

Thermal Biology, Torpor, and Activity in Free-Living Mulgaras in Arid Zone Australia during the Winter Reproductive Season

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ABSTRACT

Little is known about the energy conservation strategies of free-ranging marsupials living in resource-poor Australian deserts. We studied activity patterns and torpor of free-living mulgaras (*Dasyercus blythi*) in arid central Australia during the winter of 2006. Mulgaras are small (~75 g), nocturnal, insectivorous marsupials, with a patchy distribution in hummock grasslands. Mulgaras (six males, three females) were implanted intraperitoneally with temperature-sensitive transmitters and monitored for 6–55 d. Temperature profiles for different microhabitats and the thermal properties of soil and a number of burrows were also measured. Air temperature ranged from -3°C at night to 30°C during the day. Although burrows buffered temperature extremes, the thermal diffusivity of the sandy soil was high, and many burrows were shallow. Hence, soil and burrow temperatures averaged about 15°C . The activity of mulgaras was often restricted to a few hours after sunset, before they retired into their burrows. Mulgaras employed torpor frequently, often entering torpor during the night and arousing around midday, with arousals occurring later on cooler days. Shallow burrows allowed cooling below mean T_{soil} . Consequently, body temperatures as low as 10.8°C were observed. The longest torpor bout was 20.8 h. Torpor patterns changed seasonally and differed between males and females. From June to August, females entered torpor almost daily despite mating and gestation, but from the end of the gestation period onward, they remained normothermic. In contrast, males showed only shallow and short torpor during the mating season, but from mid-July, a transition to more frequent and deeper torpor re-

sembling that of females was observed. Apparently, in both sexes, the reproductive effort entails energetic costs, but torpor, as an energy-saving mechanism, and reproduction are not exclusive in mulgaras. In a resource-poor environment during the least productive part of the year, frequent torpor seems to provide the means to compensate for the increased energetic costs associated with reproduction.

Introduction

For mammals, the maintenance of a high body temperature (T_b) via endogenous heat production entails a high energy turnover, which, in resource-poor desert environments, has distinct disadvantages. Desert mammals therefore not only excel in water conservation but also are characterized by a low metabolic rate and low reproductive output in comparison to their mesic counterparts (Eisenberg 1963; Dawson and Hulbert 1970; Yom-Tov 1985; Lovegrove 2003; Withers et al. 2006). Consequently, despite these energetic constraints, the mammal fauna in arid environments can be diverse, and in Australia, small dasyurid marsupials contribute significantly to this diversity (Dickman 2003). Being predominantly insectivorous, food availability for dasyurids is presumably affected by season and specific climatic conditions such as rain and temperature. It is perhaps because of this relatively narrow dietary niche that many dasyurids have evolved the ability to enter daily torpor (Geiser 2003). Daily torpor is a controlled reduction in T_b and metabolic rate, whereby T_b is lowered to an average of about 17°C and metabolic rate to about 30% of basal metabolic rate (BMR; Geiser and Ruf 1995), and in dasyurids can be employed even during the reproductive season (Geiser 1996). Unlike hibernators, animals that exhibit daily torpor arouse from torpor each day, and energy balance is predominantly achieved by foraging rather than relying on accumulated energy stores such as body fat or food caches (Körtner and Geiser 2000a).

Although metabolic rate during torpor is reduced substantially, daily arousals are energetically costly, and it has been proposed that such arousals offset the majority of energy savings from torpor if torpor bouts are short (Prothero and Jürgens 1986). However, estimations of energy savings during torpor and arousal costs are predominantly based on laboratory studies where animals were exposed to constant low ambient temperatures (T_a). In contrast, recent field-based studies demonstrate that torpid animals, even when sheltered in tree hollows, burrows, and rock crevices, are exposed to considerable daily T_a fluctuations and, in some cases, use the different thermal char-

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acteristics of various microhabitats to minimize energy expenditure during torpor and arousal (Körtner et al. 2001; Chruszcz and Barclay 2002; Geiser et al. 2002; Mzilikazi et al. 2002; Turbill et al. 2003; Cooper and Withers 2004; Dausmann et al. 2005; Brigham et al. 2006; Willis et al. 2006; Warnecke et al. 2008). Of course, the opportunities for exploiting daily T_a fluctuations depend on prevailing climatic conditions. Specifically, daily fluctuations in T_a are most pronounced in arid environments because of intense solar radiation, minimal cloud cover, and high thermal diffusivity of sandy soils (Buxton 1924; van Wijck 1963).

We tested the hypothesis that employment of daily torpor is an important functional trait for the survival of Australian desert marsupials. We examined the influence of daily T_a fluctuations on torpor patterns during winter in a desert mammal inhabiting sand plains. We used the nocturnal, insectivorous brush-tailed mulgara (*Dasyercus blythi*) as the study organism because the species is sedentary, and individuals are known to enter torpor in the laboratory (Geiser and Masters 1994; Masters 2003). Because this species uses burrows, we were interested in examining the interrelation between soil temperature and torpor variables. Furthermore, because juvenile development and growth are slow in mulgaras (4–5 mo from mating to independence; Michener 1969; Tyndale-Biscoe and Renfree 1987), reproduction usually commences during winter, when energy conservation is most critical because of high thermoregulatory costs and low food availability.

Two species of mulgaras, both scheduled as threatened, inhabit grasslands on sandy soils across extensive parts of South Australia, the Northern Territory, and Western Australia (Menkhorst and Knight 2001). However, the taxonomy and naming conventions of the two closely related forms of mulgaras are currently under review. Here, we follow Woolley (2005) in recognizing the taxon as *Dasyercus blythi* Waite, 1904.

Material and Methods

The study was conducted in Uluru-Kata Tjuta National Park, Northern Territory (25°20'S, 131°02'E), during the Austral winter (June–August 2006). The study area was located on a sand plain interspersed with low dunes. Mature dense spinifex (*Triodia basedowii*) covered some of the area, but large parts of the study area had been burned in a wildfire in 2002, and in these areas, spinifex was still sparse.

Mulgaras were captured using box aluminum traps (type A; Elliott Scientific Equipment, Upwey, Australia) baited with peanut butter and rolled oats and also contained some polyester fiber material for insulation (for details, see Körtner et al. 2007). To measure core T_b , nine mulgaras were implanted intraperitoneally with sterilized temperature-sensitive radio transmitters (2.4–3.9 g; <5% of body mass; Sirtrack, Havelock, New Zealand) under general oxygen/isoflurane anesthesia. Two different loop antenna configurations were used to account for the difference in size and weight of the transmitters. Heavy males received transmitters with a larger loop antenna boosting re-

ception range. All transmitters were coated with inert wax and then calibrated over a temperature range of 9°–40°C to the nearest 0.1°C before implantation against a mercury thermometer traceable to a national standard. The incision into the abdominal cavity was closed using Chromic Gut (2.0 metric, Ethicon, Sommerville, NJ) for the muscle layer and Coated Vicryl (3.0 metric, Ethicon) for the skin before a topical anesthetic (Ban Itch, Apex Laboratories, Sommerby, New South Wales) and Leuko Spray Bandage (BSN Medical, Clayton, Victoria) was applied. Anesthetized animals were also injected subcutaneously with an identification transponder (PIT tags, Des-tron Technologies, South St. Paul, MN). After surgery, mulgaras were given liquid Children's Panadol (Ermington, New South Wales) and were held for the following night and day while being provided with fresh kangaroo mince ad lib. They were then released the following evening at the point of capture. Overall, seven (five still functional, allowing recalibration) of the nine deployed transmitters were retrieved. One female was carrying newly born pouch young (August 17), precluding a second surgery, and one male "disappeared" or its transmitter failed and was not retrapped. Two animals were retrapped after their transmitters had expired.

Radio tracking and recording of T_b was performed between June 10 and August 21, 2006. All implanted individuals were radio tracked daily to their burrows shortly after sunrise. Burrows were marked and the location recorded with a handheld GPS (Garmin 12X, Garmin, Olathe, KS). For each animal, a mobile data-logging system measuring the interval between two transmitter pulses every 10 min was placed close to the burrow (Körtner and Geiser 1998). After several days, data were downloaded to a personal computer. Log-transformed interval data were then converted to T_b values using a second-order polynomial equation based on the original calibration of the transmitter. Torpor was defined by a T_b threshold of 30°C and the timing of entry and arousal by T_b falling below and rising above 30°C, respectively; torpor bout length was calculated for the time that T_b remained below 30°C (Körtner and Geiser 2000b). Rate of rewarming during arousal was averaged over the time period from the start of the arousal process to when a maximum T_b had been reached (usually above 30°C). In addition, the maximal arousal rate was defined as the maximal temperature difference over a 10-min interval (i.e., between two logger readings). Because mulgaras spent most of the activity phase away from both their burrows and the data loggers, normothermic resting T_b values for the activity phase were obtained daily by averaging the T_b values for the last half-hour before animals left their burrows.

We predicted that the variance of T_b minima during torpor for a given burrow would be smaller (more uniform) than the overall variance of T_b minima across all burrows if the torpor T_b minimum was determined by the thermal characteristics of a burrow. To test this prediction, the variances of T_b minima for each burrow (provided it was used for torpor more than once) were calculated. These were then averaged. This mean value was then compared with 500 averages of variances gen-

erated for randomized subsets of T_b minima. These random subsets were similarly structured to the original data set for burrows (i.e., calculated for the same number of burrows and for the same number of data points for each of the burrows as the original data set). The randomized data points were selected with replacement (i.e., bootstrapped). Only deep torpor bouts long enough (>2 h) to have reached a relatively stable T_b minimum were included in this analysis (i.e., all torpor bouts for females and, for males, bouts from the second half of July onward).

Given the relatively short range of the transmitter-logger combinations, onset of activity was inferred from the time when the transmitter signal disappeared from the logger records. Likewise, end of activity refers to the reappearance of a signal, but this could be quantified only on those days when an animal returned to the same burrow.

The T_a and relative humidity (RH) were measured with miniature data loggers at 30-min intervals (Thermochron and Hydrochron, temperature resolution 0.5°C, humidity 0.6% hydrochron only; i-Buttons, Maxim Integrated Products, Sunnyvale, CA). Air temperature and RH were measured in the shade of a tree trunk at a height of about 1.5 m above the ground. Surface temperature (T_{surf}) was measured at four locations either in the open without shade or under dense spinifex. In addition, soil temperature (T_{soil}) at a site without vegetation cover was recorded with loggers buried in the sand at depths of 17, 27, 37, and 57 cm for 40 d.

To describe the propagation of temperature in the soil formally, the thermal diffusivity was calculated. The thermal diffusivity (α ; cm^2/s) of a substrate is a measure of the degree and speed at which temperature fluctuations at the surface penetrate the substrate. This value allows comparing the sandy soils of Uluru-Kata Tjuta National Park with other soil types, and on the basis of our measurements, predictions for annual soil temperature fluctuations can also be made.

The amplitude of the daily temperature fluctuation at a given depth (z) equals

$$\text{amplitude}_{(z)} = \frac{\text{amplitude}_{(\text{surface})}}{\exp [z/(\alpha 86,400/\pi)^{0.5}]}$$

The delay specifying the time required for temperature changes to penetrate the substrate (phase angle in seconds) equals

$$\text{delay}_{(z)} = \frac{z}{(\alpha 86,400/\pi)^{0.5} 86,400/(2\pi)}$$

For annual variations in temperature, the term defining the cycle length, 86,400 (number of seconds per day) has to be multiplied by 365 (formulas modified from van Wijk 1963). To characterize the apparent thermal diffusivity of the soil at the study site, the daily temperature profile at 17 cm depth as the upper boundary layer was modeled by the first five harmonics of a Fourier series (van Wijk 1963; Horton et al. 1983) using a fast Fourier transformation (Lindfield and Penny 1989).

We chose to use the 17-cm-depth profile as the upper boundary instead of T_{surf} to avoid complications by nonperiodic events such as changes in cloud cover, wind speed, and potential artifacts from the different reflectivity of loggers compared with the surrounding soil. On the basis of the amplitude and phase angle of the five harmonics for the upper boundary, another model was constructed for the 27-cm profile, with the apparent thermal diffusivity α as the variable. The α with the best fit was determined by iteration according to the least sum of squared differences. For details, see Horton et al. (1983). Thermal diffusivity was averaged over the last 32 d measured (July 18–August 19), avoiding the nonperiodic fluctuation during the rainfall period in early July.

Finally, burrow temperature (T_{burrow}) and RH profiles were measured in three mulgara burrows. A combined temperature/humidity logger was loosely taped to the tail of each of four recaptured mulgaras, and the animals were released into one of their known burrows. Of the four attempts, three succeeded and one failed because the mulgara returned to the surface after a few hours and deposited the logger at the burrow entrance. Provided the animal removed the tape in the burrow ($n = 3$), the logger was retrieved at the end of the study via an attached fishing line. Burrow length was assumed to be similar to the length of fishing line (i.e., distance from entrance to nest chamber), and burrow depth was estimated by comparing the temperature profile with that of soil temperature.

Rainfall records were obtained from the weather stations at Yulara and Uluru at a distance of approximately 11 and 13 km from the study site, respectively. We used the average of these two sites as an approximation of rainfall at the study area.

Unless stated otherwise, data are presented as means \pm 1 SD, whereby the mean for a group of animals was calculated as the average of the means for each individual. Data analyses were performed in Excel (Microsoft), Minitab (Minitab), and a variety of programs written in Visual Basics V1 and V6 (Microsoft) by G. Körtner. Means were compared using Student's t -test with percentage values arcsine transformed. Curve fits were performed via regression analyses in Sigmaplot 7.0 (SPSS). The variable n refers to the number of animals, and N refers to the number of measurements.

Results

Air and Soil Temperature

The weather was predominantly fine with clear skies, except for overcast conditions during July 12–20, when approximately 45 mm of rain fell. On days without cloud cover, T_a regularly fell below 0°C at night and exceeded 20°C during the day. On average, T_a increased slightly from the second half of July onward. However, when summarized over the study period (June 10–August 18), mean daily T_a was $11.7^\circ \pm 2.1^\circ\text{C}$, maximum daily T_a was $21.1^\circ \pm 3.9^\circ\text{C}$ (reached on average 7.8 ± 1.2 h after sunrise), and minimum daily T_a was $3.0^\circ \pm 3.3^\circ\text{C}$ (at 1.8 ± 2.3 h before sunrise). During dry weather, RH was inversely related to T_a ($\text{RH} [\%] = 68.6 - 2.14T_a [^\circ\text{C}]$, $F_{1,2,567} = 5.873$,

$R^2 = 0.70$, $P < 0.001$) and before the rain period regularly fell to a minimum of $23.8\% \pm 5.5\%$ during midday and reached a mean maximum of $71.8\% \pm 10.6\%$ during the night (29 d). With the rain, RH increased; at night, RH often reached 100%, and morning dew or frost was initially common. This postrain period lasted for about 16 d before RH returned to pre-rain levels.

The daily mean T_{surf} of sand was $12.8^\circ \pm 2.3^\circ\text{C}$, the maximum daily T_{surf} was $34.1^\circ \pm 6.8^\circ\text{C}$, and the minimum daily T_{surf} was $0.7^\circ \pm 3.5^\circ\text{C}$ (June 10–August 18). Daily fluctuations of T_{surf} were more pronounced than T_{a} , particularly during the day when the sun heated the sand to $>30^\circ\text{C}$ (Fig. 1). Excluding the 9 d of rainy and overcast weather, the amplitude in T_{surf} (day–night differential) was $35.8^\circ \pm 5.3^\circ\text{C}$, and the maximum recorded amplitude was 48°C . On average, the maximum T_{surf} was reached at 1400 ± 0.51 hours or, when corrected for the change in photoperiod, 6.6 ± 0.5 h after sunrise (June 10–August 18; Fig. 1).

As expected, spinifex cover reduced T_{surf} fluctuations to some extent (Fig. 1). The daily temperature profile resembled that of T_{a} : daily mean $11.5^\circ \pm 2.1^\circ\text{C}$, minimum $2.2^\circ \pm 3.5^\circ\text{C}$, and maximum $24.3^\circ \pm 3.9^\circ\text{C}$. The daily temperature amplitude under spinifex was $23.7^\circ \pm 4.0^\circ\text{C}$, excluding the rain period.

The daily temperature cycle in sand was further dampened with increasing depth. Mean daily T_{soil} over the course of the experiment was similar at all depths ($15.8^\circ \pm 0.4^\circ\text{C}$, $n = 4$, 70 d). The apparent thermal diffusivity of the predominantly sandy soil was $9.21 \pm 0.83 \cdot 10^{-3} \text{ cm}^2/\text{s}$. Consequently, at a depth of 17, 27, 37, and 57 cm, the daily amplitude of T_{surf} was reduced by a calculated factor of 0.34, 0.18, 0.1, and 0.03, respectively, which closely matched the observed values (Fig. 1). The calculated phase delays for daily fluctuations in respect to T_{surf} at these depths were 4.1, 6.5, 8.9, and 13.7 h, respectively (Fig. 1). Hence, for example, daily maxima of T_{soil} for each depth would occur on average 10.7 (10.9 ± 0.9), 13.1 (13.4 ± 1.5), 15.2 (16.1 ± 0.6), and 20.3 (22.6 ± 0.6) h after sunrise at 17, 27, 37, and 57 cm (actual measured values in parentheses). In contrast, assuming stable soil conditions (i.e., moisture level) at a depth of 57 cm, annual changes in mean daily T_{surf} should be reduced by a factor of only 0.83, and the delay of the annual cycle should be about 11 d.

Burrow Temperature and Relative Humidity

Mean T_{burrow} in three burrows was $15.5^\circ \pm 1.2^\circ\text{C}$, similar to mean T_{soil} . However, in burrow B1, daily fluctuations of T_{burrow} with an amplitude of $5.6^\circ \pm 3.7^\circ\text{C}$ (maximum: $17.2^\circ \pm 2.4^\circ\text{C}$; minimum: $11.6^\circ \pm 1.9^\circ\text{C}$) were pronounced, and daily minima below 10°C were observed. In contrast, in the other two burrows, the amplitudes of the fluctuations of T_{burrow} were both only 0.8°C (maxima: $16.9^\circ \pm 1.1^\circ\text{C}$, $16.0^\circ \pm 0.8^\circ\text{C}$; minima: $16.1^\circ \pm 1.2^\circ\text{C}$, $15.2^\circ \pm 0.7^\circ\text{C}$, respectively). According to these amplitudes, burrow depths were estimated to be 30 cm (B1, 190 cm long), 50 cm (B2, 220 cm long), and 50 cm (B3, 60 cm long). Apparently, the first two burrows descended at a shallow angle

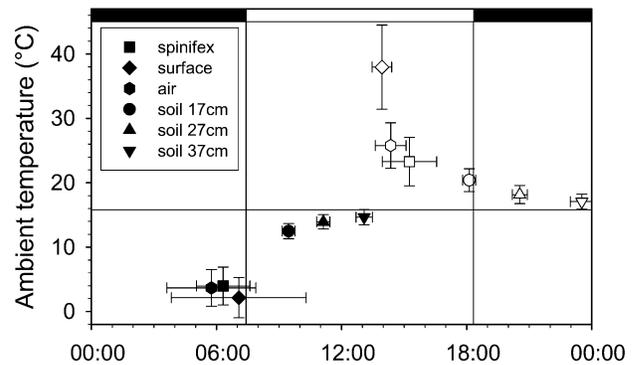


Figure 1. Minima (solid symbols) and maxima (open symbols) of ambient temperatures plotted against the respective time of day of their occurrence. Temperature profiles were measured at different locations above- and belowground as indicated. The rain period during mid-July was excluded from the analysis. Temperature fluctuations measured at 57 cm depth were too small to determine the times of maximum and minimum. The horizontal line represents mean soil temperature at all depths. The dark phase is depicted as solid bars.

and the third rather steeply. Determining burrow depth via destructive excavation was neither desirable nor permitted, given the rarity of mulgaras. Therefore, only one animal, which could not be retrapped, was dug up at the end of the study to remove the transmitter. This burrow had two entrances and was 24 cm deep, with a length of approximately 1 m.

The RH in burrows was generally higher than aboveground. RH in the two deeper burrows was around 100% even before the rainfall event in July. In contrast, in the shallow burrow (B1), RH fluctuated inversely with T_{burrow} between 30% and 65% before rain. During this period, average daily RH inside this burrow was correlated with average RH of outside air ($\text{RH}_{\text{burrow}} [\%] = 0.35\text{RH}_{\text{air}} [\%] + 34.3$, $F_{1,25} = 27.97$, $R^2 = 0.54$, $P < 0.001$). After the rain, RH in this burrow also reached 100% and remained so until the end of the study.

Trapping and Radiotelemetry

Over the course of the study, we trapped 12 individual mulgaras. On average, males (85 ± 12.7 g, $n = 8$) were heavier than females (57.4 ± 3.9 g, $n = 4$, $T_9 = 5.6$, $P < 0.001$). Of these animals, nine individuals (6M : 3F) were radio tracked for periods ranging from 6 to 55 d, resulting in 277 radio tracking days (Fig. 2). Short monitoring periods were attributed to premature transmitter failure and some predation (Körtner et al. 2007). Of the five recalibrated transmitters, the three with short deployments (14–34 d) were within $0.31^\circ \pm 0.11^\circ\text{C}$ of the original calibration (maximum deviation from the original calibration over the whole temperature range), with an inconsistent direction of the drift. The two transmitters with the longer working life (54 and 56 d) had drifted by $0.96^\circ \pm 0.10^\circ\text{C}$, whereby the original calibration returned slightly lower values. Because these drifts were minor and the time course of the

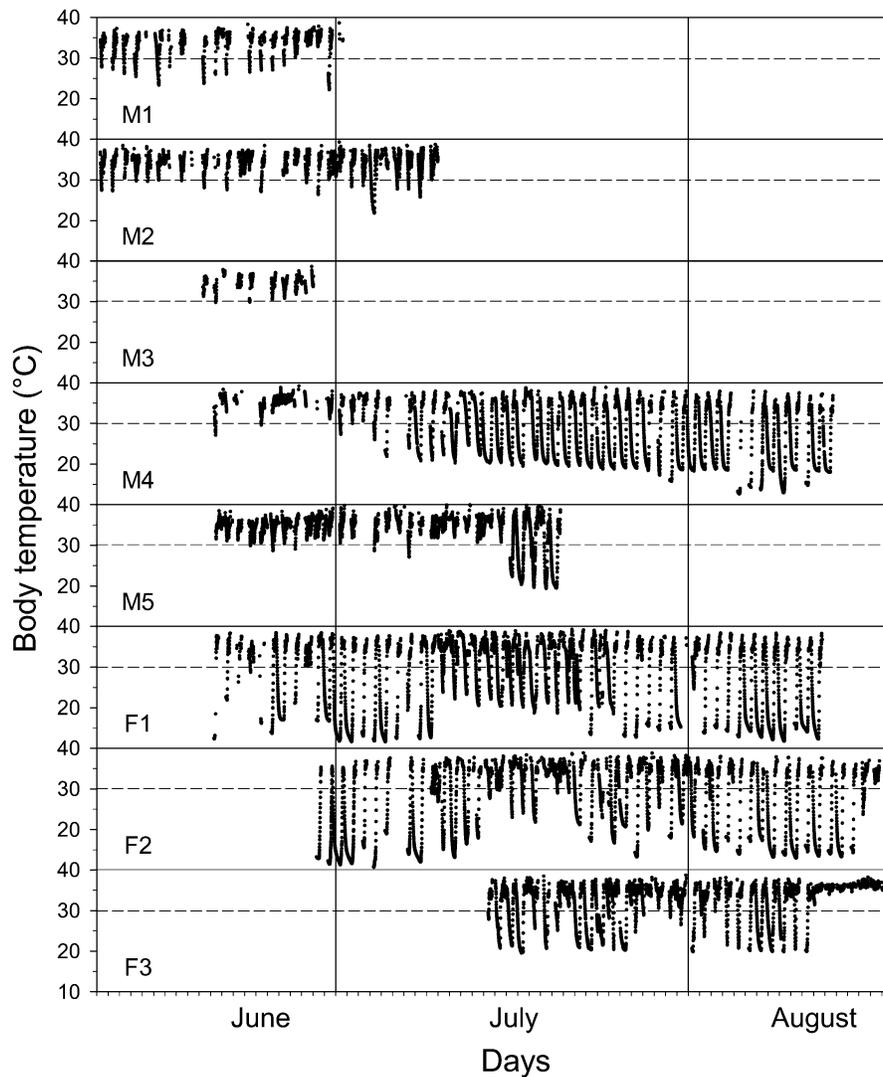


Figure 2. Summary of all body temperature measurements obtained for five male and three female mulgaras. M6 has been omitted because its transmitter failed 4 d after implantation. Torpor threshold of 30°C is indicated by horizontal dashed lines.

drift remained unknown, no correction of the original calibration was performed.

Activity

Neither the timing of activity onset ($T_{179} = 2.0$, $P = 0.05$) nor that of the end of activity ($T_{98} = 0.9$, $P = 0.37$) differed between males and females. In 84% of all observations, activity commenced within an hour of sunset (Fig. 3). Occasionally, individuals left their burrow earlier, up to 3.5 h before sunset. Late onset of activity, several hours after sunset, was usually observed in animals sharing burrows and was possibly associated with mating. The end of the activity period was less well defined and occurred throughout the night. End of activity was weakly correlated with T_a and T_{surf} , but mean night T_a was the best predictor (end of activity [hours to sunrise] = $-0.45T_a$

avg [°C] + 9.94, $F_{9,127} = 6.92$, $R^2 = 0.05$, $P < 0.01$). The frequency distribution (Fig. 3) diverged significantly from normality (Kolmogorov-Smirnov test for normality, $P < 0.01$) and appears to be weakly bimodal, suggesting that mulgaras often retreated into their burrows after a short activity period or much later around sunrise. In fact, on several occasions, two or more activity bouts were observed separated by prolonged resting periods sometimes including torpor. On six out of 277 occasions, mulgaras were observed to remain in their burrows for the entire nighttime activity phase.

Body Temperature Patterns and Torpor

The T_b of mulgaras showed pronounced daily fluctuations. At the beginning of the activity phase at dusk, T_b values were on average $36.3^\circ \pm 0.6^\circ\text{C}$ ($n = 9$, $N = 267$). When animals were

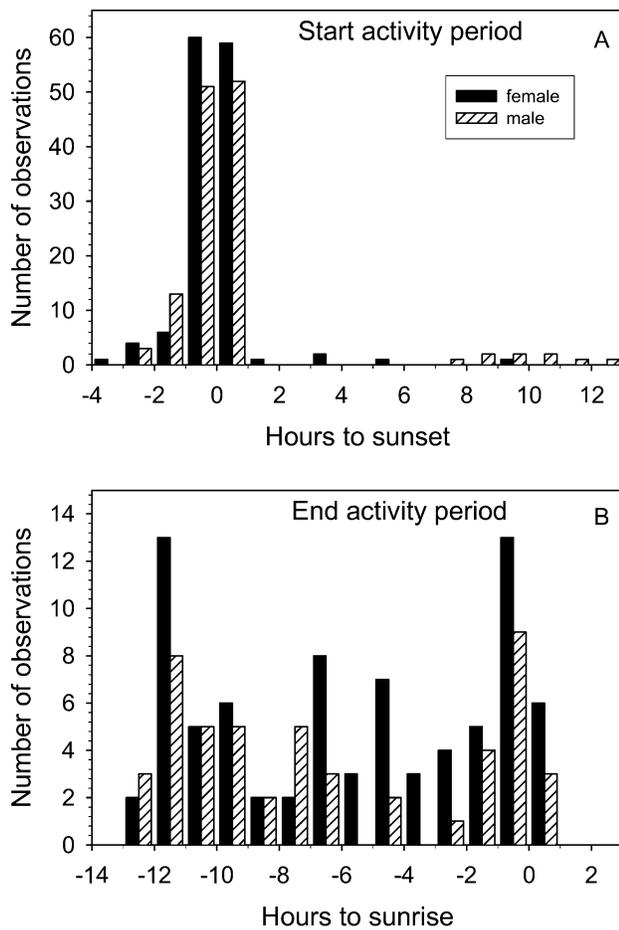


Figure 3. Onset of activity in relation to sunset (A) and end of activity in relation to sunrise (B).

active close to the monitored burrow at night, values above 38°C were commonly recorded. In contrast, T_b was generally lower during the day. The frequency distribution of minimal T_b values reached during the day differed between males and females (Fig. 4). On the majority of tracking days, females became torpid, and hence low T_b 's were observed more often for females than for males (Fig. 4). By comparison, males remained normothermic more frequently, and torpor was shallower and usually restricted to the daytime rest phase. However, in males, torpor frequency and depth appeared to increase over the course of the study (Fig. 2). In the two males that were monitored into the middle of July and onward (M4, M5), a relatively sudden transition occurred from regular normothermy and shallow daytime torpor to deep, daily torpor that commenced during the night. Excluding the two males, which were monitored for less than 8 d, not long enough to assess torpor frequency (M3 [one bout in 7 d], M6 [three bouts in 4 d]), torpor frequency of males before the transition was $50.8\% \pm 25.9\%$ ($n = 4$, $N = 79$), whereas after the transition, it was 100% ($N = 44$) for both males ($T_3 = 5.7$, $P = 0.011$). Toward the end of the study, the reverse trend was observed

in one female (F3) with newly born pouch young. This individual remained normothermic after the young were born, whereas it regularly entered deep torpor before birth of the young (Fig. 2). Excluding the pouch young phase of this female, torpor frequency for females was $95.8\% \pm 2.5\%$ ($n = 3$, $N = 134$).

Mulgaras entered daily torpor exclusively (i.e., torpor bout length did not exceed 24 h), and timing of arousal from torpor ($T_{169} = 2.2$, $P = 0.03$) and entry into torpor ($T_{150} = 1.9$, $P = 0.06$) was similar for both males and females. Torpor was not necessarily restricted to the daytime rest phase of mulgaras. The timing of torpor entry showed two peaks (Fig. 5), and only the second peak around sunrise was consistent with rest phase torpor. A large number of torpor bouts commenced during the night often only a relatively short time into the dark phase (Fig. 5). On a number of days, two torpor bouts per day were observed; the first during the night and, separated by a period of activity, a second bout toward morning. However, because mulgaras could have entered torpor in an alternate burrow during the night and, on occasion, were observed to do so, it remains unclear how often daily double bouts occurred. Torpor entry appeared to occur slightly earlier on cold nights (torpor entry [hours from sunset] = $0.28T_a \text{ min } [^{\circ}\text{C}] - 3.73$, $F_{9,165} = 5.34$, $R^2 = 0.03$, $P = 0.02$), but the low R^2 indicates a poor predictive power of this regression. Arousal timing was more uniform, with most arousals taking place 3–7 h after sunrise (+3 to +7 in Fig. 5; mean: 5.6 ± 1.6 h) for bouts extending beyond sunrise. On nine occasions, torpor was extended to dusk, and these arousals, which occurred >9 h after sunrise, were all observed during the rainy overcast period in July (Fig. 5). The time elapsed between arousal and sunrise was inversely correlated with maximum T_{surf} of that day (time of arousal [hours to sunrise] = $-0.07T_{\text{surf}} \text{ max } [^{\circ}\text{C}] + 7.8$, $F_{9,203} = 19.1$, $R^2 = 0.086$, $P < 0.001$). Hence, arousals tended to occur slightly earlier on hot days. Mean arousal rate was $0.12^{\circ} \pm 0.04^{\circ}\text{C}/\text{min}$

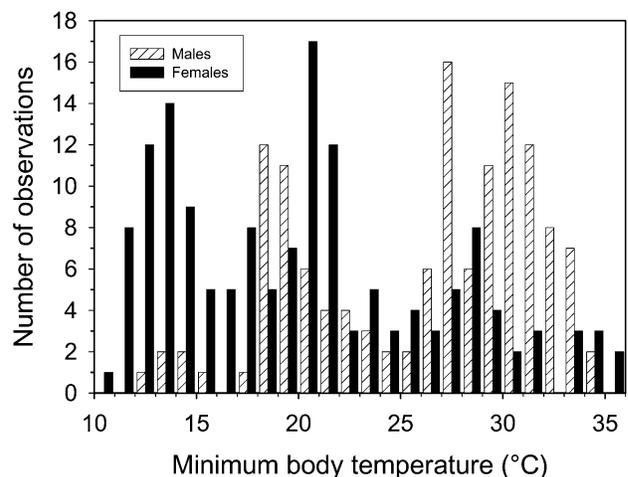


Figure 4. Frequency distribution of minimum body temperature (T_b) reached during the day for male and female mulgaras.

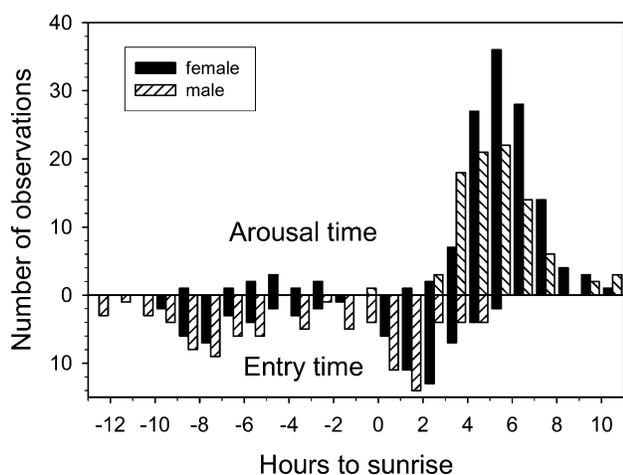


Figure 5. Timing of torpor in relation to sunrise. Bars below the line depict torpor entry times, and those above zero depict arousal times from torpor.

($n = 8$, $N = 211$), and the maximal rate of rewarming during arousal was $0.24 \pm 0.09^\circ\text{C}/\text{min}$ ($n = 8$, $N = 212$). The overall maximum rewarming rates observed over a 10-min period was $0.62^\circ\text{C}/\text{min}$. Only maximum arousal rate was weakly correlated with maximum T_a (arousal rate [$^\circ\text{C}/\text{min}$] = $0.003T_a \text{ max } [^\circ\text{C}] + 0.174$, $F_{8,211} = 4.0$, $R^2 = 0.02$, $P = 0.047$).

The minimum T_b reached during torpor decreased with increasing torpor bout length, and this relationship was well described by an exponential function (Fig. 6; males: $y = 17.58 + 12.67e^{(-0.163x)}$, $F_{6,72} = 584.9$, $R^2 = 0.94$, $P < 0.001$; females: $y = 9.33 + 20.06e^{(-0.084x)}$, $F_{3,88} = 166.3$, $R^2 = 0.79$, $P < 0.001$; combined: $y = 13.77 + 16.14e^{(-0.117x)}$, $F_{9,161} = 350.9$, $R^2 = 0.82$, $P < 0.001$). However, scatter increased for torpor bouts > 8 h. Apparently, T_b reached a plateau during longer bouts, although the level of this plateau varied widely between bouts. In most cases, males maintained T_b above 17°C and, hence, above mean T_{soil} , whereas females regularly showed T_b 's below 14°C . The lowest T_b and longest torpor bout recorded for females were F1 (11.6°C , 17.5 h), F2 (10.8°C , 20.8 h), and F3 (19.6°C , 14.3 h) and for the two males after the transition to deep torpor were M4 (12.7°C , 18.6 h) and M5 (19.4°C , 14.2 h). Neither torpor bout length ($R^2 = 0.01$, $P = 0.21$) nor minimum T_b during torpor ($R^2 = 0.01$, $P = 0.11$) was correlated with minimum T_a .

Our T_b data strongly suggest that the minimum T_b during long torpor bouts (i.e., in females and after the transition in males; $N = 155$) was influenced by the thermal characteristics of a burrow. The average variance for long torpor bouts in burrows that were used for torpor by an individual at least twice (range: two to 30 times) was 1.33°C^2 ($n = 5$, 25 burrows), whereas those of random subsets range from 8.85°C^2 to 24.85°C^2 . Hence, T_b minima for any given burrow were more uniformly distributed than expected from the overall range. This is illustrated in Figure 7, where the mulgara (M4) used two different burrows during alternating days. The torpor bouts in burrow

B2, used on August 8 and 10, reached a stable plateau above mean T_{soil} , indicating a burrow depth of > 50 cm. This burrow was used by this animal for torpor on a total of 30 d with consistent torpor patterns. However, other burrows were occasionally used, and some of these appeared to be much shallower (B1). In the example of August 9, T_b fell below the T_{soil} at ≤ 27 cm, but below approximately 16°C , T_b matched the T_{soil} profile measured at a depth of 17 cm (Fig. 7). It is therefore tempting to assume that on this day before arousal, the phase of slow rewarming, which traced the increase of T_{soil} at 17 cm, constituted passive rewarming.

Discussion

The generally low and unpredictable rainfall that is characteristic of desert environments results in an overall low food availability. In winter, this situation is exacerbated for insectivorous mammals such as the mulgara because the activity and reproduction of their predominantly ectothermic prey is curtailed (Holm and Edney 1973). Reducing energy expenditure is therefore highly desirable. Consequently, mammals adapted to desert environments are characterized by a relatively low BMR (Lovegrove 2003; Withers et al. 2006). However, for small, nocturnal desert mammals, thermoneutrality and therefore BMR remains elusive during winter nights with often subzero T_a 's. Although burrows provide resting mulgaras some protection from temperature extremes and reduce the risk of dehydration, their ability to provide a thermally buffered environment is limited by the high thermal diffusivity of the sandy soil. Hence, during the nadir of the annual T_a cycle (i.e., winter), T_{soil} was on average only about 15°C , a temperature that for mulgaras is substantially below the thermoneutral zone ($\geq 30^\circ\text{C}$; MacMillen and Nelson 1969; Kennedy and MacFarlane 1971). In addition, pronounced daily T_a fluctuation penetrate to a depth of about 60 cm, albeit with a progressively reduced amplitude. Hence, in burrows close to the surface, T_{soil} and T_{burrr} regularly fell below

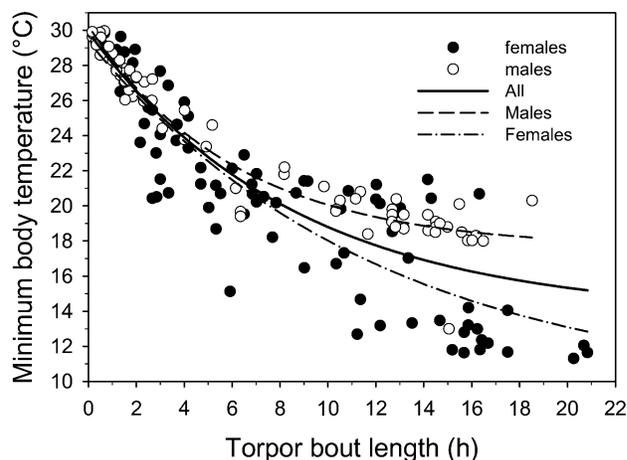


Figure 6. Minimum body temperature (T_b) reached during torpor plotted against torpor bout length for males and females.

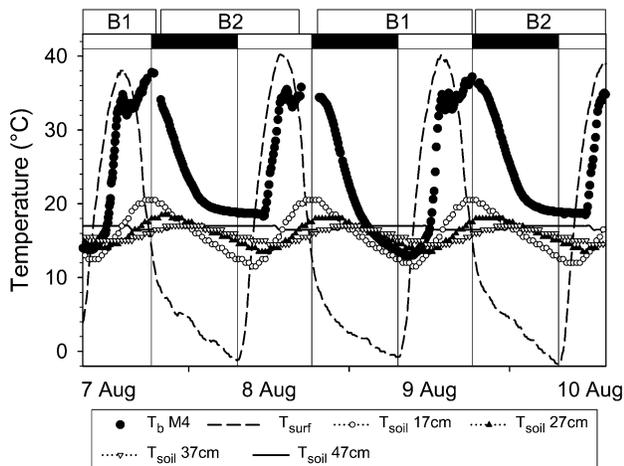


Figure 7. Three-day example of body temperature patterns (circles) of a male mulgara and soil temperature. Solid lines with decreasing amplitude show temperature profiles measured at the surface and 17, 27, 37, and 57 cm underground, respectively. Over the time period shown here, this animal entered torpor on all 4 d and used two different burrows. As illustrated, the first burrow (B1) was used on August 7 and 9, when T_b fell as low as 13°C, and the second (B2) on August 8 and 10, when T_b remained >18°C. Short activity periods around dusk are indicated by gaps in the data. The dark phase is depicted as solid bars.

10°C. Consequently, during winter, normothermic mulgaras that shelter in burrows still require considerable amounts of energy for thermoregulation.

Because heat loss is proportional to the $T_b - T_a$ gradient, any reduction in T_b will reduce heat loss and hence costs for thermoregulation. By entering torpor, mulgaras are able to reduce the costs of endogenous heat production and, by allowing T_b to fall below normothermic resting levels, maintain energy expenditure at levels well below BMR (Geiser and Masters 1994; Geiser and Ruf 1995). Furthermore, for mulgaras as well as the closely related fat-tailed dunnart (*Sminthopsis crassicaudata*; Warnecke et al. 2008), torpor in the field can be substantially deeper (field 10.8°C vs. laboratory 13.2°C) and longer (field 20.8 h vs. laboratory 12.3 h) than previously observed in the laboratory (Geiser and Masters 1994). Considering that torpid mulgaras do not thermoregulate above a T_a of about 10°C (Geiser and Masters 1994), shallow burrows with low minimum T_{burrr} could assist in further reducing energy expenditure during torpor. Remaining close to the surface allows mulgaras to cool below mean T_{soil} , whereby torpor metabolic rate decreases with T_b by a factor of two to three for every 10°C (Geiser 2004). This energetic advantage could be partly offset by potentially shorter torpor bouts and increased arousal costs if rewarming were achieved exclusively via endogenous heat production. However, if active arousal is delayed until after T_{burrr} in shallow burrows begins to increase (Fig. 7), arousals can be potentially passive and costs could be substantially reduced. For example, in stripe-faced dunnarts (*Sminthopsis macroura*), energy expenditure during torpor was almost halved when subjected to

a T_a cycle with a 10°C amplitude instead of a constant T_a (Lovegrove et al. 1999). Incidentally, mulgaras rarely realize maximal rewarming rates, which can be as high as 0.6°C/min (Morrison 1965; data in this study), and arousal was usually slower, potentially maximizing passive heat gain from the environment. During overcast/rainy weather when soil and burrows did not heat up during the day and passive rewarming was not possible, arousals were on average delayed, and then torpor was occasionally extended to dusk.

The patterns of early arousal from torpor probably facilitated by high afternoon T_a 's are shared by all arid zone dasyurids studied to date and also by some small African heterothermic mammals (Geiser 1986; Geiser and Baudinette 1988; Lovegrove and Raman 1998; Lovegrove et al. 1999; Schmid 2000; Geiser et al. 2002; Mzilikazi and Lovegrove 2005; Warnecke et al. 2008). After arousal, normothermic mulgaras could select mild, energy-conserving conditions along their burrow system, given that on sunny days T_{soil} close to the surface continues to rise. Mulgaras could also facilitate heat uptake by sun basking as they do in captivity (Fleay 1961). However, perhaps because of the difficult observational conditions among the spinifex hummocks and the vigilance of mulgaras, we were unable to observe basking in our study animals, but at least two other arid zone dasyurids are known to sun bask in the wild and even to use solar radiation to facilitate arousal from torpor (Geiser et al. 2002; Warnecke et al. 2008). Nevertheless, even when mulgaras are able to select thermoneutral conditions on or close to the surface, afternoon normothermia is energetically still more expensive than extended torpor, which still would be feasible at greater depths. It therefore appears that desert heterotherms usually do not have to maximize energy savings by always employing long torpor bouts, provided that temperature conditions allow thermoregulatory costs for normothermia to remain low. Moreover, in mulgaras, the use of torpor was apparently not essential for short-term survival because, at different times of the winter, both sexes either ceased to use torpor altogether or reduced torpor length and depth substantially. Females that employed torpor extensively during gestation ceased to use torpor close to the time of parturition (see also Geiser and Masters 1994). Some additional costs might have been incurred if the extensive use of torpor prolonged gestation, which is variable, ranging from 30 to 48 d (Fleay 1961; Michener 1969; Woolley 1971; Geiser and Masters 1994). The reverse applied to males, which frequently showed deep prolonged daily torpor later during winter and only occasionally entered shallow torpor during the mating season in early winter. Incompatibility between torpor and mating in males is often attributed to either physiological constraints for spermatogenesis (e.g., most rodents) or to the necessity to increase competitiveness during the mating season (Barnes 1996; Geiser 1996; Fietz et al. 2004). As far as the latter is concerned, the large home ranges of males indicate that they play the more active role in mate seeking, and therefore activity might have to be elevated (Masters 2003; Körtner et al. 2007).

Because torpor was intertwined with reproduction, torpor

might have allowed free-ranging mulgaras to achieve a positive energy balance to gain or to recoup body energy stores, as has been observed in the laboratory (Geiser and Masters 1994). In a similar fashion, kangaroo mice (*Microdipodops pallidus*) increasingly employ torpor in response to food restriction, enabling them not only to maintain body mass but also to accumulate food stores (Brown and Bartholomew 1969). It therefore appears that, similar to hibernation, in some species, daily torpor can be used to shift energetic costs between seasons beyond simply balancing daily energy requirements. However, we predict that in mulgaras, torpor is restricted during the summer months. Because annual T_a fluctuations of 18°C (Australian Bureau of Meteorology) will penetrate the soil by several meters, even at a depth of 57 cm, mean T_{soil} during summer will increase by about 15°C, reducing the scope for cooling and potential energy savings but probably also the necessity for torpor. With mean T_{soil} 's expected to be around 30°C, shallow burrows used to an advantage in winter will become dangerously hot during the day, and mulgaras would have to retreat to deep burrows to escape the risk of hyperthermia.

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