aroused largely passively until T_a had reached 28°C.

Discussion

Our study demonstrates the importance of behavioural and physiological responses to environmental challenges on the energetic demands of dunnarts. It shows for the first time that dunnarts always move to an available radiant heat source both when normothermic and torpid, which substantially reduces energy expenditure. Our findings suggest that the combination of basking and torpor may reduce energy demands in these and other small mammals in the wild.

Energetics of basking and torpor

Basking has been observed in many mammalian species (e.g. Bartholomew and Rainy 1971; Schwaibold and Pillay 2006; Brown and Downs 2007; Schradin et al. 2007), but

only a few studies have visually confirmed that basking occurs during arousal from torpor (Geiser et al. 2002; Warnecke et al. 2008; Körtner and Geiser 2009) and only one study has quantified the impact of basking on energetics during arousal from torpor (Geiser and Drury 2003). Importantly, our study has added a behavioural component to the experiment by providing animals the choice to either avoid or gain access to radiant heat. All dunnarts at all measurements sought shelter when no radiant heat was provided and all moved under the heat lamp to bask when radiant heat was available. The observed extent of basking by captive individuals underscores the importance of this thermoregulatory strategy for this species, and supports previous predictions of its frequent use in the wild (Warnecke et al. 2008).

Our data furthermore show that basking significantly reduces energy expenditure of dunnarts (Fig. 3). Maximum savings were gained by resting individuals at 15°C, where RMR was reduced by 74%. This means that basking allows dunnarts to maintain RMR near basal metabolic rate, while T_a is >16°C below their thermal neutral zone (MacMillen and Nelson 1969). The finding that normothermic T_b was unaffected by basking shows that all energy gained by radiant heat is directly invested in reducing the amount of endogenous heat production necessary for maintaining, rather than raising, normothermic T_b. Uptake of radiant heat of course will affect the energy budget of a small mammal enormously. The energetic costs for the arousal from torpor measured here were reduced by 67% due to basking, when compared to endogenous arousals at the same T_a, which is similar to findings for *S. macroura* (Geiser and Drury 2003). Obviously, natural conditions can only be simulated, and heat gain of animals basking in the wild may vary. However, the finding that basking was used extensively, resulting in significant energy savings, is a strong indicator for the importance of basking in free-ranging dunnarts. In fact, our measurements are possibly underestimates because of the much higher light intensity of the sun compared to the heat lamp used, a possible different spectral composition of the light, and absorbance of parts of the spectrum by the chamber. Therefore, basking potentially allows substantial energy savings in dunnarts and other similar-sized species and radiant heat plays an important role in reducing energy demands, especially in combination with torpor.

Torpor occurrence in dunnarts was highly variable and greatly influenced their energy budget. The overall torpor use was 59%, with torpor duration ranging from under 2 h to over 16 h. ADMR was up to more than twice as high when dunnarts remained normothermic, which is similar to other species (Ruf and Heldmaier 1992; Coburn and Geiser 1998). This shows that the use of torpor becomes especially effective when resting at low T_a. The finding that dunnarts are highly flexible in the way they manage energy expenditure by adjusting torpor bout length is supported by previous studies. In the laboratory, torpor bout length was dependent on T_a (Holloway and Geiser 1995) and in the field it appears to differ between habitats. In a semi-arid habitat, dunnarts regularly enter long torpor bouts of up to 17 h (Warnecke et al. 2008), whereas in cool-temperate mesic habitats torpor appears to occur only occasionally (Morton 1978; Frey 1991). Hence, by varying torpor use, dunnarts seem to be able to adjust energy expenditure to cope with unpredictable environmental conditions and food supplies.

The dependence of locomotor activities on T_b is well studied in reptiles (e.g. Bennett 1990), but reports on mammals' performance at low T_bs are scarce (Brice et al. 2002; Geiser et al. 2002; Arnold et al. 2004). Results of our study support previous reports that dunnarts are capable of coordinated movements at very low T_bs (Warnecke et al. 2008). Torpid dunnarts were observed to move under the lamp before the arousal phase began with T_bs as low as 17.5°C. Field observations describe torpid individuals leaving their resting sites in deep soil cracks to position themselves on the bare surface to bask with T_bs as low as 14.6°C (Warnecke et al. 2008). Based on a correlation of a blackbody temperature and T_b of elephant shrews, Mzilikazi et al. (2002) stated that their "animals are somehow able to emerge into the sun from under the rocks to bask while in a torpid state". This interpretation is supported by our observations, but highlights the general lack of knowledge about the thermal dependence of mammalian locomotion.

Implications for free-ranging animals

Estimations of energy expenditure of free-ranging mammals can be based on continuous T_b readings (Cooper and Withers 2004; Willis et al. 2004; Körtner and Geiser, 2009). For dunnarts, the ADMR calculated this way was 45.3 ml O_2 g^{-1} day^{-1} (Warnecke et al. 2008), which was confirmed by data collected in the present study. Using data measured at 15°C, based on the same time budget (15 h torpor, 1 h basking during arousal, 2 h normothermic basking, 4 h rest under the surface and 2 h activity), the resulting ADMR is 40.8 ml O_2 g^{-1} day^{-1}, within 10% of our previous estimate. However, caution must be used when comparing laboratory data with field energy expenditure, due to the more complex environment and behaviour of wild animals.

Our study confirms that the range of ADMR measured in dunnarts is large, as previously shown (Holloway and Geiser 1995). The minimum individual ADMR, obtained from an animal that employed a long torpor bout and passive arousal, was only 38% of the maximum individual

ADMR measured for a normothermic individual. These differences may possibly help explain variations in energy expenditure between habitats, as literature data show that the ADMR of dunnarts in arid habitat is only 22% of that used by their mesic counterparts. While dunnarts in arid Australia, which have to cope with an unreliable food supply, showed long daily torpor bouts as published data indicate (Warnecke et al. 2008), the high insect abundance in the mesic grassland habitat during spring possibly enabled dunnarts to remain normothermic (Morton 1978; Nagy et al. 1988). Thus, ADMR is highly variable and can possibly be adjusted to the prevailing food supply by the use of torpor.

Basking duration was affected by thermal conditions in the laboratory and these findings may help understand previous observations of this behaviour in the wild. During winter, dunnarts rested in deep soil cracks and used torpor and basking extensively, while in autumn the duration of basking and torpor was much shorter and animals remained close to the surface (Warnecke et al. 2008). In the present study, dunnarts exposed to winter conditions (stable $T_a = 15°C$) remained under the heat lamp until it was turned off and expressed a high peak in MR afterwards, similar to MR_{ar} (Fig. 2b). In contrast, when exposed to autumn conditions (T_a cycle), basking started immediately after the lamp was turned on. Interestingly, dunnarts retreated back into the covered part of the respirometry chamber when T_a had reached 27°C and T_b had reached normothermic values (Fig. 5b). The energetic benefits from basking apparently were, at that point, outweighed by the advantages of a low normothermic RMR at a high T_a and likely by the opportunity to seek cover. Therefore, for wild dunnarts the decreased basking duration during autumn may not necessarily imply energetic disadvantages as animals gain enough external heat by resting at a shallow depth while decreasing the risk of predation.

In conclusion, dunnarts show high flexibility in their ability to adjust energy expenditure according to environmental conditions by regulating behavioural (basking length) and physiological (torpor use) strategies. This is likely to be a key factor for their ability to inhabit hostile environments and may explain their widespread distribution over different climatic zones of the Australian continent. Dunnarts in the laboratory show well-defined basking behaviours comparable to that of wild animals. Thus, basking appears to be an important thermoregulatory strategy that affects energy expenditure substantially and is adjusted depending on the thermal environment.

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