

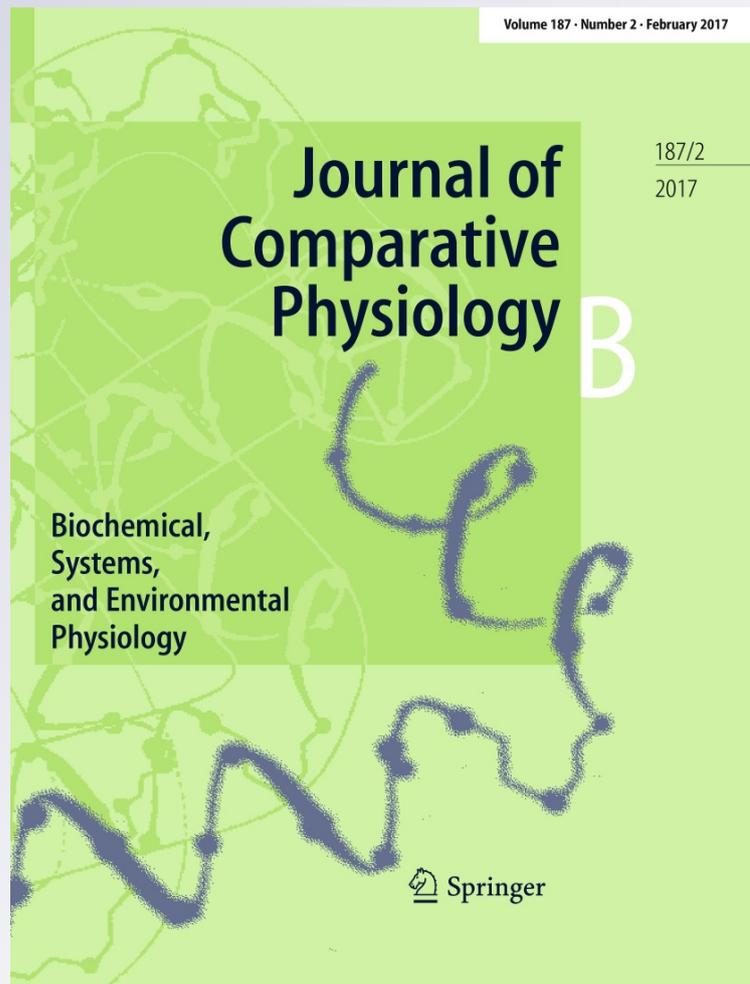
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# Torpor and basking after a severe wildfire: mammalian survival strategies in a scorched landscape

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**Abstract** Wildfires can completely obliterate above-ground vegetation, yet some small terrestrial mammals survive during and after fires. As knowledge about the physiological and behavioural adaptations that are crucial for post-wildfire survival is scant, we investigated the thermal biology of a small insectivorous marsupial (*Antechinus flavipes*) after a severe forest fire. Some populations of antechinus survived the fire in situ probably by hiding deep in rocky crevices, the only fire-proof sites near where they were trapped. We hypothesised that survival in the post-fire landscape was achieved by decreasing daytime activity and using torpor frequently to save energy. Indeed, daytime activity was less common and torpor expression was substantially higher ( $\geq 2$ -fold) at the post-fire site than observed in an unburnt control site and also in comparison to a laboratory study, both when food was provided ad libitum and withheld. Basking in the post-fire site was also recorded, which was likely used to further reduce energy expenditure. Our data suggest that torpor and basking are used by this terrestrial mammal to reduce energy and foraging requirements, which is important in a landscape where food and shelter are limited and predation pressure typically is increased.

**Keywords** Antechinus · Climate change · Fire · Heterothermy · Marsupial · Physiology

## Introduction

For mammals living in resource-restricted habitats, such as temperate, arid, or post-flood/fire environments, the high energetic cost of endothermy can become problematic. To maintain a high body temperature ( $T_b$ ), endothermic mammals must exert metabolic energy for heat production; this is especially pronounced for small mammals, which have a large surface/volume ratio and high resting metabolic rate (RMR) (Hill et al. 2008). Over prolonged periods, this cost can be prohibitively high, and many small mammals employ daily torpor or hibernation to conserve energy (Ruf and Geiser 2015).

Torpor is characterised by substantial but controlled reductions in metabolic rate (MR),  $T_b$ , and water loss (Cooper et al. 2009; Ruf and Geiser 2015), and, therefore, reduces energy and foraging requirements. Importantly, torpor in many mammals from Australia and other regions is not only employed in winter, but also in response to drought, weather extremes, reduced food availability and even in summer when ambient temperatures ( $T_a$ ) are high (Geiser and Brigham 2012; Levin et al. 2015; Nowack and Dausmann 2015). Torpor often is also used together with basking to further minimise energy expenditure, as arousals from torpor without an external heat source are energetically expensive (Geiser et al. 2002; Warnecke et al. 2008; Currie et al. 2015; Thompson et al. 2015).

In a post-fire environment, terrestrial mammals that survive in situ (Banks et al. 2011) often have to cope with food shortage, a reduced number of shelters, and increased exposure to predators during foraging (Körtner

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et al. 2007; McGregor et al. 2014), all of which could potentially be mitigated by using torpor. Indeed, empirical evidence demonstrates that the use of torpor via a reduction in energy and thus foraging requirements decreases mortality from exposure to predation and limits starvation (Geiser and Turbill 2009; Turbill et al. 2011; Ameca y Juarez et al. 2012; Hanna and Cardillo 2014). In Australia, every year, wildfires burn large areas of the continent and, in conjunction with anthropogenic habitat fragmentation and the introduction of placental carnivores, may have contributed to the disproportionately high number of extinctions of mammals over the past 200 years (Woinarski et al. 2015). Importantly, it is predicted that changes in global weather patterns will increase the frequency and intensity of wildfires in Australia, as in other regions with fire-prone vegetation (Moritz et al. 2015).

Recent work has shown that torpid mammals can arouse in response to smoke stimuli (Stawski et al. 2015; Nowack et al. 2016a) and that the use of torpor appears important for survival of terrestrial mammals after controlled low-intensity management burns that remove most ground cover, but leave trees largely unaffected (Nowack et al. 2016b; Stawski et al. 2016). However, the role of torpor in terrestrial mammals soon after an intense and extremely destructive wildfire has never been examined. We, therefore, tested the hypotheses that after a severe bushfire, yellow-footed antechinus (*Antechinus flavipes*), a small marsupial mammal, will (a) decrease daytime foraging activity due to a reduction in ground cover and an associated increase in predation pressure, (b) use torpor more often in response to limited foraging opportunities, and (c) also engage in basking because of the enhanced availability of sun and the need to save energy.

## Methods

### Study site and animals

All procedures in our study were approved by the University of New England Animal Ethics Committee and the New South Wales National Parks and Wildlife Service.

The post-fire study was conducted in May/June 2013 (austral autumn/early winter) in Warrumbungle National Park (31°17'S 149°0'E; 23,312 hectares); a volcanic mountain range that is surrounded by wheat fields and pastures near Coonabarabran, New South Wales. From 12 to 28 January 2013, a severe wildfire burnt approximately 88 % of the park. The fire was ended by heavy rain, which caused flooding, erosion, and uprooted many of the still standing trees (see electronic supplementary material). Consequently, access to the park was initially prohibited and was



**Fig. 1** Photo of the study area showing the rocky outcrop and burnt trees with basal regrowth

still restricted to small sections of the park when our study commenced 3 months after the fire.

We selected the yellow-footed antechinus (*Antechinus flavipes*: Dasyuridae), a small, insectivorous marsupial known to use daily torpor (Geiser 1988; Rojas et al. 2014) for our investigation, because they succeed in fragmented landscapes and early post-fire environments (Thompson et al. 1989; Banks et al. 2011). *Antechinus flavipes* are terrestrial and arboreal and, although generally nocturnal, are often active during the day; they are mainly insectivorous but may eat small vertebrates, eggs, nectar, and flowers (Menkhorst and Knight 2001).

Trapping was conducted at two severe burn sites (total  $2 \times 450 = 900$  trap nights), but animals were only trapped at the one of these. This site was characterised by fissured rock ledges and outcrops, sandy soil covered in ash, dead tree stems and with sparse, small sprouting ground cover of mainly *Acacia* spp., and some *Eucalyptus* trees with basal regrowth (Fig. 1). We were able to trap a total of nine individuals and to collect data for six of them (5 males 23.8–34.4 g capture mass, 1 female 23.4-g capture mass) in late May/early June. The six animals were tracked for  $29.5 \pm 7.0$  days on average. Fresh scats from traps could be collected on only two occasions and these were analysed for dietary composition (Scats about, PO Box 45, Majors Creek, NSW, Australia). Trapping at this particular site was replicated for the following year (see electronic supplementary material).

In addition, extensive trapping (450 trap nights) was conducted in the few remaining pockets of unburnt vegetation mainly along creek lines with unburnt *Acacia* trees, a layer of leaves and some debris (from the flooding event), shrubbery, and rock fissures (see electronic supplementary material). Despite the apparent suitability of the habitat, the areas were small and no antechinus could be obtained. Therefore, initially, our only control reference for torpor

expression was from a laboratory study that provides data on both spontaneous (food ad libitum) and induced (food withheld) torpor occurrence in the species (Geiser 1988;  $n = 9$  females,  $n = 6$  males) and a winter field study from a colder habitat (Rojas et al. 2014;  $n = 2$  males). However, subsequently, we were able to collect comparable field-data from an unburned field site with similar environmental and thermal conditions, but at a different location. This control data set comprised six male *A. flavipes* (25.9–32.8 g capture mass, 36 animal days) measured over 6 study days at Aberbaldie Nature Reserve (31°04'24"S, 151°25'34"E, July 2016) that also features rocky outcrops and primarily *Eucalypt* woodland. Mean (post-fire  $T_a = 12.5 \pm 2.6$  °C,  $n = 43$ ; control  $T_a = 11.4 \pm 1.3$  °C,  $n = 6$ ;  $p = 0.341$ ,  $t = 0.9$ ,  $df = 47$ ) and minimum (post-fire  $T_a = 8.4 \pm 2.9$  °C,  $n = 43$ ; control  $T_a = 8.8 \pm 2.5$  °C,  $n = 6$ ;  $p = 0.765$ ,  $t = -0.3$ ,  $df = 47$ )  $T_a$ s were similar for the post-fire and control studies. A similar  $T_a$  is important for comparisons as the previous studies (Rojas et al. 2014; Stawski and Rojas 2016) and the current study have shown that  $T_a$  significantly affects torpor bout duration in antechinus.

### Telemetry and data acquisition

Core  $T_b$  of free-ranging antechinus at both field sites was measured using temperature-sensitive radio-transmitters (1.9–2.2 g Sirtrack, Havelock North, New Zealand) that were <10 % of body mass as recommended (Rojas et al. 2010). Transmitters with individual radio frequencies for identification of individuals were coated with inert wax (Paraffin/Elvax, Mini Mitter, Respironics Inc. OR, USA), calibrated to the nearest 0.1 °C, disinfected in 70 % ethanol, and implanted intraperitoneally under general isoflurane/oxygen anesthesia as described (Rojas et al. 2010). Following implantation, a topical anaesthetic (Xylocaine, AstraZeneca Pty Ltd, North Ryde, NSW, Australia) and Leuko Spray Bandage (BSN medical Pty Ltd, Clayton, Vic, Australia) were applied to the incision site, and Children's Pandol (Ermington, NSW, Australia) was administered with food. Animals were held overnight provided with canned cat food (Whiskas, Wodonga, VIC, Australia) and mealworms, and released at the site of capture the following morning.

Antechinus were radio-tracked daily from the early morning with receivers (TR-4 Telonics, Mesa, USA or ICOM IC-R10, Icom Inc., Osaka, Japan) and Sirtrack Yagi antennae. Manual temperature readings with a stopwatch were taken each time a transmitter signal was received. A mobile receiver/logging system was placed near the nest site and the time interval between two transmitter pulses was recorded automatically every 10 min (Körtner and Geiser 2000). Data were downloaded every few days and time intervals between transmitter pulses converted to  $T_b$

using a second-order polynomial equation ( $r^2 > 0.999$ ) based on the transmitter calibration. Data from transmitters were used to determine  $T_b$  and activity patterns. Individuals were deemed active if they were out of reception range of the data loggers placed near their nest sites; only days when individuals returned to a nest with a data logger were used for analyses. Nest locations were recorded using a handheld GPS (Garmin Inc., Olathe, NS, USA).

$T_a$  at both study sites was measured at 10-min intervals using calibrated temperature data loggers ( $\pm 0.5$  °C, iButton DS1921G, Maxim Integrated Products, Sunnyvale, CA, USA). These were placed at a number of locations near nests of study animals, ~1 m above ground in an inverted Styrofoam cup for shade. At the Warrumbungle National Park post-fire site, the temperature of rock crevices ( $T_{\text{crevice}}$ ) was measured with iButtons in two locations at ~1-m depth and temperature inside a basking log ( $T_{\text{log}}$ ) was measured in one location.

### Data analysis

Antechinus were considered to be torpid when  $T_b$  fell below 32.0 °C for males and 31.0 °C for females. These thresholds were derived using Eq. 4 from Willis (2007) and rounded to the nearest integer. The thresholds were used to include small but energetically important reductions in  $T_b$  (Brigham et al. 2011), and as active  $T_b$  of antechinus often approach or even exceed 40 °C (Rojas et al. 2014 and present study), these torpor thresholds (i.e. a drop of  $T_b$  by >8 °C) seem appropriate. Torpor entry and arousal times and torpor bout duration (TBD) were calculated from times that  $T_b$  remained below these thresholds for periods longer than 30 min (Körtner and Geiser 2000). This definition of the torpor threshold was also used to re-define torpor in the laboratory study (Geiser 1988) that we used for comparison with our current data. Mean  $T_b$  during torpor (torpor  $T_{b \text{ mean}}$ ) was calculated as the mean of all  $T_b$ s below the threshold. For torpor bouts with missing values, torpor  $T_{b \text{ mean}}$  was calculated by resampling the  $T_b$  trace at the longest available interval during the torpor bout. If large proportions of data were missing, the torpor bout was excluded from this analysis.

The number of individuals ( $n$ ) and the number of observations ( $N$ ) are provided when applicable. Means are presented  $\pm 1$  standard deviation (SD) and a significance level of 0.05 was used for all statistical tests. As post-fire data were available for only one female, these were not included in any of the statistical analyses, but because females are crucial in post-fire recovery and data were available for 29 days for this individual, the data are presented nevertheless. Torpor expression and distribution of  $T_b$  integers for males were tested against independent variables of  $T_a$  using  $t$  tests and Chi-square test. Differences in daytime activity,

torpor use, and daily  $T_{b\ min}$  in males between the post-fire, control, and laboratory studies were tested using an analysis of variance (ANOVA) followed by Fisher's pairwise comparison. An analysis of covariance (ANCOVA) was performed initially with body mass (BM) at capture as a covariate, which had no significant effect, and BM was, therefore, not further considered for analyses. Percentage values were arcsine transformed before testing. Temporal distribution of entry and arousal times for each torpor bout was analysed with Raleigh's test. The relationship of TBD,  $T_b$ , and  $T_{b\ mean}$  with  $T_{a\ min}$  was assessed using the linear mixed-effects models with individual as a random factor to account for the repeated measures design (R 2.10.1. R Development Core Team, 2009). Mean TBD was calculated for each animal separately; following this, the mean was calculated for males collectively.

**Results**

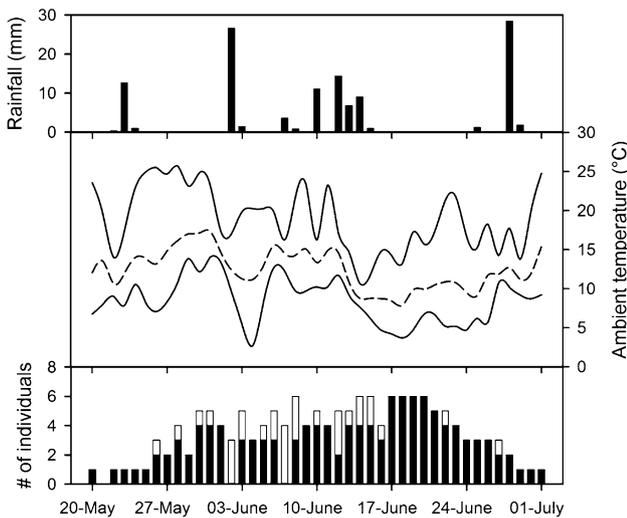
Throughout the post-fire study, the daily mean outside (air)  $T_a$  was  $12.5 \pm 2.6\ ^\circ\text{C}$  and the mean  $T_{crevice}$  was only slightly higher with  $13.0 \pm 2.4\ ^\circ\text{C}$  (Fig. 2). However,  $T_{crevice}$  fluctuated daily by  $5.2 \pm 2.4\ ^\circ\text{C}$ , whereas outside  $T_a$  fluctuated by  $9.1 \pm 4.3\ ^\circ\text{C}$  (Fig. 2). Most nest sites were at the top or halfway down rocky slopes characterised by deep cracks and crevices, these all had an easterly aspect, facing the rising sun.

The preliminary dietary analysis indicated that a large part of the antechinus diet consisted of ants (80 % in the male, 40 % in the female), which were the only terrestrial

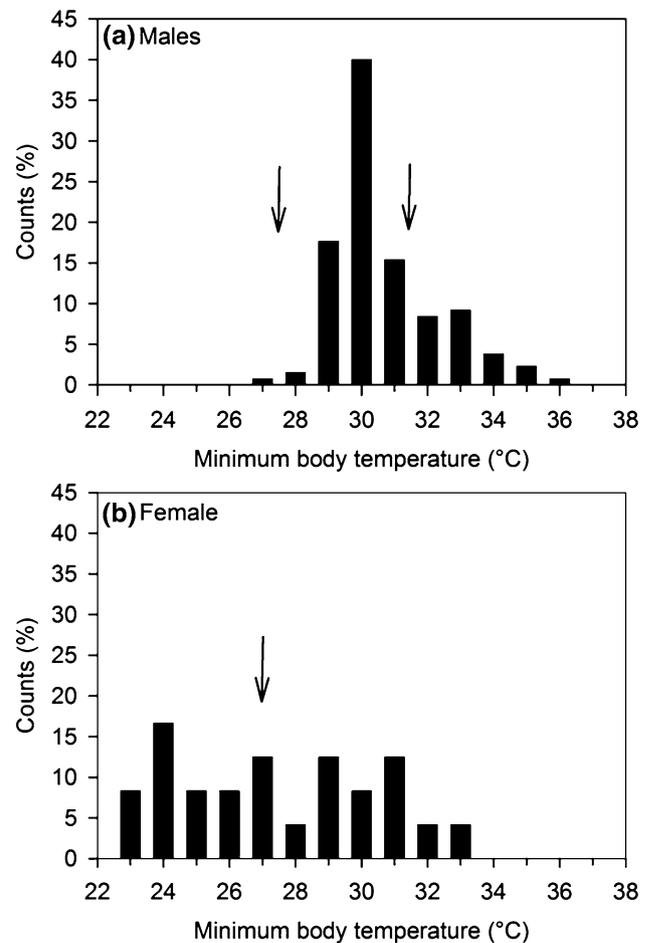
insect group present in numbers after the fire. Leaves (monocot and dicot) and seeds contributed to the rest of the diet.

At both field sites, *Antechinus flavipes* were predominantly active during the night. At the post-fire site, they expressed daytime activity on only  $6.0 \pm 2.6\ %$  ( $n = 5$ ) of days, whereas at the unburnt site the percentage of days antechinus were active during the daytime, was significantly higher ( $39.0 \pm 10.5\ %$ ,  $n = 6$ ;  $p = 0.02$ ,  $f_{1,9} = 8.56$ ).

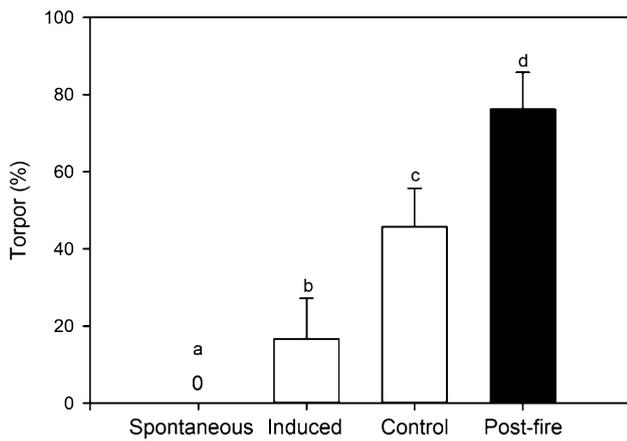
Overall, free-ranging antechinus demonstrated strong daily fluctuations of  $T_b$ , which in the post-fire female ranged from a minimum of  $23.4\ ^\circ\text{C}$  (torpid) to a maximum of  $38.9\ ^\circ\text{C}$  (active). In the post-fire males,  $T_b$  ranged from  $26.8\ ^\circ\text{C}$  (torpid) to  $40.7\ ^\circ\text{C}$  (active), similar to the males from the control site ( $27.4\ ^\circ\text{C}$ , torpid, to  $40.8\ ^\circ\text{C}$ , active). Daily  $T_{b\ min}$  ranged from  $23.4$  to  $33.5\ ^\circ\text{C}$  (mean:  $27.5 \pm 3.1\ ^\circ\text{C}$ ,  $N = 24$ ; Fig. 3b) in the female; in



**Fig. 2** Rainfall, ambient temperature (minimum, average, and maximum), and the total number of individuals on the day of measurement (white bars) and individuals expressing torpor (black bars) against time (May–June 2013) from the post-fire site



**Fig. 3** Frequency distribution of percent of all  $T_{b\ min}$  integers of *A. flavipes* from the post-fire site. Males are represented by **a** and the arrows are the  $T_{b\ min}$  for a male observed at the control site (left) and (right) during induced torpor in the laboratory (Geiser 1988). The female is represented by **b** and the arrow is the  $T_{b\ min}$  measured for a female during induced torpor in the laboratory (Geiser 1988)



**Fig. 4** Post-fire torpor use (% of days) in male *A. flavipes* in comparison to that in the control field site and in the laboratory when food was available (spontaneous torpor) or food was withheld (induced torpor) (Geiser 1988). Means differed among groups ( $p < 0.0001$ ); differences among groups were determined by a post hoc Fisher's pairwise comparison and are indicated by different letters

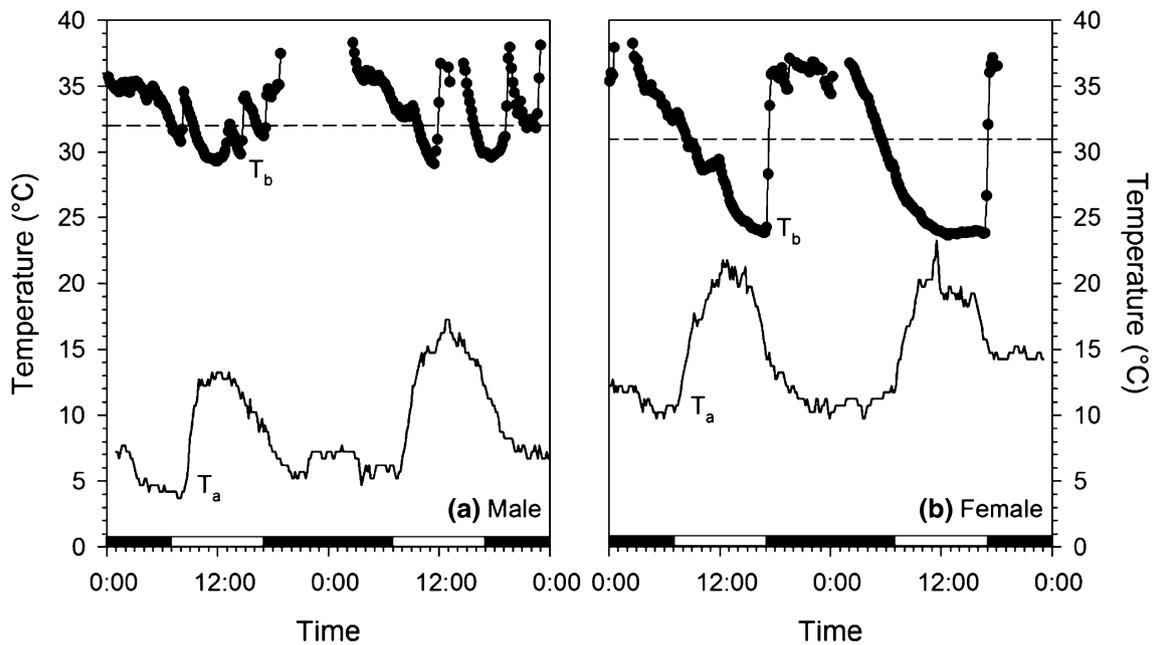
males from the post-fire site from 26.8 to 36.3 °C (mean  $30.7 \pm 0.3$  °C,  $n = 5$ ,  $N = 130$ ; Fig. 3a) and in males from the control site from 27.4 to 37.9 °C (mean  $31.9 \pm 1.8$  °C,  $n = 6$ ,  $N = 34$ ) and these means did not differ significantly ( $p = 0.13$ ,  $f_{1,9} = 2.77$ ).

*Antechinus flavipes* at the post-fire site expressed torpor on most days of the study period ( $76.2 \pm 9.6$  % for the five

males, 87.5 % for the female), with some individual variation (Fig. 2). In males, this high level of torpor use was significantly greater ( $p < 0.0001$ ,  $f_{3,22} = 21.09$ ) than that measured at the control field site ( $45.7 \pm 10.0$  %) and also than both spontaneous (food ad libitum: 0 %) and induced torpor (food withheld:  $16.7 \pm 10.5$  %) measured in a laboratory study (Geiser 1988; Fig. 4).

When male *A. flavipes* entered torpor, at the post-fire site, they expressed a single torpor bout on 48 % and two or more torpor bouts on 52 % of torpor days (Fig. 5a). This ratio was slightly different at the control field site, with males expressing a single torpor bout on 65 % of torpor days and two or more torpor bouts on 35 % of days. The female at the post-fire site expressed a single torpor bout on 52 % of torpor days; two or more torpor bouts occurred on 48 % of days (Fig. 5b).

At both field sites, days on which torpor was expressed were on average cooler, with a lower  $T_{a \text{ min}}$  than those without torpor (post-fire:  $p = 0.01$ ,  $t = 3.84$ ; control:  $p = 0.01$ ,  $t = -2.72$ ,  $df = 25.6$ ). Similarly, in the burnt habitat, individual torpor bout durations (TBD) for male *A. flavipes* increased with decreasing  $T_{a \text{ min}}$  ( $p = 0.01$ ,  $R^2 = 0.43$ ;  $\text{TBD (h)} = 4.212 - 0.160 T_{a \text{ min}} (\text{°C})$ ;  $n = 5$ ) and not surprisingly the torpor  $T_{b \text{ mean}}$  ( $p < 0.001$ ,  $R^2 = 0.55$ ;  $\text{TBD (h)} = 51.112 - 1.593 \text{ torpor } T_{b \text{ mean}} (\text{°C})$ ;  $n = 5$ ). Accordingly, at the post-fire site, the frequency distribution of all  $T_b$  integers indicated a shift in  $T_b$  range as  $T_a$  changed ( $p < 0.0001$ ,  $R^2 = 77.25$ ). On the day with the lowest



**Fig. 5** Body temperature ( $T_b$ , dots) of a male (a) and female (b) *A. flavipes* from the post-fire site, torpor threshold (dashed line), and ambient temperature ( $T_a$ , solid line) plotted over 2 days in June 2013.

The dark and light bars at the bottom of the graph indicate night and day, respectively

$T_{a \text{ min}}$  of 2.7 °C, 62 % of all  $T_b$  integers were between 23 and 35 °C. In contrast, on the day with the highest  $T_{a \text{ min}}$  of 14.0 °C, 64 % of all  $T_b$  integers were in the  $T_b$  range of 33–36 °C and the lowest recorded  $T_b$  was 28 °C.

At the post-fire site, the mean TBD of individual bouts was  $4.4 \pm 3.6$  h ( $N = 33$ ) for the female and  $1.8 \pm 1.5$  h ( $n = 5$ ,  $N = 180$ ) for the males, similar to the mean TBD recorded for males at the control site ( $1.9 \pm 1.4$  h,  $n = 6$ ,  $N = 27$ ). However, the longest individual torpor bout at the post-fire site was 13.8 h in a male, lasting ~twice that recorded in the control site (6.3 h). In addition, the maximum TBD in captive males was only 0.8 h (Geiser 1988), much shorter than those recorded in the field.

For male antechinus, times for torpor entry (post-fire site:  $p < 0.001$ ,  $Z = 28.81$ ; control site:  $p < 0.0001$ ,  $Z = 63.99$ ) and arousal (post-fire site:  $p < 0.001$ ,  $Z = 30.04$ ; control site:  $p < 0.0001$ ,  $Z = 63.99$ ) were non-randomly distributed and very similar at the post-fire and control sites. The average torpor entry time at the post-fire site was 12:56 h  $\pm$  325 min ( $n = 5$ ,  $N = 214$ ) and at the control site was 12:36 h  $\pm$  267 min ( $n = 6$ ,  $N = 64$ ). Average arousal time at the post-fire site was 15:23 h  $\pm$  321 min ( $n = 5$ ,  $N = 212$ ) and that at the control site was 14:22 h  $\pm$  277 min ( $n = 6$ ,  $N = 64$ ). Although these averages indicate that the initial entries and final arousals from torpor predominantly occurred during daytime, torpor bouts during the night were not uncommon at both sites.

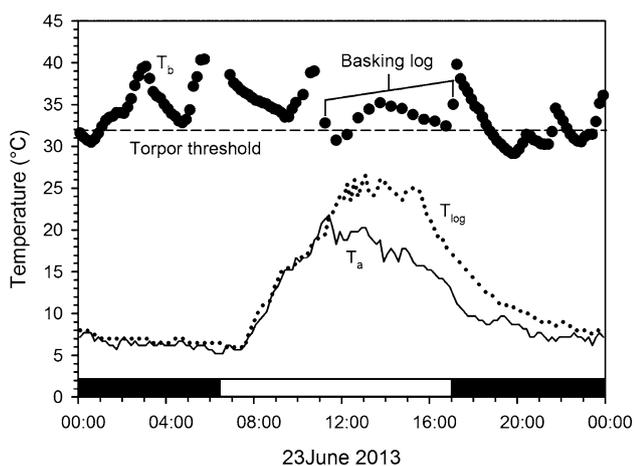
Interestingly, one male (M1) from the post-fire site was found in a log 33 m away from its nest site at similar times in the afternoon on 9 days during the tracking period. On one occasion, another male was also located resting in a different log in the afternoon. The logs were both fairly

small in diameter (~20 cm), burnt, and hollowed from the fire and situated in the direct afternoon sunlight, and  $T_{\text{log}}$  of M1 was up to 10 °C higher than  $T_a$  during the afternoon (Fig. 6). A consistent behavioural and thermal pattern was evident when M1 visited the basking log. After a brief morning activity period (81  $\pm$  41 min), M1 arrived at the log at 11:16 h  $\pm$  31 min (Fig. 6). Onset of shallow torpor began once M1 was inside the log and mean  $T_{b \text{ min}}$  during the torpor bout was 30.1  $\pm$  0.5 °C. Final arousal occurred at 16:46 h  $\pm$  62 min and M1 usually returned to the original nest site within 5–12 min of leaving the log (once after 86 min). After return to the nest site, M1 entered between 1 and 3 torpor bouts during the night.

## Discussion

Our study provides the first detailed account of the thermal biology and activity of a free-ranging small terrestrial mammal after a severe wildfire. Extensive trapping in several burnt and unburnt areas at Warrumbungle National Park after the wildfire surprisingly yielded antechinus only in one high severity burn site. However, this site was characterised by rocky outcrops containing deep crevices, whereas the few unburnt forest remnants were situated along gullies. This suggests that in this species, immediate survival was linked to the safe underground refuges in the rocky outcrops. Without these, mortality would have likely been high, if not catastrophic, with the remaining small pockets of vegetation being too small to sustain viable populations of antechinus. This scenario appears to be in contrast to low-intensity management burns without crown fires when most of the monitored congeners, *A. stuartii*, and also echidnas (*Tachyglossus aculeatus*) survived (Nowack et al. 2016b; Stawski et al. 2016). However, irrespective of fire intensity, site fidelity after a fire appears to be a general trend in antechinus. While in the present case of a severe wildfire, the link between underground refuges and trap success strongly suggests that the study animals survived the fire and remained at this particular site for months after the fire, monitoring the same individuals of a closely related species before, during, and after a control burn provides direct evidence (Stawski et al. 2016). In any case, it is virtually impossible that *A. flavipes* recolonised the study area from outside Warrumbungle National Park, as it is surrounded by cleared agricultural land and these small mammals do not travel large distances and rarely display between-site movements (Marchesan and Carthew 2008; Stawski et al. 2016).

*Antechinus flavipes* is deemed the most diurnal species of the genus *Antechinus* (Menkhorst and Knight 2001), and during winter, they can occasionally be seen foraging during the daytime, a behaviour consistent with the activity



**Fig. 6** Example of basking at the post-fire site displaying body temperature ( $T_b$ , dots), torpor threshold (dashed line), ambient temperature ( $T_a$ , solid line), and log temperature ( $T_{\text{log}}$ , dotted line) measured on 23 June 2013. The time the animal was basking in the log exposed to sun is indicated by the bracket

pattern displayed by individuals from the unburnt control site. In contrast, activity in the post-fire habitat was to a large extent restricted to the night, and while some individuals did move to basking sites, we very rarely recorded animals foraging during the day. This result is similar to a recent study conducted in a low severity burn site on *A. stuartii*, which substantially reduced daytime activity after the fire (Stawski et al. 2016). A shift to more nocturnal activity may have occurred in response to a perceived or real increased exposure to predators due to diminished ground cover following the fire. Certainly, foxes and their tracks were seen regularly at the post-fire study site and we also trapped many introduced mice (*Mus musculus*) (see electronic supplementary material), an irruptive species following fire or rain events that can attract predators to an area (Fox and McKay 1981; Letnic et al. 2005; McGregor et al. 2014). The combined population increase of introduced mice and predators often coincides with a decrease in native species richness and abundance (Letnic et al. 2005; Letnic and Dickman 2006). Increased use of torpor, which permits a reduction in foraging, should have compensated for that effect to a degree, but a substantial decline in antechinus numbers was observed at the post-fire study site in the years following the study (see electronic supplementary material). Consequently, either reproduction in this semelparous species (antechinus can have only one litter per year) was not very successful following the fire and/or successive generations dispersed into adjacent areas with now dense understory due to the recovering vegetation.

We found that torpor was much more frequent, and maximum torpor bout duration was longer in the post-fire site than that recorded in the control site, in the laboratory and also from a previous winter field study (Geiser 1988; Rojas et al. 2014). These results are similar to that found in their congener, *A. stuartii*, which also increased torpor use after a prescribed fire (Stawski et al. 2016). In addition, the correlation of torpor use with  $T_{a\text{ min}}$  demonstrates that, like many heterothermic species (Ruf and Geiser 2015), *A. flavipes* use energy-conserving torpor especially at low  $T_a$  (Rojas et al. 2014; Stawski and Rojas 2016). Torpor is often more common at low  $T_a$ , because heat loss is proportional to the  $T_b - T_a$  differential; therefore, a reduction in  $T_b$  at low  $T_a$  in thermoregulating torpid animals reduces heat loss and the associated costs of thermoregulation (Ruf and Geiser 2015).

Interestingly, although torpor use in *A. flavipes* increased with decreasing  $T_a$ , torpor was predominantly used during the warmest part of the day in both the post-fire and control sites. At first glance, this timing of torpor in *A. flavipes* is rather unusual for dasyurids which usually enter torpor in the second half of the night or in the early morning (Körtner et al. 2010). However, most of these were studied in a desert environment that, because of lack of ground and

cloud cover, is characterised by extreme daily fluctuations in  $T_a$ , with a rapid fall in  $T_a$  constricting night-time activity and a rapid rise of  $T_a$  in the morning truncating torpor by around midday. In contrast, antechinus inhabit mesic environments with rather moderate daily  $T_a$  cycles and, besides the shift in torpor timing in comparison to desert dasyurids, have a higher threshold  $T_b$  for thermoregulation in torpor that matches the warmer daytime  $T_a$ s. However, a post-fire environment, at least after a severe fire that burns the canopy of trees, somewhat resembles deserts because of the unimpeded sun exposure on clear days.

Accordingly, some *A. flavipes* basked in sun-exposed hollow charred logs during the daytime with  $T_{\text{log}}$  elevated by the lack of canopy, the small diameter of the logs, and the blackened surface. These observations are restricted to only two males, perhaps, because small diameter hollow logs were rare after the fire. So far, basking during torpor and especially rewarming have been observed predominantly in desert dasyurids, which have predictable access to sun (Geiser et al. 2002; Warnecke et al. 2008) and also elephant shrews from grass and shrub lands of southern Africa (Thompson et al. 2015). In the laboratory, basking under a heat lamp can substantially reduce energy costs of rewarming from torpor (by up to 85 %), which without access to radiant heat or increasing  $T_a$ , and can be extremely expensive and compromise energy savings achieved by torpor (Geiser and Drury 2003). In our study, in which the animals entered torpor in a warm log, the reduction of  $T_b$  while in the log reduced the  $T_b - T_a$  differential to about 6 °C, which should decrease MR by approximately half in comparison to normothermic resting animals at a  $T_a$  of 15 °C outside the basking log (Geiser 1988). Even in normothermic animals, basking can reduce the MR of the animal to near basal levels resulting in large energy savings (Currie et al. 2015; Geiser et al. 2016).

We present data on patterns of torpor use, basking, and activity in *A. flavipes* in an environment following a severe wildfire. Torpor use is clearly related to ambient temperature conditions, but when these are accounted for torpor occurred at a higher frequency at the severely burnt site than in the control habitat. We expect that the resource-restricted post-fire environment played a role in basking and the observed torpor differences. Scat analyses revealed that the majority of the diet of the antechinus in this post-fire habitat consisted of ants, which were the only terrestrial insects observed in large numbers. The previous dietary studies have revealed that beetles and spiders generally constitute the largest proportion of an antechinus diet with very small amounts of ants (Hall 1980; Fox and Archer 1984; Green 1989; Lunney et al. 2001), suggesting that the antechinus in our study were, indeed, energetically constrained. However, while the present results provide a strong indication for a positive link between wildfire and

torpor expression, to establish a causal relationship, further work is required. Interestingly, the opposite response to the same wildfire at Warrumbungle National Park was recorded in volant bats, such that bats expressed less torpor after the wildfire in comparison to 2 years later, likely due to the increase in flying insects and open foraging spaces after the fire (Doty et al. 2016). These differing results suggest that studies on more species are required to determine the functional role of mammalian torpor and the interrelations between torpor and activity following severe wildfires.

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