

# Basking and torpor in a rock-dwelling desert marsupial: survival strategies in a resource-poor environment

Fritz Geiser · Chris R. Pavey

Received: 30 April 2007 / Revised: 24 June 2007 / Accepted: 27 June 2007  
© Springer-Verlag 2007

**Abstract** Australian deserts are characterized by unpredictability, low primary productivity, and high temperature fluctuations. Despite these adverse conditions the diversity of small insectivorous marsupials of the family Dasyuridae is surprisingly high. We quantified the thermal biology of the dasyurid *Pseudantechinus madonnellensis* (body mass ~30 g) in the wild to gain some understanding of whether the success of dasyurids in the arid zone may be related to some extent to their use of energy conservation strategies. In winter, most free-ranging *Pseudantechinus* frequently (58.3% of 131 animal days) entered daily torpor after midnight (mean 0157 hours) in rock crevices when outside ambient temperatures ( $T_a$ ) were low. Most animals remained torpid until the next morning when they moved while still torpid from rock crevices to sun-exposed basking sites. We visually observed basking during rewarming from torpor (mean commencement at 0943 hours) at body temperatures ( $T_b$ ) as low as 19.3°C when radiant heat was high and  $T_a$  was rising. Basking continued for the rest of the day. Torpor use was not strongly correlated with  $T_a$ , but the temporal organization of daily torpor and activity were apparently linked to the thermal characteristics of basking sites.

Our study suggests that by frequently employing daily torpor and basking and by appropriately coordinating their thermal biology with that of specific locations in their environment, *Pseudantechinus* can reduce daily energy expenditure and thus can live and reproduce in a challenging environment. It is likely that the success of other small dasyurids and perhaps many other small mammals living in deserts is linked to employment of torpor and basking for energy conservation.

**Keywords** Activity patterns · Basking · Desert mammals · Daily torpor · Energy conservation · *Pseudantechinus macdonnellensis* · Thermal environment

## Abbreviations

MR	Metabolic rate
$T_a$	Air temperature
$T_{a \text{ bask}}$	Basking temperature
$T_{a \text{ cave}}$	Cave temperature
$T_b$	Body temperature

## Introduction

Arid regions represent extreme environments for the persistence of animal and plant life particularly as a result of low primary productivity, limited supply of food and water, and pronounced daily and seasonal fluctuations of  $T_a$ . Australia is a dry continent with almost half its land area experiencing mean annual rainfall of less than 250 mm (Trewin 2006) and with infertile soils (Stafford Smith and Morton 1990), but despite these adverse conditions the diversity of small mammals in the Australian arid zone is high (Dickman 2003). The most successful group of mammals are small insectivorous/carnivorous marsupials of the family

---

Communicated by I.D. Hume.

F. Geiser (✉)  
Centre for Behavioural and Physiological Ecology,  
Zoology, University of New England, Armidale,  
NSW 2351, Australia  
e-mail: fgeiser@une.edu.au

C. R. Pavey  
Biodiversity Conservation, Department of Natural Resources,  
Environment and of the Arts, P.O. Box 1120, Alice Springs,  
NT 0871, Australia

Dasyuridae with about half of the 53 Australian species living entirely or partially in the arid zone (Menkhorst and Knight 2001; Dickman 2003).

Small endothermic mammals living in deserts face several challenges because of extreme  $T_a$  and frequent lack of food and water (Schmidt-Nielsen 1979; Bradshaw 2003). The large relative surface area of small endotherms requires high metabolic rates (MR) and results in high water loss when their  $T_b$  is regulated at homeothermic levels particularly when they are exposed to extreme environmental conditions. Especially in insectivorous endotherms food availability declines with  $T_a$  while energy requirements increase (Speakman and Thomas 2003), and food, but also water requirements, may exceed available resources. These limitations appear to be the primary reason why not all endotherms are permanently homeothermic. Many small species are heterothermic and are capable of entering a state of torpor, characterised by substantial reductions of  $T_b$ , MR, water loss and other physiological processes that reduce water and food requirements (MacMillen and Hinds 1983; Wang 1989; Withers 1992; Frank 1994; Geiser 2004; Gutman et al. 2006).

Arid zone dasyurid marsupials employ daily torpor under laboratory conditions, some even when food is freely available. Others use torpor during the reproductive season, when most mammals maintain strict homeothermy, suggesting that torpor is a crucial adaptation that allows these small mammals to live and reproduce in Australian deserts (Geiser 2003). Dasyurids reduce  $T_b$  from  $\sim 35^\circ\text{C}$  during normothermia (high MR and high regulated  $T_b$ ) to  $\sim 15^\circ\text{C}$  during torpor. The MR during daily torpor is on average reduced to  $\sim 30\%$  of the basal MR (Geiser 2003), and water loss during torpor is reduced to one third of that in normothermic individuals (Cooper et al. 2005). While torpor in arid zone dasyurids has been studied in several species, almost all of this knowledge is based on laboratory measurements quantified under constant thermal conditions. However, recent evidence shows that laboratory data on torpor can differ substantially from those obtained in the field and often torpor is less frequent, shallower, and of shorter duration in captivity than in the field (Geiser et al. 2000). Thus, laboratory data may underestimate the ecological and functional significance of torpor for survival in a challenging desert environment.

The purpose of our study was to investigate the ecology and thermal biology of a free-ranging arid zone dasyurid, the fat-tailed antechinus (*Pseudantechinus macdonnellensis*) in relation to its diverse and changing thermal environment. In particular we sought to determine how natural daily variation in thermal conditions influenced thermal biology, daily activity patterns and space use of these rock-dwelling marsupials. *P. macdonnellensis* is a rare, small ( $\sim 30$  g), largely insectivorous, and supposedly nocturnal

dasyurid living in arid regions of Australia with a stronghold in the MacDonnell Ranges where they typically inhabit rocky areas, use multiple rock crevices as shelters and, for desert dasyurids (Dickman et al. 2001), show a strong site-fidelity (Gilfillan 2001; Menkhorst and Knight 2001; Dickman 2003; Pavey et al. 2003). We were especially interested in understanding how in the wild these mammals employ torpor and other energy saving mechanisms such as basking (Geiser et al. 2002) and appropriate timing of daily activity and rest phases to permit life in an environment with limited food supply. Use of basking in torpid mammals has been discovered only recently as a strategy for energy conservation (Geiser et al. 2002, 2004; Mzilikazi et al. 2002; Warnecke et al. 2007) and laboratory data on a small dasyurid marsupial suggest that it can substantially reduce the energy cost associated with arousal from torpor (Geiser and Drury 2003).

## Methods

The study was conducted in winter (June/July 2001) at Ormiston Gorge ( $23^\circ 37' \text{S}$ ,  $132^\circ 45' \text{E}$ , altitude  $\sim 600$  m), in the West MacDonnell National Park, Northern Territory, in central Australia. The study site was located largely on north-facing steep slopes covered in sandstone rocks and spinifex (*Triodia brizoides*) that contained high vertical sandstone cliffs and some caves. We caught seven adult fat-tailed antechinus (two females, five males) using Elliott box traps along sandstone cliffs. Capture body mass of males and females was indistinguishable ( $t$  test,  $t = 0.7$ ,  $df = 5$ ,  $P > 0.5$ ) and the overall mean body mass was  $30.8 \pm 5.0$  g ( $n = 7$ ). Animals were transferred to a field laboratory and temperature-sensitive transmitters were implanted intraperitoneally (using a small,  $< 1$  cm, ventral incision) into six individuals under Oxygen/Isoflurane anaesthesia. The incision was sutured with a self-absorbing sterile chromic gut suture. Animals recovered quickly from surgery, which typically lasted  $\sim 20$  min. Incisions were clean and partially healed when animals were released. Prior to surgery, transmitters (Sirtrack, New Zealand, FM single stage, mass 2 g) were coated in Paraffin/Elvax (Minimitter, USA) and calibrated against a precision thermometer to the nearest  $0.1^\circ\text{C}$  in a water bath from  $10$  to  $40^\circ\text{C}$  to derive an equation of pulse rate as a function of temperature ( $r^2 > 0.99$ ), which was used to calculate  $T_b$  of free-ranging individuals. Animals were released at their site of capture after recovery for one night in captivity. The seventh individual (male) was equipped with an external transmitter glued to the dorsal skin, however, because this transmitter was dislodged within one day, data from this individual, with the exception of body mass, are not included in analyses. After release animals were tracked/located at least once daily

with manual receivers (Telonics TR4, with a Sirtrack folding Yagi antenna) to identify their exact location. Radio-tracking commenced soon after sunrise (~0720 hours) and well before (~3 h) basking commenced. We used transmitter signals to determine the approximate location of the animals and then scanned the likely areas with binoculars to determine when and where animals emerged from torpor sites to bask and at what  $T_b$  basking commenced. *Pseudantechinus* entered torpor in rock crevices and caves and moved while still torpid from the sites they entered torpor to basking sites. Transmitter pulse rate was recorded manually and animals were observed with binoculars usually several times/day; however, most continuous thermal data were recorded at 10-min intervals with receiver/loggers (Körtner and Geiser 2000) for periods of 18–27 days (mean  $23 \pm 4$  days, representing a total of 137 animal days). To maximise recording of continuous data from the small implanted transmitters, which had a short transmission range, we employed more than one receiver/logger (usually 2 near likely torpor sites) for each individual and frequently relocated the receiver/loggers especially in the early morning when animals often had moved to a new resting/torpor site.

The outside air  $T_a$  was measured at the study site to the nearest  $0.5^\circ\text{C}$  using data loggers (Thermochron, iButton, Dallas Semiconductor) placed 1 m above the ground in the shade. In addition, iButtons were used to measure  $T_a$  in the centre of a  $1.3 \times 1.5\text{-m}$  spinifex hummock ( $T_{a \text{ Spinifex}}$ )

because such clumps were occasionally used as shelter sites, and at known basking sites ( $T_{a \text{ bask}}$ ) used in the morning (AM, facing NE,  $n = 3$ ) and afternoon (PM, facing NW,  $n = 3$ ). Three *Pseudantechinus* (#1♀, #1♂, #2♂) were observed using these basking sites. Animals usually basked on rock surfaces and thus we placed iButtons at sites where basking was observed. Basking sites usually consisted of a narrow rock crevice or overhang that was exposed to the sun, but with close access to an underground crevice.  $T_a$  was also measured in a shallow rock crevice ( $T_{a \text{ crevice}}$ , 1 m deep) and in rock crevices at the end of caves ( $T_{a \text{ cave}}$ , 3 m deep and 6 m deep) near the area where animals rested or entered torpor as determined by radio-tracking (Table 1). Animals entered torpor in rock crevices that were <6 m from basking sites, but transmitter signals indicated that torpor sites were often within ~1 m of basking sites; we do not know whether animals used nests. All iButtons were wrapped in a sheet of white paper to minimise uptake of radiant heat and to measure predominantly convective  $T_a$ . Obviously,  $T_a$ s measured by black body devices, especially at basking sites would have resulted in a further increase in  $T_a$  maxima than measured here, but these were not used because *Pseudantechinus* fur is light sandy brown. Data were collected at hourly intervals with the exception of the  $T_a$  in a 3-m cave, which was recorded in 2-h intervals over the time of study, and at 4-h intervals over an entire year in a 6-m cave (details in Table 1). Throughout the study period, the weather was sunny with the exception of a

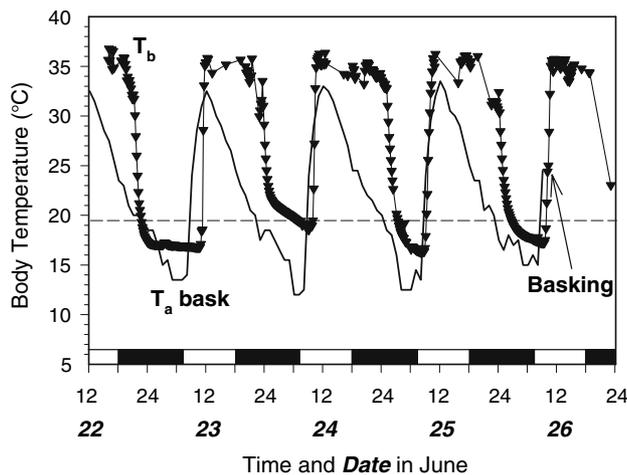
**Table 1** The thermal environment of *Pseudantechinus macdonnellensis*

	Mean $\pm$ SD ( $^\circ\text{C}$ )	Minimum ( $^\circ\text{C}$ )	Maximum ( $^\circ\text{C}$ )	Date	N
$T_a$ (measured in shade)	$12.6 \pm 5.8$	2.0	24.0	14/06/01 to 10/07/01	659
$T_a$ Spinifex	$12.1 \pm 6.1$	2.0	26.5	01/07/01 to 09/07/01	194
Morning basking sites					
$T_{a \text{ bask}}$ #1♂	$18.8 \pm 7.1$	8.0	34.5	05/07/01 to 09/07/01	92
$T_{a \text{ bask}}$ #2♂	$20.8 \pm 7.0$	12.5	38.5	01/07/01 to 05/07/01	93
$T_{a \text{ bask}}$ #1♀	$22.3 \pm 6.4$	12.0	33.5	22/06/01 to 26/06/01	95
Afternoon basking sites					
$T_{a \text{ bask}}$ #1♂	$18.7 \pm 6.8$	10.0	38.5	05/07/01 to 09/07/01	84
$T_{a \text{ bask}}$ #2♂	$18.5 \pm 7.7$	10.0	37.5	01/07/01 to 05/07/01	93
$T_{a \text{ bask}}$ #1♀	$17.1 \pm 10.8$	5.0	39.5	26/06/01 to 01/07/01	122
Torpor sites					
$T_{a \text{ crevice}}$ 1 m deep	$17.2 \pm 0.5$	16.5	18.0	15/06/01 to 01/07/01	361
$T_{a \text{ cave}}$ #2♂ 3 m deep	$19.6 \pm 0.4$	19.0	20.0	28/06/01 to 09/07/01	138
$T_{a \text{ cave}}$ #2♀ 6 m deep	$19.5 \pm 0.8$	17.5	21.0	01/07/01 to 09/07/01	193
$T_{a \text{ cave}}$ #2♀ 6 m (year)	$25.2 \pm 3.6$	16.0	30.5	09/07/01 to 15/06/02	2047
$T_{a \text{ cave}}$ #2♀ 6 m (WI)	$20.1 \pm 3.5$	16.0	25.5	09/07/01 to 31/08/01 01/06/02 to 15/06/02	406
$T_{a \text{ cave}}$ #2♀ 6 m (SP)	$23.7 \pm 1.9$	17.5	27.5	01/09/01 to 30/11/01	545
$T_{a \text{ cave}}$ #2♀ 6 m (SU)	$27.7 \pm 1.5$	24.0	30.5	09/07/01 to 15/06/02	512
$T_{a \text{ cave}}$ #2♀ 6 m (AU)	$28.1 \pm 1.3$	22.0	29.5	01/02/02 to 31/05/02	551

$T_a$  was measured every hour with the exception of  $T_{a \text{ cave}}$  #2♂ 3 m deep (every 2 h), and  $T_{a \text{ cave}}$  #2♀ cave 6 m deep measured over a year (every 4 h). Distance of temperature logger from cave entrance is indicated in meters.  $T_{a \text{ bask}}$  #1♂ indicates that this basking site was used predominantly by this male, but occasionally the same basking sites were used by different individuals on different days  
WI winter, SP spring, SU summer, AU autumn

single day, which was overcast early in the morning and then intermittently for much of the day.

Numeric values presented are means  $\pm$  1 standard deviation (SD) for the number of individuals 'n' investigated. 'N' denotes the number of observations. Differences between means were determined using a *t* test; times were transformed to angular direction before testing (Zar 1984). Linear regressions ( $T_a$  as independent variable) were fitted by using the method of least squares. When observed, animals were well coordinated immediately after release, and movements were like those of non-tagged individuals seen basking and foraging at the study site, and did not appear to be affected by the transmitters. Nevertheless, we excluded day 1 after release (i.e. 2 days after surgery) from the data analysis to ensure that behaviour was not affected by surgery. Torpor was defined as a  $T_b < 30^\circ\text{C}$  (Körtner and Geiser 2000); the duration of torpor bouts was defined as the time with  $T_b < 30^\circ\text{C}$ . Commencement of arousal was defined as the time when  $T_b$  began to increase from low torpor  $T_b$  to normothermic values; arousal completion as the time when the normothermic plateau of  $T_b$  was first reached (Fig. 1). More arousals than torpor entries were available for analysis because animals moved over night and loggers were out of transmitter range during some torpor entries.



**Fig. 1** Body temperature ( $T_b$ , triangles) and ambient temperature at a morning basking site ( $T_{a \text{ bask}}$ , solid line) of an individual female *Pseudantechinus macdonnellensis* measured over 4.5 days in June. The horizontal broken line at  $19.5^\circ\text{C}$  indicates the mean  $T_{a \text{ cave}}$  near a torpor site, which was higher than the minimum  $T_b$  on 3 of 4 days. The horizontal black and white bars indicate day and night. The arrow indicates when the animal was observed basking with a body temperature of  $25.3^\circ\text{C}$ . Note the similar pattern of decreasing  $T_b$  after the fall of  $T_{a \text{ bask}}$  at night and that of increasing  $T_b$  shortly after the increase in  $T_{a \text{ bask}}$  in the morning on all days

## Results

### Torpor variables

*Pseudantechinus* employed torpor frequently in the field (Fig. 1). Torpor was characterised by a rapid fall of  $T_b$  from values at or above  $\sim 35^\circ\text{C}$ , to  $T_b$  ranging from less than  $20^\circ\text{C}$  to just below  $30^\circ\text{C}$ . Typically after several hours at low  $T_b$ , torpid animals rewarm and  $T_b$  rose to active values of at or above  $35^\circ\text{C}$ . The average torpor occurrence was  $58.3 \pm 25.7\%$  of animal days ( $n = 6$ ,  $N = 131$  animal days), but females ( $82.5 \pm 13.4\%$ ,  $n = 2$ ) employed torpor almost twice as frequently as males ( $46.3 \pm 21.4\%$ ,  $n = 4$ ). Most individuals ( $n = 5$ ) did not enter torpor on the first day after release.

The duration of torpor bouts ranged from short bouts lasting only for 50 min to a maximum of 855 min (14.25 h). Most arousals occurred in the morning (Fig. 1) and the mean torpor bout duration was  $350 \pm 139$  min ( $n = 6$ ,  $N = 46$ ). Females ( $490 \pm 34$  min,  $n = 2$ ,  $N = 20$ ) displayed longer torpor bouts (*t* test,  $t = 3.4$ ,  $df = 4$ ,  $P < 0.05$ ) than males ( $280 \pm 111$  min,  $n = 4$ ,  $N = 26$ ).

The minimum  $T_b$ , a measure of torpor depth, averaged over all torpor bouts was lower in females ( $T_b = 21.0 \pm 1.5^\circ\text{C}$ ,  $n = 2$ ,  $N = 30$ ) than males ( $T_b = 26.8 \pm 1.3^\circ\text{C}$ ,  $n = 4$ ,  $N = 27$ ; *t* test,  $t = 4.7$ ,  $df = 4$ ,  $P < 0.01$ ). The overall mean minimum  $T_b$  was  $24.8 \pm 3.2^\circ\text{C}$  ( $n = 6$ ,  $N = 57$ ). The mean minimum  $T_b$  from the deepest torpor bout of each individual was  $16.0 \pm 0.4^\circ\text{C}$  in females ( $n = 2$ ,  $N = 2$ ) and  $24.4 \pm 3.0^\circ\text{C}$  in males ( $n = 4$ ,  $N = 4$ ) and these means also differed between sexes (*t* test,  $t = 5.5$ ,  $df = 4$ ,  $P = 0.012$ ). The single lowest individual  $T_b$  was  $15.7^\circ\text{C}$  in a female and  $20.4^\circ\text{C}$  in a male.

### Torpor and the thermal environment

The thermal environment of *Pseudantechinus* was highly variable (Figs. 1, 2; Table 1). In Fig. 2, the outside  $T_a$  measured in the shade over 4 days in July fluctuated from daily minima of  $6.3 \pm 1.8^\circ\text{C}$  to maxima of  $22.8 \pm 0.9^\circ\text{C}$ . The  $T_{a \text{ bask}}$  over the same time period of a morning (AM) basking site ranged from  $14.4 \pm 1.9^\circ\text{C}$  to  $37.4 \pm 1.7^\circ\text{C}$ , and that of an afternoon (PM) basking site from  $11.4 \pm 1.3^\circ\text{C}$  to  $35.5 \pm 1.8^\circ\text{C}$  (Fig. 2). Thus, the  $T_{a \text{ bask}}$  minima at basking sites were on average  $5\text{--}8^\circ\text{C}$  above the outside  $T_a$ . While the maximum  $T_{a \text{ bask}}$  was indistinguishable between morning and afternoon basking sites, the time when the maxima were reached differed significantly (*t* test,  $t = 8.3$ ,  $df = 5$ ,  $P < 0.001$ ) for morning ( $T_a$  maximum at 1230 hours  $\pm$  35 min) and afternoon ( $T_a$  maximum at 1545 hours  $\pm$  32 min) basking sites (Fig. 2, Table 1). Moreover, the mean daily amplitude of  $T_{a \text{ bask}}$  (minimum  $T_{a \text{ bask}}$   $13.3 \pm 1.3^\circ\text{C}$ , maximum  $T_{a \text{ bask}}$   $32.9 \pm 0.5^\circ\text{C}$ , amplitude  $19.6^\circ\text{C}$ ) measured

between 22 and 26 June (Fig. 1) was almost identical to that of  $T_b$  (minimum  $T_b$   $17.2 \pm 0.9^\circ\text{C}$ , maximum  $T_b$   $36.1 \pm 0.5^\circ\text{C}$ , amplitude  $18.9^\circ\text{C}$ ) measured over the same time period. Surprisingly, even the mean  $T_{a \text{ bask}}$  ( $22.2 \pm 6.4^\circ\text{C}$ ) and the mean  $T_b$  ( $25.1 \pm 7.8^\circ\text{C}$ ) from 22 to 26 June were similar (Fig. 1). In contrast, the cave  $T_a$  ( $T_{a \text{ cave}}$  #2♀ 6 m deep) near a resting site when our field measurements were conducted was  $19.5 \pm 0.2^\circ\text{C}$  (range  $17.5\text{--}21.0^\circ\text{C}$ ) and thus showed only small daily fluctuations. The daily fluctuations of  $T_{a \text{ Spiniifex}}$  were similar to the outside  $T_a$ , but the maximum  $T_{a \text{ Spiniifex}}$  was on average  $2.5^\circ\text{C}$  higher (Table 1). The longer term means of these and other  $T_a$ s and the minima and maxima recorded are listed in Table 1.

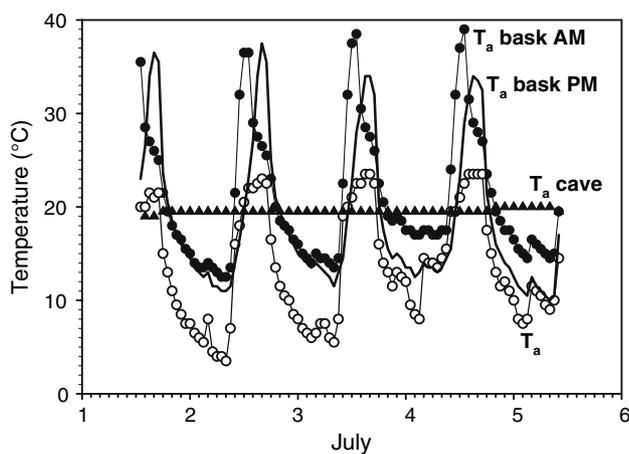
*Pseudantechinus* often rested and entered torpor in deep rock crevices, such as near the end of a cave (Fig. 2), where thermal conditions were stable, therefore it is not surprising that the daily minimum or maximum outside  $T_a$  did not strongly affect occurrence of torpor. Overall, torpor occurrence (dependent variable) of all individuals showed a trend towards a correlation with the daily minimum and maximum outside  $T_a$ , but both regressions were not significant ( $r^2 = 0.14$ ,  $P = 0.085$  and  $r^2 = 0.15$ ,  $P = 0.079$ , respectively). Moreover, variables of torpor (i.e. torpor bout duration and minimum  $T_b$ ) were not correlated with the daily minimum or maximum outside  $T_a$ . However, timing of torpor entry and especially that of arousals were related to  $T_{a \text{ bask}}$  at basking sites (Figs. 1, 2). Torpor usually commenced around or soon after midnight (Fig. 1) with a mean time of  $0157 \pm 0228$  hours ( $n = 6$ ,  $N = 47$ ) when  $T_{a \text{ bask}}$  had substantially declined by  $23.2^\circ\text{C}$  from maximum values to  $13.8 \pm 2.2^\circ\text{C}$  ( $n = 6$ ), which were only  $4.2 \pm 2.8^\circ\text{C}$  above the nocturnal  $T_{a \text{ bask}}$  minima of  $9.6 \pm 2.8^\circ\text{C}$  ( $n = 6$ ) (Table 1). Torpor in the females

commenced at  $0029$  hours  $\pm 8$  min and in males at  $0240$  hours  $\pm 0246$  hours; these means were indistinguishable ( $t$  test,  $t = 1.4$ ,  $df = 4$ ,  $P > 0.2$ ).

Arousal from all torpor bouts commenced at  $0741 \pm 0340$  hours ( $n = 6$ ,  $N = 52$ ), on average about 20 min after sunrise ( $\sim 0721$  hours). On average, males began the arousal process earlier ( $0707 \pm 0433$  hours,  $\sim 15$  min before sunrise) than females ( $0850 \pm 0116$  hours,  $\sim 90$  min after sunrise), however, the means were statistically indistinguishable ( $t$  test,  $t = 0.7$ ,  $df = 4$ ,  $P > 0.5$ ).

Most arousals (81% of all arousals observed) commenced in the morning after sunrise, with the exception of one male that always aroused at night ( $N = 5$ ), and a total of five arousals ( $N = 5$ ) by three other individuals. Post-sunrise arousals commenced at  $0943$  hours  $\pm 50$  min ( $n = 5$ ,  $N = 42$ ). These arousals began significantly later ( $t$  test,  $t = 4.1$ ,  $df = 6$ ,  $P < 0.01$ ) than the start of the steepest  $T_{a \text{ bask}}$  increase at morning basking sites ( $0753$  hours  $\pm 29$  min, from  $T_{a \text{ bask}} = 13.6 \pm 2.8^\circ\text{C}$ ,  $n = 3$ ,  $N = 11$ ). However, the time of commencement of post-sunrise arousals was similar ( $t$  test,  $t = 0.8$ ,  $df = 5$ ,  $P > 0.4$ ) to the time when the  $T_{a \text{ bask}}$  at basking sites had reached the mid-point between minimum and maximum values ( $1003$  hours  $\pm 20$  min,  $T_{a \text{ bask}} = 22.3 \pm 2.5^\circ\text{C}$ ,  $n = 4$ ,  $N = 11$ ). The time when post-sunrise arousals commenced was correlated with both the time when  $T_{a \text{ bask}}$  began to increase ( $r^2 = 0.34$ ,  $P < 0.005$ ) and the temperature of  $T_{a \text{ bask}}$  at that time ( $r^2 = 0.54$ ,  $P < 0.001$ ). The rewarming process was completed at  $1106$  hours  $\pm 44$  min ( $T_b \sim 35^\circ\text{C}$ ), which was significantly earlier ( $t$  test,  $t = 2.8$ ,  $df = 5$ ,  $P < 0.05$ ) than the time when the  $T_{a \text{ bask}}$  at morning basking sites had reached the daily maximum ( $1213$  hours  $\pm 27$  min,  $T_a = 31.2 \pm 5.5^\circ\text{C}$ ,  $n = 4$ ,  $N = 11$ ). Thus, post-sunrise arousals typically occurred after basking sites were warmed to  $T_a > 20^\circ\text{C}$  at  $\sim 1000$  hours (Figs. 1, 2) and were completed during the time the  $T_{a \text{ bask}}$  increased steeply, suggesting that many or all of these arousals involved basking.

Direct evidence of basking came from observing five individual *Pseudantechinus* exposing themselves to the sun with a  $T_b < 30^\circ\text{C}$  (e.g. Fig. 1, on 26 June). This was observed for 18% of all torpor bouts. The mean  $T_b$  when torpid individuals were first observed basking was  $27.5 \pm 1.6^\circ\text{C}$  ( $n = 5$ ,  $N = 14$ ) at  $1039$  hours  $\pm 50$  min, somewhat later than the time arousals commenced. Basking in torpid individuals commenced earlier ( $t$  test,  $t = 4.3$ ,  $df = 5$ ,  $P < 0.01$ ) on sunny days ( $0947$  hours  $\pm 42$  min,  $n = 4$ ,  $N = 11$ ) than on the single cloudy day ( $1136$  hours  $\pm 12$  min,  $n = 3$ ,  $N = 3$ ). The lowest  $T_b$  that was observed in a basking individual was  $19.3^\circ\text{C}$ . After normothermic  $T_b$  of  $\sim 35^\circ\text{C}$  had been reached, *Pseudantechinus* continued to bask for most of the afternoon. They were also seen foraging during the day and continued to forage for the first, warmer (Figs. 1, 2) half of the night.



**Fig. 2** Ambient temperatures ( $T_a$ , circles), the cave temperature near a torpor site ( $T_{a \text{ cave}}$ , triangles), the ambient temperature at a morning basking site ( $T_{a \text{ bask}}$  AM, filled circles) and an afternoon basking site ( $T_{a \text{ bask}}$  PM, solid line) over 4 days in July

## Discussion

Survival in deserts requires frugal use of energy and consequently ectothermic reptiles with their low energy requirements are the most common desert vertebrates (Bradshaw 2003). Our study suggests that by employing torpor and basking and by appropriately coordinating its thermal biology to that of specific locations in their environment, the endothermic arid zone dasyurid marsupial *P. macdonnellensis* can minimise energy expenditure and thus also can live in this challenging environment.

*Pseudantechinus* in winter organise their daily activity, rest, and torpor phases and select sites with appropriate thermal conditions for various functional states apparently to minimise daily energy expenditure. The occurrence of daily torpor on 82.5% of animal days we observed in females is well above that observed for free-ranging daily heterotherms from mesic areas, however, data on the latter are currently scarce (Geiser et al. 2000; Körtner and Geiser 2000; Christian and Geiser 2007). Laboratory data show that spontaneous daily torpor (food ad libitum) occurs predominantly in small arid zone dasyurids (*Sminthopsis* spp., *Antechinomys laniger*, *Planigale gilesi*) suggesting that in these species torpor is a strategy that is regularly employed to reduce daily energy expenditure (Geiser and Baudinette 1987; Geiser 2003). In contrast, mesic dasyurids (*Antechinus* spp.) mainly enter torpor after withdrawal of food (induced torpor) (Geiser 1988, 2003), suggesting that in these species, living in richer, more predictable environments, daily torpor is used during acute energetic stress and is predominantly an emergency strategy.

*Pseudantechinus* basked during rewarming from torpor when solar radiation was high and  $T_a$  was rising, continued to bask for much of the day and commenced foraging in the afternoon, which continued during the first half of the night when  $T_a$  was relatively high (Fig. 2) and insects were likely to be active (Speakman and Thomas 2003). Torpor entry commenced soon after midnight in thermally buffered rock crevices when outside  $T_a$  and  $T_{a \text{ bask}}$  at basking sites were low. Torpor usually lasted until the morning when torpid individuals returned again to basking sites with increasing  $T_{a \text{ bask}}$  and high radiant heat. Overall, the  $T_b$  of *Pseudantechinus* on days they entered torpor and the  $T_{a \text{ bask}}$  showed similar daily fluctuations both in timing and amplitude.

We did not observe basking during all arousals likely because animals often basked in sun-exposed crevices along high vertical sandstone cliffs and were difficult to approach and see. However, interrelations between  $T_b$  and  $T_a$  at basking sites and the ~110-min delayed commencement of basking during the single cloudy day in comparison to the sunny days strongly suggest that most, if not all, post-sunrise arousals did indeed involve basking.

Our study provides further evidence that arousals from torpor in endotherms do not always rely entirely on endothermic heat production, but rather use fluctuations in  $T_a$  (Lovegrove et al. 1999; Chruszcz and Barclay 2002; Brice et al. 2002; Turbill et al. 2003; Dausmann et al. 2005; Geiser et al. 2004; Willis et al. 2006) or exposure to radiant heat (Geiser et al. 2002, 2004; Mzilikazi et al. 2002; Brigham et al. 2006) to facilitate passive rewarming. As endothermic rewarming from daily torpor requires a substantial increase in MR, often to about twice that during rest and >10-fold of that during torpor (Geiser and Drury 2003), and thus compromises energy savings gained from employing torpor, these findings are important for estimating energy expenditure in the wild. In *S. macroura*, another small dasyurid marsupial from arid Australia, passive rewarming in captivity via radiant heat can reduce energetic costs of rewarming to only 15% of that required during active endothermic rewarming because during much of the rewarming process MR could be maintained below basal values (Geiser and Drury 2003). Nevertheless, movement from torpor sites to basking sites requires coordinated locomotion. We observed a torpid individual running up a vertical cliff with a  $T_b$  of 19.3°C, which is remarkable for a mammal, but in comparison to endothermic rewarming, locomotion is associated with little energetic costs especially if basking sites are near resting/torpor sites.

Obviously, basking during the normothermic resting phase, as we observed in *Pseudantechinus*, also can contribute to minimisation of energy expenditure. Even at low  $T_a$ , radiant heat can maintain MR near basal levels and reduce energy requirements by ~50–80% (Ohmart and Lasiewski 1971; Geiser and Drury 2003). Overall, it has been estimated that a combination of daily torpor and basking during rewarming and rest can reduce daily energy expenditure of small mammals with a comparable daily thermal cycle and similar size as *Pseudantechinus* by about 50% (Geiser et al. 2004), with resulting low food and thus foraging requirements. Whereas this may appear moderate in comparison to energy saving made during hibernation, which generally reduces energy expenditure by >80% (Wang 1989), species employing daily torpor, unlike most hibernators who rely on stored fat or food, can forage between torpor bouts and replenish fuels from external resources (Geiser 2004).

While solar energy is used by *Pseudantechinus* during arousal from torpor and rest as an alternative source of energy in an environment with low primary productivity, the question remains as to why *Pseudantechinus* rewarm in the morning rather than staying torpid at even lower MR for longer and rewarm passively in the afternoon shortly before their main activity phase. Arousals may occur in the morning for several reasons detailed below. (1) Even in winter, *Pseudantechinus* may need to avoid reptile predators such

as varanid lizards (unpublished observations), which also rewarm in the morning and forage only after they reach a high  $T_b$  when they could capture *Pseudantechinus* if these were to rewarm in the afternoon and thus would not be fully coordinated. (2) Our study was conducted near the beginning of the mating season of *Pseudantechinus* (Gilfillan 2001; McAllan 2003); rewarming in the morning may have allowed prolonged interactions with other individuals. (3) Normothermic phases may facilitate capture of and digestion of food captured the previous night. Thus, while passive rewarming from torpor in the morning may not afford all the energy savings of a longer torpor bout, energy expenditure during basking is still low and allows animals to undertake important daily activities.

Although  $T_b$  during rewarming and the  $T_{a\text{ bask}}$  at basking sites were tightly linked, the  $T_b$  minima observed during torpor were lower than the  $T_{a\text{ cave}}$  measured in a cave near a shelter where animals entered torpor on some days as determined by radio-telemetry (Fig. 1). The  $T_{a\text{ cave}}$  near the shelter remained near 19.5°C throughout the period of measurement whereas the  $T_b$  of *Pseudantechinus* fell to a minimum of 15.7°C, and on 18% of occasions (all in females) the minimum  $T_b$  fell below 19.5°C. These low  $T_b$  suggests that *Pseudantechinus* do not always select the warmest available  $T_a$  during torpor as is often suggested from laboratory studies, but rather select resting sites with a lower  $T_a$ , which likely are closer to the surface and nearer a basking site, to further reduce  $T_b$  and thus minimise energy expenditure during torpor as has been observed in bats and echidnas (Brown and Bernard 1994; Nicol and Andersen 2007). A reduction of  $T_b$  by a further 4°C below the available shelter  $T_{a\text{ cave}}$  of 19.5°C should result in a MR reduction by ~40% assuming a mean  $Q_{10}$  of 2.3 for daily heterotherms (Geiser 2004). Thus, it appears that even during torpor, when MR is already substantially reduced, *Pseudantechinus* attempt to further minimise energy expenditure on some days in winter. On the other hand in the warm season, the  $T_{a\text{ cave}}$  was near the lower critical  $T_a$  of the thermo-neutral zone of *Pseudantechinus* (lower critical  $T_a = 30.1^\circ\text{C}$ , MacMillen and Nelson 1969; mean  $T_{a\text{ cave}}$ : 27.7°C summer, 28.1°C autumn), suggesting that for much of the year the species can live without heat stress under conditions approximating thermo-neutrality and therefore should require little energy for thermoregulation. It would be interesting to determine whether even under these apparently favourable thermal conditions *Pseudantechinus* employ torpor to further minimise energy expenditure and how the daily activity patterns change in the hot season.

Male and female *Pseudantechinus* showed similar daily cycles in  $T_b$  fluctuations, but some differences with regard to timing of torpor and arousal and torpor depth emerged. On average, males entered torpor about 2 h later than females and aroused about 15 min earlier than females.

Since our study was conducted during the beginning of the reproductive season of the species (Gilfillan 2001; McAllan 2003), it is likely that males extended the period of activity in search of females or in territorial defence or vigilance (Buck and Barnes 1999). Deep and long torpor bouts by female dasyurids during the mating season and prior to parturition and lactation have been interpreted as an energy conserving strategy to enhance fat storage during mating and especially pregnancy. During pregnancy female marsupials require only little energy for growth of their small (<0.5% body mass of mother) altricial young, and apparently therefore can afford to enter torpor and store energy that then can be consumed during the energy-demanding time of lactation (Geiser and Masters 1994). We observed females and males sharing shelter and basking sites on several occasions supporting our interpretation that reproductive behaviour may explain differences in torpor patterns between the sexes.

Our study shows that the arid zone *Pseudantechinus* uses torpor and basking during arousal from torpor and the rest phase to lower energy expenditure. While this is likely to have immediate positive effects on survival, torpor use also appears to prolong life span (Wilkinson and South 2002), which is important in a desert environment where reproduction may not be possible every year. Thus, torpor not only may contribute directly to the animal's short-term survival, but may also facilitate persistence of populations in the harsh and unpredictable Australian desert.

**Acknowledgments** We thank Michael Barritt, Silke Beckedorf, Nicola Goodship, Karen May, and Parks and Wildlife Service of the Northern Territory staff based at Ormiston for assistance and logistic support during the study. Mark Brigham and Bronwyn McAllan provided constructive comments on the manuscript. The Animal Ethics Committee of the University of New England and the Parks and Wildlife Service of the Northern Territory provided permits for the study. The research was supported by grants from the Australian Research Council and The University of New England.

## References

- Brice PH, Grigg GC, Beard LA, Donovan JA (2002) Patterns of activity and inactivity in echidnas (*Tachyglossus aculeatus*) free-ranging in a hot dry climate: correlates with ambient temperature, time of day and season. *Aust J Zool* 50:461–475
- Brigham RM, Woods CP, Lane JE, Fletcher QE, Geiser F (2006) Ecological correlates of torpor use among five caprimulgidiform birds. In: Proceedings, 23rd international ornithological congress, *Acta Zool Sin* 52(Suppl):401–404
- Buck CL, Barnes BM (1999) Temperatures of hibernacula and changes in body composition of arctic ground squirrels over winter. *J Mammal* 80:1264–1276
- Bradshaw D (2003) Vertebrate ecophysiology. Cambridge University Press, UK
- Brown CR, Bernard RTF (1994) Thermal preference of Schreiber's long-fingered (*Miniopterus schreibersii*) and Cape horseshoe (*Rhinolophus capensis*) bats. *Comp Biochem Physiol* 107A:439–499

- Christian N, Geiser F (2007) To use or not to use torpor? Activity and body temperature as predictors. *Naturwissenschaften* 94:483–487
- Chruszcz BJ, Barclay RMR (2002) Thermoregulatory ecology of a solitary bat, *Myotis evotis*, roosting in rock crevices. *Funct Ecol* 16:18–26
- Cooper CE, McAllan BM, Geiser F (2005) Effect of torpor on the water economy of an arid-zone marsupial, the striped-faced dunnart (*Sminthopsis macroura*). *J Comp Physiol B* 175:323–328
- Dausmann KH, Glos J, Ganzhorn JU, Heldmaier G (2005) Hibernation in the tropics: lessons from a primate. *J Comp Physiol B* 175:147–155
- Dickman CR (2003) Distributional ecology of dasyurid marsupials. In: Jones M, Dickman C, Archer M (eds) *Predators with pouches: the biology of carnivorous marsupials*. CSIRO publishers, Melbourne, pp 318–331
- Dickman CR, Haythornthwaite AS, McNaught GH, Mahon P, Tamayo B, Letnic M (2001) Population dynamics of three species of dasyurid marsupials in arid central Australia: a 10-year study. *Wildl Res* 28:493–506
- Frank CL (1994) Polyunsaturate content and diet selection by ground squirrels (*Spermophilus lateralis*). *Ecology* 75:458–463
- Geiser F (1988) Daily torpor and thermoregulation in Antechinus (Marsupialia): influence of body mass, season, development, reproduction, and sex. *Oecologia* 77:395–399
- Geiser F (2003) Thermal biology and energetics of carnivorous marsupials. In: Jones M, Dickman C, Archer M (eds) *Predators with pouches: the biology of carnivorous marsupials*. CSIRO publishers, Melbourne, pp 234–249
- Geiser F (2004) Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annu Rev Physiol* 66:239–274
- Geiser F, Baudinette RV (1987) Seasonality of torpor and thermoregulation in three dasyurid marsupials. *J Comp Physiol B* 157:335–344
- Geiser F, Masters P (1994) Torpor in relation to reproduction in the Mulgara, *Dasyercus cristicauda* (Dasyuridae: Marsupialia). *J Therm Biol* 19:33–40
- Geiser F, Drury RL (2003) Radiant heat affects thermoregulation and energy expenditure during rewarming from torpor. *J Comp Physiol B* 173:55–60
- Geiser F, Goodship N, Pavey CR (2002) Was basking important in the evolution of mammalian endothermy? *Naturwissenschaften* 89:412–414
- Geiser F, Holloway JC, Körtner G, Maddocks TA, Turbill C, Brigham RM (2000) Do patterns of torpor differ between free-ranging and captive mammals and birds? In: Heldmaier G, Klingenspor M (eds) *Life in the cold: 11th international hibernation symposium*. Springer, Berlin, pp 95–102
- Geiser F, Drury RL, Körtner G, Turbill C, Pavey CR, Brigham RM (2004) Passive rewarming from torpor in mammals and birds: energetic, ecological and evolutionary implications. In: Barnes BM, Carey HV (eds) *Life in the cold: evolution, mechanisms, adaptation, and application*. 12th international hibernation symposium. Biological Papers of the University of Alaska #27. Institute of Arctic Biology, University of Alaska, Fairbanks, pp 51–62
- Gilfillan SL (2001) An ecological study of a population of *Pseudantechinus macdonnellensis* (Marsupialia: Dasyuridae) in central Australia. I. Invertebrate food supply, diet and reproductive strategy. *Wildl Res* 28:469–480
- Gutman R, Choshniak I, Kronfeld-Schor N (2006) Defending body mass during food restriction in *Acomys russatus*: a desert rodent that does not store food. *Am J Physiol* 290:R881–R891
- Körtner G, Geiser F (2000) Torpor and activity patterns in free-ranging sugar gliders *Petaurus breviceps* (Marsupialia). *Oecologia* 123:350–357
- Lovegrove BG, Körtner G, Geiser F (1999) The energetic costs of arousal from torpor in the marsupial *Sminthopsis macroura*: benefits of summer ambient temperature cycles. *J Comp Physiol B* 169:11–18
- MacMillen RE, Nelson JE (1969) Bioenergetics and body size in dasyurid marsupials. *Am J Physiol* 217:1246–1251
- MacMillen RE, Hinds D (1983) Water regulatory efficiency in heteromyid rodents: a model and its application. *Ecology* 64:152–164
- McAllan BM (2003) Timing of reproduction in carnivorous marsupials. In: Jones M, Dickman C, Archer M (eds) *Predators with pouches: the biology of carnivorous marsupials*. CSIRO publishers, Melbourne, pp 147–168
- Menkhorst P, Knight F (2001) *A field guide to the mammals of Australia*. Oxford University Press, Melbourne
- Mzilikazi N, Lovegrove BG, Ribble DO (2002) Exogenous passive heating during torpor arousal in free-ranging elephant shrews, *Elephantulus myurus*. *Oecologia* 133:307–314
- Nicol SC, Andersen NA (2007) Cooling and body temperature regulation of hibernating echidnas (*Tachyglossus aculeatus*). *J Exp Biol* 210:586–592
- Ohmart RD, Lasiewski RC (1971) Roadrunners: energy conservation by hypothermia and absorption of sunlight. *Science* 172:67–69
- Pavey CR, Goodship N, Geiser F (2003) Home range and spatial organization of the rock-dwelling carnivorous marsupial, *Pseudantechinus macdonnellensis*. *Wildl Res* 30:135–142
- Schmidt-Nielsen K (1979) *Desert animals*. Dover Publications, New York
- Speakman JR, Thomas DW (2003) Physiological ecology and energetics of bats. In: Kunz TH, Fenton MB (eds) *Bat ecology*. University of Chicago Press, Chicago, pp 430–490
- Stafford Smith DM, Morton SR (1990) A framework for the ecology of arid Australia. *J Arid Environ* 18:255–278
- Trewin B (2006) Australian deserts, climatic aspects of Australia's deserts. In: 2006 year book Australia, Australian Bureau of Statistics, Canberra
- Turbill C, Law BS, Geiser F (2003) Summer torpor in a free-ranging bat from subtropical Australia. *J Therm Biol* 28:223–226
- Wang LCH (1989) Ecological, physiological, and biochemical aspects of torpor in mammals and birds. In: Wang LCH (ed) *Animal adaptation to cold*. Springer, Berlin, pp 361–401
- Warnecke L, Turner JM, Geiser F (2007) Torpor and basking in a small arid zone marsupial. *Naturwissenschaften* (in press)
- Wilkinson GS, South SM (2002) Life history, ecology and longevity of bats. *Ageing Cell* 1:124–131
- Willis CKR, Brigham RM, Geiser F (2006) Deep, prolonged torpor by pregnant, free-ranging bats. *Naturwissenschaften* 93:80–83
- Withers PC (1992) *Comparative animal physiology*. Saunders, Fort Worth
- Zar JH (1984) *Biostatistical analysis*. 2nd edn. Prentice Hall, Englewood Cliffs