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ORIGINAL PAPER

Torpor in free-ranging antechinus: does it increase fitness?

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Abstract Antechinus are small, insectivorous, heterothermic marsupial mammals that use torpor from late summer to early winter and reproduce once a year in late winter/early spring. Males die after mating, most females produce only a single litter, but some survive a second winter and produce another litter. As it is not known how these females manage to survive the second winter after the energetically demanding reproductive period and then reproduce a second time, we aimed to provide the first data on thermal biology of free-ranging antechinus by using temperature telemetry. Male *Antechinus stuartii* and *Antechinus flavipes* rarely entered torpor in autumn/early winter in the wild, expressing only shallow bouts of <2 h. Female *A. stuartii* used torpor extensively, employing bouts up to 16.7 h with body temperatures as low as 17.8 °C. Interestingly, although first and second year females used similar torpor patterns, torpor occurrence was almost twofold in second year (93 % of days) than first year females (49 %), and the proportion of the overall monitoring period animals spent torpid was 3.2-fold longer in the former with a corresponding shorter activity period. Our study suggests that intensive use of torpor is crucial for second year females for autumn and winter survival and production of a second litter. We provide the first evidence of an age-related pattern in daily torpor expression in free-ranging mammals and show that torpor use is a complex process that is affected not only by the current energy availability and thermal conditions but also by the reproductive history and age of individuals.

Keywords Age · *Antechinus* · Body mass · Free ranging · Marsupial · Torpor · Reproduction

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Abbreviations

T_a	Ambient temperature
T_b	Body temperature
MR	Metabolic rate

Introduction

Torpor is employed by many small endotherms and is characterised by a controlled and temporal reduction of body temperature (T_b), metabolic rate (MR), water loss and other physiological functions (Boyer and Barnes 1999; Cooper et al. 2005). The most widely recognised form of torpor is hibernation, which is characterised by a sequence of multi-day torpor bouts with extremely low T_b, often between 0 and 10 °C, and MR throughout winter (Boyer and Barnes 1999). The other common form of torpor is daily torpor, during which T_b usually falls to between ~10 and 25 °C, lasts only for a few hours and in many species may be used at any time of the year (Geiser and Ruf 1995). Torpor use can reduce energy costs by more than 90 % compared to normothermia (maintenance of high T_b) at the same ambient temperature (T_a) (Geiser 2013). Both forms of torpor have been extensively studied in many small mammals and birds (Lyman et al. 1982). However, most work, especially on daily torpor, has been conducted in the laboratory, and the data available suggest that captive studies may underestimate the use, depth and duration of torpor in comparison to that expressed in the wild (Geiser et al. 2007).

Laboratory studies conducted mainly in the northern hemisphere also resulted in the widely held view that survival of winter is the main function of torpor (Lyman et al. 1982). However, recent evidence shows that torpor use is much more complex and is used to deal with a number of other energetically demanding periods. Functions of torpor include enhancement of pre-migratory fattening, predator avoidance and also bridging periods of increased energy expenditure despite limited resources such as during development and reproduction (Calder and Booser 1973; Racey 1973; Audet and Fenton 1988; Geiser et al. 2006; Körtner et al. 2008; Bieber and Ruf 2009; Stawski and Geiser 2010; Turbill et al. 2011; Geiser and Brigham 2012; Giroud et al. 2012; Dzal and Brigham 2013; Klug and Barclay 2013; Kronfeld-Schor and Dayan 2013).

With regard to energy use during reproduction, marsupials of the genus *Antechinus* have a most unusual life history (Fisher et al. 2011). These insectivorous mammals of the family Dasyuridae breed once a year, and mating occurs over a short 2-week period during late winter/early spring when thermoregulatory energy expenditure is high. The mating period is followed by a complete male die-off (Woolley 1966; Dickman 1985; McAllan et al. 2006), attributed to a combination of stress-related factors (Barker 1978; Bradley et al. 1980). Females, on the other hand, all of which reproduce and most carry full litters determined by the number of teats (Woolley 1966; Wood 1970; Lee and Cockburn 1985), must survive at least until the end of summer when their large litter of ~8 young are weaned. Interestingly, some, despite an extremely taxing time of lactation, may live for a second year (Wood 1970; Fleming et al. 1981; Lee and Cockburn 1985; Green et al. 1989). Although about one third of the female population survive this energetically demanding period of reproduction, little is known about how they are able to cope with a post-reproductive, second winter to produce another litter of 8 in the following spring and thus potentially double their reproductive output. While torpor and reproduction are widely assumed to be incompatible (Barnes 1986; Blank and Desjardins 1986; Goldman et al. 1986; Ouarour et al. 1991), several mammals, including dasyurid marsupials, are known to use torpor during or for preparation for the reproductive period (Körtner et al. 2010; Geiser and Brigham 2012). However, although antechinus are able to express daily torpor, this has been established only for captive individuals (Geiser 1988), and the ecological and energetic implications of torpor, especially with regard to reproduction, are therefore not fully appreciated.

The purpose of our study was to provide the first data on thermal biology and torpor use in free-ranging antechinus in relation to reproduction. Our main aim was to determine sex differences and quantify whether and how second year females differ in their use of torpor in comparison to first year females considering their differences in age and reproductive history. However, we were also interested in whether thermal biology of free-ranging antechinus differs from published work on captive antechinus.

Material and methods

Location and trapping

The study area was located on the slope of Mount Duval situated on Newholme Field Station, University of New England, approximately 12 km north of Armidale, NSW, Australia (30°24′S; 151°38′E). Animals were caught using aluminium box traps (330×90×90 mm; Elliott Scientific Equipment, Upwey, Australia) baited with a mix of rolled oats and peanut butter, and contained polyester fibre for insulation. Trapping was conducted during April/May (autumn) in 2011, 2012 and 2013. Traps were set in the late afternoon and checked for captures in the morning soon after dawn. During inclement weather, traps were closed until conditions improved.

Animals and measurements

In 2011, T_b data were obtained from four animals (two male *Antechinus flavipes* and two female *Antechinus stuartii*). In 2012, five animals (two male and three female *A. stuartii*) were implanted with transmitters, and data were collected from each. In 2013, only one female *A. stuartii* was caught and implanted with a transmitter. As the temperature characteristics of this last transmitter drifted over time, T_b readings were adjusted using an average of the maximum daily T_b of other females (the most consistent values across individuals). These data were then used for statistical analysis because the derived variables were consistent with those of other individuals. Animals were tracked for 16.4 days on average, most for >9 days, but the female caught in 2013 only for 4 days because of transmitter failure.

Species, sex, body length and body mass of captured animals were determined. Females were aged according to their pouch appearance; as the teats never completely regress after lactation, those females with easily visible teats and sparse fur in the pouch area were classified as second year females, whereas females with no/minimally visible teats and furred pouch area were classified as first year females (Woolley 1966). All males were considered to be less than 1 year of age. Body condition was assessed using the scaled mass index calculated using the scaling exponent from standardised major axis regression of the natural log of mass and length taken from all individuals captured (data obtained over 3 years; n=42; body mass range 13.6–41 g) (Peig and Green 2010).

Transmitters and implantation

The T_b of each animal was measured using small VHF temperature-sensitive transmitters with individual transmission frequencies for identification of individuals (Sirtrack, Havelock North, New Zealand, or Biotrack, Dorset, UK). The transmitters were implanted into the intraperitoneal cavity under isoflurane/oxygen anaesthesia in a field laboratory. Before implantation, each transmitter (mass range 1.25–2.40 g; <10 % of body mass as recommended by Rojas et al. 2010) was calibrated to the nearest 0.1 °C in a water bath between 10 and 40 °C in 5 °C increments. The pulse interval was then used to determine T_b based on transmitter-specific calibration curves ($r^2>0.99$). The transmitters were sterilised in 70 % ethanol and implanted as described by Rojas et al. (2010). Pain killer (Metacam, Boehringer Ingelhein, North Ryde, NSW, Australia) was added to their food post surgery. The animals were fed canned cat food (Whiskas, Wodonga, Victoria, Australia) and kept for 24–72 h depending on their recovery and weather conditions and were then released at their point of capture.

Tracking and data loggers

Every morning, the animals were radio tracked with a handheld receiver (Icom IC-R10, Osaka, Japan) and Yagi antenna (Titley Scientific, Australia) to their nest site. Each location was determined using a handheld GPS (eTrex, Garmin Inc., Olathe, KS, USA). Signal detection range of the transmitters was dependent on the animals' location and nest type; however, it ranged from approximately 50 to 200 m.

When animals were initially located, several stopwatch readings of T_b were taken each day using the handheld receiver. Field receiver/loggers were set up for each animal at their nest site to automatically record the time interval between two transmitter pulses every 10 min (Körtner and Geiser 2000). Each recording system was placed in a waterproof box close to the nest. Data from the receiver/loggers were downloaded onto a laptop computer every 2–10 days after set-up. The pulse intervals recorded and the coefficients from the regressions of individual calibration curves were used to determine T_b. Due to a short detection range, receiver/loggers had to be moved when the animals moved location.

T_a at the field site was measured to the nearest 0.1 °C using an iButton (humidity/temperature logger, DS1923, Maxim Integrated Products, Sunnyvale, CA, USA) every 10 min. Rainfall data were obtained from the Australian Bureau of Meteorology for Armidale.

Data analysis and statistics

Torpor bout duration was calculated as the time that T_b remained below 30 °C for >20 min (Geiser and Masters 1994). Resting T_b was calculated as the minimum T_b recorded on days when torpor was not employed, and active T_b was calculated as the T_b on return to nest site and thus within logger range. Minimum T_b was calculated as the mean of daily minima recorded for each individual. Minimum torpor T_b was calculated using the lowest T_b recorded for each torpor bout. Time spent torpid was calculated both as percentage of days torpor was employed of the total days observations were made and percentage of time (hours) spent torpid over the same period. Onset and end of activity were calculated as the time the animal left and returned to its nest as determined by the first time the transmitter signal was absent and then again present on the receiver/logger. Data are represented as mean± standard deviations.

Data were tested for normality and equal variance. Analysis of variance (ANOVA) and Tukey's pairwise comparison were used to compare body mass, body condition, daily minimum T_b, resting T_b, active T_b, between males, first year females and second year females. A comparison of mean torpor bout duration between males, first year females and second year females was conducted using Kruskal–Wallis non-parametric tests because of unequal variances. Data of torpor occurrence (%) and time torpid (%) were arcsine transformed, and then ANOVA and Tukey's pairwise comparisons were conducted to compare across the sexes and age of females. Time of torpor entry, torpor arousal, and onset and end of activity was converted to degrees, and a Rayleigh's test (Zar 1974) was used to determine whether the timing of these activities was random; derived *r*-values (ranging from 0, not significant, to 1, highly significant) indicate the dispersion of timing records. In addition, Watson–Williams tests (Zar 1974) were performed to compare the onset and end of torpor and activity patterns between males, first year females and second year females. To test whether T_a affects torpor use the minimum T_a of days torpor was used or not used was compared with ANOVAs. Chi-squared test was used to determine whether rain was a factor affecting torpor use. Statistical analyses were conducted using R (R Development Core Team 2009) or programmes written by the authors in Visual Basic 6 (Microsoft) based on procedures listed in Zar (1974).

Results

In 2011, the average daily T_a observed during the study period was 9.0±2.9 °C and ranged from a minimum of 0.6 °C to a maximum of 15.3 °C with extremes of −2.5 to 21.6 °C (Fig. 1). The daily amplitude of T_a was 9.5±3.7 °C and ranged from 1.5 to 18.1 °C. On 26 of 61 days, rainfall events were recorded, with 21 days of <5 mm. In 2012, the average daily T_a was 11.4±3.1 °C and remained between 5.0 and 17.5 °C, with extremes of −1.5 to 24.1 °C. The average daily amplitude of T_a was 10.8±3.2 °C and ranged from 2.0 to 15.6 °C. It rained on 13 of the 29 days, but only on 4 days precipitation was >5 mm. In 2013, the average daily T_a was 9.8±0.5 °C and ranged from 9.2 to 10.2 °C, with extremes of 2 to 16.5 °C (not shown); the average daily amplitude of T_a was 11±2.7 °C and

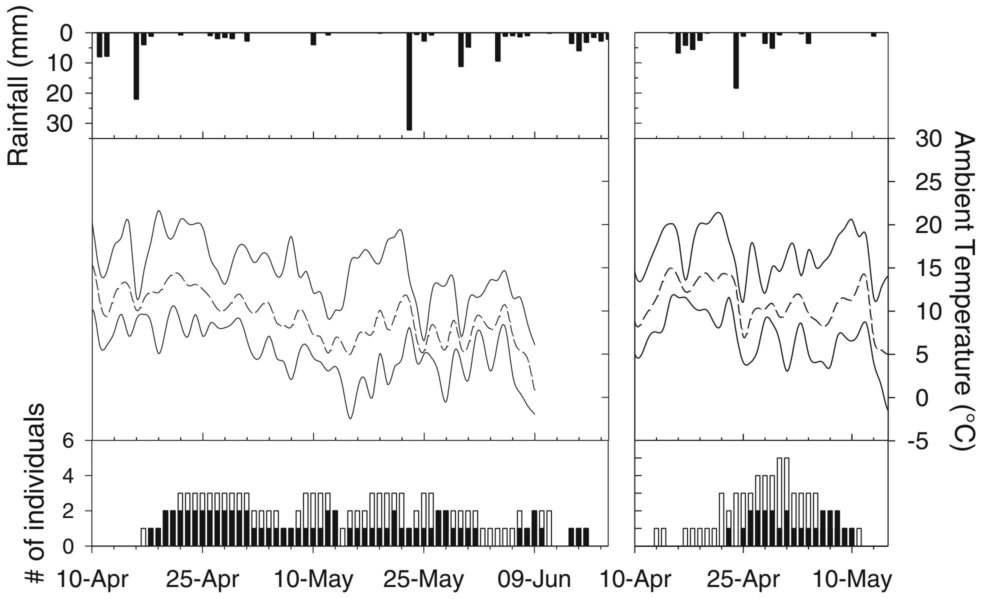


Fig. 1 Rainfall, ambient temperature (minimum, average and maximum) and the total number of individuals (*white bars*) and torpid individuals (*black bars*) against time in 2011 (*left*) and 2012 (*right*)

ranged from 8 to 14.5 °C. No rainfall events were recorded in 2013.

Body mass differed between males (*A. stuartii* similar to *A. flavipes*) and females, as well as between first and second year female *A. stuartii* (Table 1; $P<0.001$). In contrast, body condition did not differ between the three groups ($F_{2,\,7}=2.12$, $P=0.19$). Resting T_b of all animals dropped to low normothermic T_b of 32.0±0.7 °C and did not differ between males, first

Table 1 Body mass, torpor occurrence, minimum T_b and maximum torpor bout duration for individual antechinus

Animal	Body mass	Total days measured	Days torpid	Torpid (% of days)	Time torpid (% of hours)	Min. T_b (°C) [mean (min)] during torpor	Torpor bout duration (hours) [mean (max)]
♂							
A. flavipes 1	28.2	12	1	8.3	0.3	29.8[b]	0.8
A. flavipes 2	29.2	32	6	18.8	1.0	28.8 (28.2)	1 (1.8)
A. stuartii 1	25.9	9	0	0	0	—	—
A. stuartii 2	30.2	9	0	0	0	—	—
	28.4±2.3	16.7±13.3	2.0±3.5	6.3±10.9	0.3±0.5	28.9±0.5	1.0±0.4
1st year ♀							
A. stuartii 4	20.9	16	5	31.3	4.6	27.3 (24.6)	2.5 (4.3)
A. stuartii 5	21.1	9	6	66.7	14.7	24.5 (21.2)	5.1 (8.5)
A. stuartii 6	20.1	4	2	50.0	2.3	29.3 (29.0)	0.8 (1.2)
	20.7±0.5	9.7±6.0	4.3±2.1	49.3±17.7	7.3±6.5	26.7±2.7	3.2±2.2
2nd year ♀							
A. stuartii 1	23.7	49	47	95.9	32.7	24.4 (17.8)	5.7 (16.7)
A. stuartii 2	24.6	11	10	90.9	19.0	27.9 (25.0)	5.0 (9.3)
A. stuartii 3	26.3	13	12	92.3	18.3	25.1 (19.9)	5.2 (8.5)
	24.9±1.3	24.3±21.4	23.0±20.8	93.0±2.6	23.3±8.1	24.8±5.5	5.5±3.3
ANOVA	$P<0.001$			<0.001	<0.001	0.24 (0.12)	0.18[a] (0.05)
Tukey's							
♂ vs 1st year ♀	$P<0.001$			0.008	0.02		(0.65)
♂ vs 2nd year ♀	$P=0.04$			<0.001	<0.001		(0.05)
1st year vs 2nd year ♀	$P=0.02$			0.02	0.03		(0.11)

[a] Kruskal–Wallis test

[b] Single value used for calculation of both mean and min

year females and second year females (Figs. 2 and 3; $P=0.94$). Active T_b increased to 38.2±0.6 °C and did not differ between sexes and ages. In contrast, average daily minimum T_b, including both normothermic and torpid values, differed between all groups ($P<0.02$), with a daily minimum T_b of 31.7±2.0 °C in males, 29.8±3.7 °C in first year females and 25.3±4.0 °C in second year females.

Animals were mainly found in tree hollows and occasionally in logs and under leaf litter. Nest sharing in tree hollows was observed between sexes and species, involving two to four individuals. Torpor was seen in all nests types, and there was no difference in torpor use. T_a did not affect whether torpor was employed in males ($P=0.66$) and second year females ($P=0.94$). However, T_a had a significant effect on torpor use in first year females ($P=0.01$), with a mean minimum T_a of 5.2±2.2 °C on days when torpor was employed versus with that of 8.1±2.2 °C on days torpor was not employed. Rainfall had no apparent effect on torpor use ($\chi^2=2.18$, $P=0.14$).

The timing of torpor entry and arousal was random in males. In females, torpor entry ($P<0.01$) and arousal ($P<0.001$) had a non-random distribution (Fig. 4). In females, although torpor entry was observed throughout the day, torpor entry generally occurred around midday with no difference between first year (12:35 h, $r=0.55$) and second year females (11:15 h, $r=0.38$; $F_{1,\,108}=0.62$, $P=0.43$). On average, arousals in females occurred in the late afternoon around sunset and was later in second year females (18:04 h, $r=0.53$) than first year females (16:14 h, $r=0.77$; $F_{1,\,104}=31.74$, $P<0.001$). Activity was non-random ($r=0.49$–0.64, $P<0.001$) in both sexes and ages (Fig. 5). Animals were generally active during the scotophase, but some activity during the photophase was

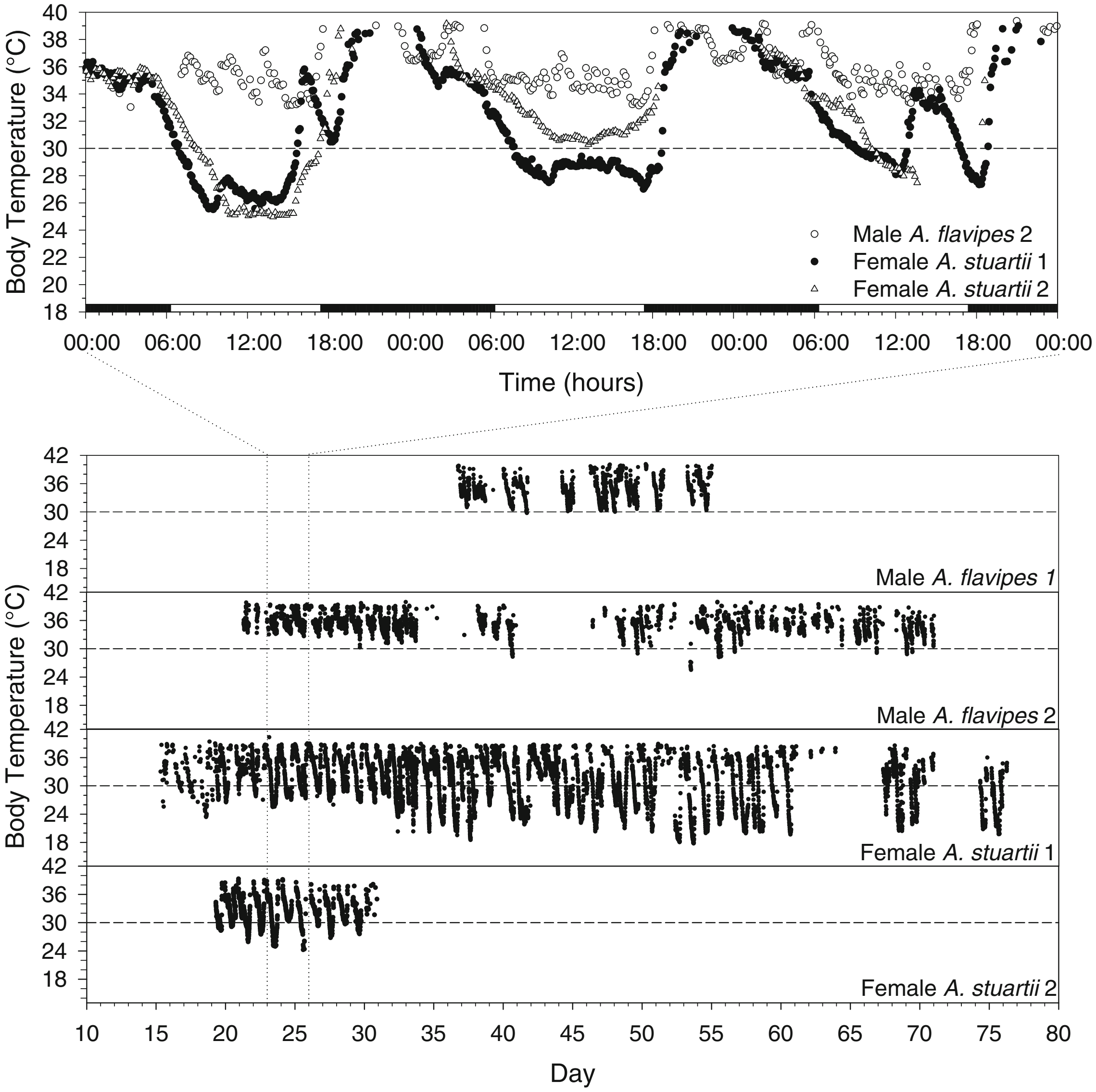


Fig. 2 Body temperature recordings for *Antechinus* during Autumn in 2011 (day 10=10th April)

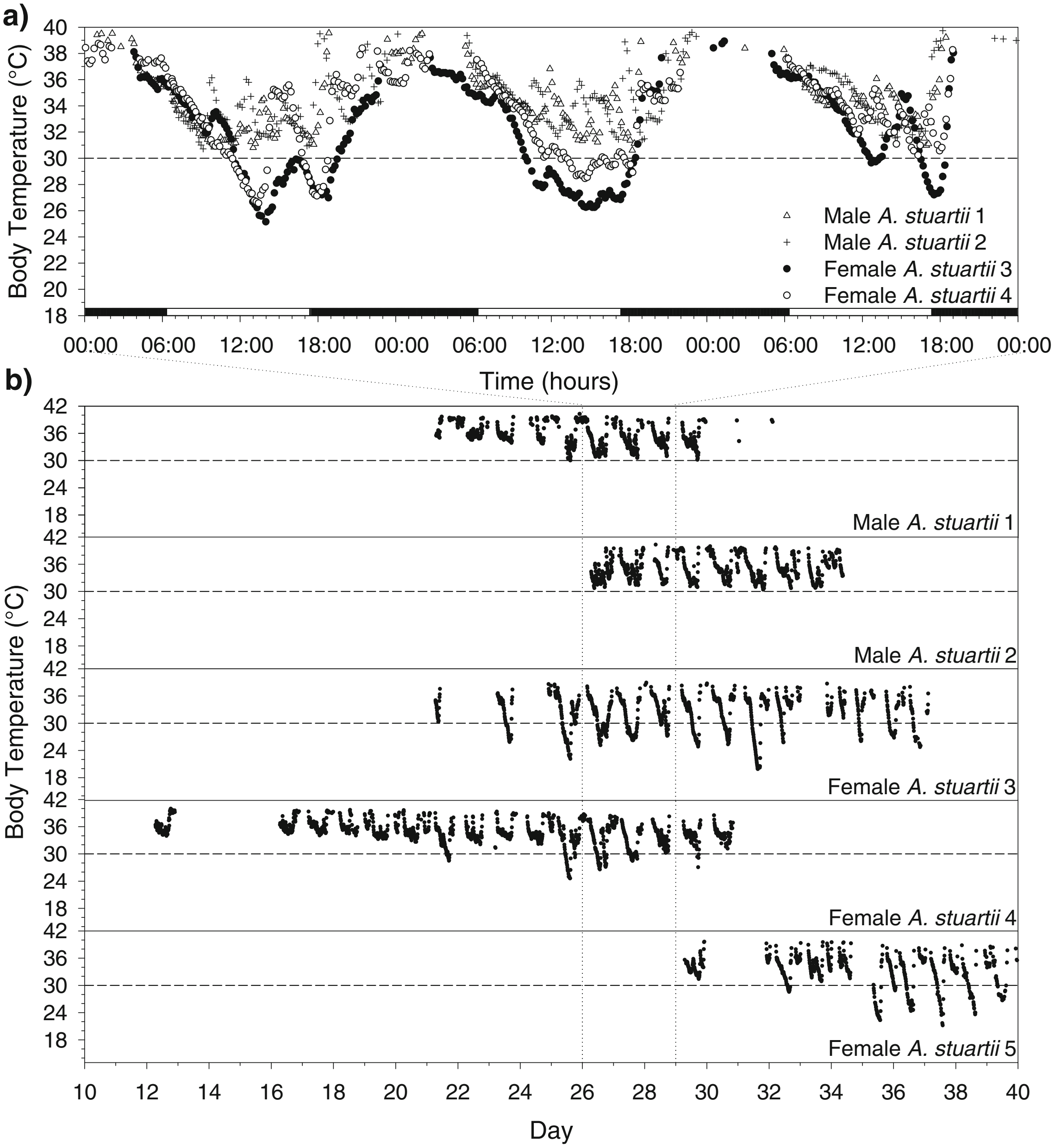
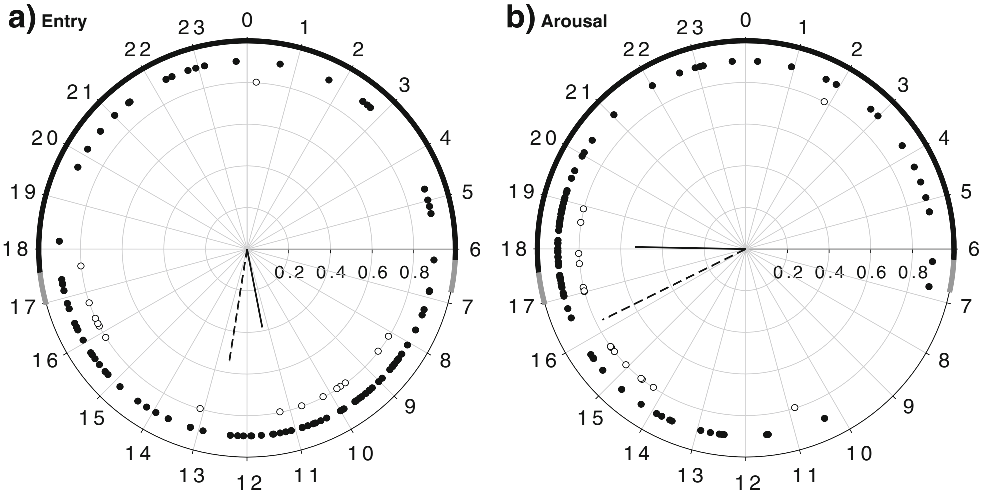


Fig. 3 Body temperature recordings for *Antechinus stuartii* during Autumn in 2012 (day 10=10th April). During the 3-day period shown (**a**), all 4 animals were found at the same location (tree hollow), except male #2 moved locations on the third day

also observed. The onset of activity was similar in males and females with a mean time of 20:34 h ($F_{2,\ 196}$=0.11, P=0.90). Differences in end of activity were observed ($F_{2,\ 165}$=125.48, P<0.001); second year females returned at 1:34 h later than males (1:05 h, P<0.001) but earlier than first year females (3:13 h, P<0.01).

All female *A. stuartii* expressed pronounced torpor throughout the study periods. In contrast, the torpor expressed by males was shallow and brief (Figs. 2 and 3). Furthermore, females used torpor more often than males (Table 1). Only two of four males (both *A. flavipes*) used torpor, and this was only for 8 and 19 % (mean for all males 6.3±10.9 %) of the total days observed. All females used torpor on 31 to 96 % of the total days observed. Moreover, the first year females used torpor on 49.3±17.7 % of all observation days, whereas the second year females used torpor for 93.0±2.6 % of the days observed. The mean proportion of days torpor was expressed differed significantly between the three groups (P<0.001). In addition, total time spent torpid differed between the three groups ($F_{2,\ 7}$=26.31, P<0.001). Overall, males spent little time torpid (0.3±0.5 %), a >24-fold difference in comparison to females. Interestingly, second year females spent considerably more time torpid than first year females with a 3.2-fold difference between the two groups (P=0.03). Nevertheless,

Fig. 4 Time of torpor **a** entry and **b** arousal of first year (*circles*) and second year female (*filled circles*) *Antechinus stuartii. Lines* indicate means, and '*r*' derived from the Rayleigh's test for first year (*dashed*) and second year (*solid*) females. Only significant vectors are shown, and a *longer length* indicates stronger clustering of events. *Black bar* indicates the scotophase at the beginning of the study, and the *grey bar* indicates the change in scotophase by the end of the study period



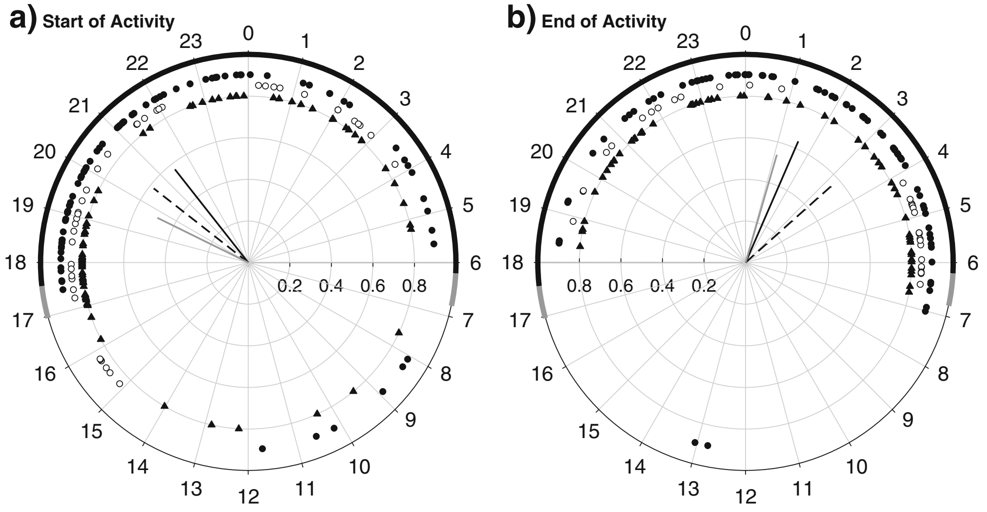
mean torpor bout duration did not differ (H=3.46, P=0.18), and maximum torpor bout duration was barely significant ($F_{2,\ 5}$=5.93, P=0.05). Torpor bouts in males lasted 1.0± 0.4 h; in females, torpor bouts lasted for 3.2±2.2 h (first year) and 5.5±3.3 h (second year). The longest torpor bout in females was 16.7 h (range 0.7 to 16.7 h) and 1.8 h in males. Torpor bouts of <2 h, similar to that of males, were also observed in females; however, most (16 of 19) occurred on days when multiple bouts of torpor were employed. Torpor also appeared to be shallower in males (minimum torpor T_b> 28 °C) than in females (absolute minimum torpor T_b<25 °C, except *A. stuartii* ♀ 6). Minimum torpor T_b of all torpor bouts employed by males ranged from 28.2 to 29.8 °C (28.9± 0.5 °C) and, in females, ranged from 17.2 to 29.7 °C (first year females: 26.7±2.7 °C; second year females: 24.8± 5.5 °C). However, mean minimum torpor T_b ($F_{2,\ 5}$=1.93, P=0.24) and absolute minimum torpor T_b ($F_{2,\ 5}$=3.37, P= 0.12) did not differ between the three groups.

Discussion

We provide the first data on torpor use and patterns by free-ranging antechinus. Torpor was employed extensively in the wild, although differences were seen between age groups and sexes. Within sexes and age groups, torpor expression was very similar. Interestingly, torpor was more pronounced in second year females than that in first year females, suggesting that these females use torpor to recover from their first reproductive period, to survive the winter, minimise foraging and thus avoid predators, and help them prepare for a second reproductive period in spring.

Previous studies have shown that the patterns and prevalence of torpor can differ between the sexes in both hibernators (Michener 1992; Healy et al. 2012; Batavia et al. 2013) and daily heterotherms (Körtner et al. 2008, 2010). Often, males exhibit shorter bouts of torpor and also have higher minimum T_b than females (Michener 1992; Körtner et al.

Fig. 5 Time of onset (**a**) and end (**b**) of activity of male (*triangles*), first year female (*circles*) and second year female (*filled circles*) *Antechinus. Lines* indicate means, and '*r*' derived from the Rayleigh's test for males (*grey*), first year females (*dashed*) and second year (*black, solid*) females. Only significant vectors are shown, and a *longer length* indicates stronger clustering of events. *Black bar* indicates the scotophase at the beginning of the study, and the *grey bar* indicates the change in scotophase by the end of the study period



2010; Healy et al. 2012). Similarly, our study showed that females not only used torpor more frequently but they also employed deeper and longer bouts than males, in agreement with captive antechinus (Geiser 1988). However, as with other comparisons of free-ranging and captive individuals (Geiser et al. 2007), data from captive antechinus did underestimate the extent of torpor use in the wild where deeper and longer torpor bouts were expressed. For example, the lowest T_b recorded in captivity was 21.0 °C, whereas the lowest recorded T_b in the wild was 17.8 °C. However, not all variables of torpor differed between captive and wild individuals: Minimum torpor T_b observed for first year females was 21.2 °C, similar to that in captivity. Moreover, mean daily minimum T_b (includes torpor and normothermia) was similar in captive and free-ranging antechinus: ~25 °C in female *A. stuartii* and ~32 °C in male *A. flavipes.*

On average, free-ranging antechinus also entered torpor more frequently than captive individuals. Spontaneous torpor (food available) was recorded only on a few occasions in captive females, whereas induced torpor by food withdrawal was more frequent occurring on >80 % of observation days in *A. stuartii* and female *A. flavipes* (Geiser 1988). Captive male *A. flavipes* were the least likely to enter torpor, whereas in the field, male *A. flavipes* were the only males expressing torpor. However, captive male *A. flavipes* were over 20 g heavier than wild males in our study. As food availability cannot be easily measured in the field, it is unknown how it affected torpor in the wild. Nevertheless, unpredictability of food has been shown to increase torpor incidence (Munn et al. 2010) and may have contributed to the observed difference in torpor prevalence between captive animals that are usually provided with a consistent ad libitum food resource and animals in the field which experience limited and variable foraging success.

In several species, a negative correlation between the extent of daily torpor and body mass has been observed (Geiser 1988; Holloway and Geiser 1996; Körtner and Geiser 2000). In captive antechinus, both minimum T_b and torpor bout duration ($\log_{10}$) showed a linear relationship with body mass with smaller individuals employing deeper and longer bouts (Geiser 1988). As male antechinus are larger than females, some of the discrepancy seen between the sexes, as well as the differences between captive and free-ranging animals, might be explained by body mass. However, although wild males used torpor on only 6 % of days, they were only slightly (~15 %) heavier than second year females. In contrast, second year females, despite being ~20 % heavier than first year females, used torpor on most days observed (93 %), about twice that in the first year females (49 %). Moreover, second year females were torpid for considerably longer periods than first year females. Thus, our data show that sex and age per se also play key roles in determining torpor use.

Arousal from torpor occurred later in the second year females, consistent with longer torpor bouts, whereas time of entry into torpor did not differ between female age groups. Timing of activity also differed between second year females, and males and first year females. With regard to second and first year females, onset of activity occurred at a similar time of day, a few hours after sunset; however, the latter remained active until later at night than the former. The shorter foraging time in second year females is possibly explained by the longer time they remained torpid and also a longer experience in optimal foraging (Buckley and Buckley 1974). Alternatively, first year females are still growing in autumn, which requires prolonged foraging and may limit torpor use, whereas second year females maintain a constant body mass (Braithwaite 1979). However, growth is not always slowed by torpor use as, for example, in fasted juvenile dormice, growth was highest when more frequent bouts of torpor were employed (Giroud et al. 2012; and see below).

Short foraging times in second year females reduce not only energy expenditure but also exposure to predators (Bieber and Ruf 2009; Turbill et al. 2011). This interpretation is further supported by data on subtropical insectivorous bats, which express summer torpor especially when fat, suggesting that in this case torpor is not used to deal with energy shortages, but rather to minimise foraging when not required for energy balance and thus minimise predation (Stawski and Geiser 2010). For second year female antechinus, which use a energetically more conservative approach than first year females, with reduced activity and longer torpor periods, torpor likely is used not only to minimise predation and energy expenditure but also to recover from their first reproductive period and to prepare for the next reproduction. In contrast, first year females which have not yet reproduced use torpor only at low T_a when energetic demands are high. Perhaps, this 'wasteful' use of energy and thus high foraging requirements is one of the reasons why so few females survive into a second year. Even more energetically wasteful than the first year females are the males, which appear to use torpor only as a last resort; perhaps, burning the candle on both ends contributes to the early demise of males immediately after reproduction. Obviously, in males, reproductive success depends on how big they are and with how many females they can mate, and consequently, they need to be active and feed during their growth period, which possibly limits torpor use. Thus, torpor not only has benefits but also has potential costs (Humphries et al. 2003).

Several studies have assessed age effects on torpor expression. However, most of these compared juveniles and adults and showed that juveniles express more pronounced torpor than adults likely to enhance survival and growth on limited resources (Geiser 1988; French 1990; Geiser and Brigham 2012; Giroud et al. 2012; Healy et al. 2012; Bieber et al. 2013), and again many of these differences can be attributed to body mass. Fewer studies have examined age of mature animals with regard to use of torpor, especially in species with a short lifespan. Edible dormice (*Glis glis*) shorten the hibernation season with each year of age, and this is thought to maximise their total reproductive output (Bieber et al. 2013). Antechinus show exactly the opposite effect of age on torpor use: The older, heavier females used torpor more often than the younger, lighter females. However, unlike the edible dormice that go through several months of inactivity, antechinus must survive through several months of daily activity/torpor cycles to reach the breeding season. The more extensive use of torpor in second year females may therefore increase their chances of surviving into another year and a second breeding period as torpor use is known to not only reduce energy demands but also increase the chance of long-term survival (Turbill et al. 2011). Although we have no direct evidence that the extensive use of torpor by second year females allowed them to produce a second litter and therefore increased fitness, antechinus reproduction is not only extremely synchronous but also highly predictable. Essentially, all females produce full litters of about 8 young (Wood 1970). Moreover, the decline in female antechinus in the wild is most pronounced in summer whereas numbers in winter remain rather stable (Wood 1970; Lee and Cockburn 1985). Thus, it is highly likely that if females survive to early winter (as in our study), they will also survive the winter into another reproductive period.

Our study presents further support of the extensive use of torpor in wild populations, not only to cope with immediate energy demands but also to deal with previous energetic history. Our observations are the first to show an age effect on daily torpor use, whereby the older females use frequent and pronounced torpor most likely to permit a second reproductive period and to increase fecundity.

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