Stawski, C, Körtner, G, Nowack, J and Geiser, F

Phenotypic plasticity of post-fire activity and thermal biology of a free-ranging small mammal

http://researchonline.ljmu.ac.uk/id/eprint/10391/

Article

Citation (please note it is advisable to refer to the publisher's version if you intend to cite from this work)

Stawski, C, Körtner, G, Nowack, J and Geiser, F (2016) Phenotypic plasticity of post-fire activity and thermal biology of a free-ranging small mammal. Physiology & Behavior, 159. pp. 104-111. ISSN 0031-9384

Phenotypic plasticity of post-fire activity and thermal biology of a small mammal

Clare Stawski*, Gerhard Körtner, Julia Nowack and Fritz Geiser

Centre for Behavioural and Physiological Ecology, Zoology, University of New England,
Armidale, 2351, NSW, Australia

***Corresponding author:** Clare Stawski, Zoology, University of New England, Armidale, 2351, NSW, Australia. Email: clare.stawski@gmail.com. Phone: +61 2 67733756.

Abstract

Ecosystems can change rapidly and sometimes irreversibly due to a number of anthropogenic and natural factors, such as deforestation and fire. How individual animals exposed to such changes respond behaviourally and physiologically is poorly understood. We quantified the phenotypic plasticity of activity patterns and torpor use—a highly efficient energy conservation mechanism—in brown antechinus (*Antechinus stuartii*), a small Australian marsupial mammal. We compared groups in densely vegetated forest areas (pre-fire and control) with a group in a burned open habitat (post-fire). Activity and torpor patterns differed among groups and sexes. Females in the post-fire group spent significantly less time active than the other groups, both during the day and night. However, in males only daytime activity declined in the post-fire group, although overall activity was also reduced on cold days in males for all groups. The reduction in total or diurnal activity in the post-fire group was made energetically possible by a ~3.4-fold and ~2.2-fold increase in the proportion of time females and males, respectively, used torpor in comparison to that in the pre-fire and control groups. Overall, likely due to reproductive needs, torpor was more pronounced in females than in males, but low ambient temperatures increased torpor bout duration in both sexes. Importantly, for both male and female antechinus and likely other small mammals, predator avoidance and energy conservation—achieved by reduced activity and increased torpor use—appear to be vital for post-fire survival where ground cover and refuges have been obliterated.

Keywords: behaviour, climate change, habitat degradation, marsupial, predation, physiology

1. Introduction

Anthropogenic environmental changes, such as habitat degradation and an increase in the variability of weather patterns, are having irreversible impacts on many ecosystems around the world. Often these changes are intertwined as, for example, land clearing destroys post-fire refuges, replaces forests with more fire-prone vegetation and also increases ambient temperature (T_a) and therefore fire frequency (McKenzie et al. 2004; Alencar et al. 2015). The ensuing fires then further contribute to deforestation, placing even more pressure on ecosystems. The global increase in fires (Stephens et al. 2013) and habitat fragmentation (Johnstone et al. 2012) are inflicting historically unprecedented levels of stress on individual animals, threatening the survival of populations and species.

Small terrestrial mammals are generally not able to flee from a fire, but they have been shown to survive *in situ* (Quinn 1979; Banks et al. 2011; Stawski et al. 2015*a*). Fire-proof refugia, such as deep burrows and rock crevices, are vital to the persistence of small terrestrial mammals not only during, but also after a fire when the absence of ground cover increases predation pressure (Banks et al. 2011; Diffendorfer et al. 2012; Robinson et al. 2013; Stawski et al. 2015*a*). Therefore, small mammal populations often do not require recolonisation after a fire, provided the remaining individuals are able to survive in a habitat that is usually depleted of food, water, vegetative cover and refuges (Friend 1993; Banks et al. 2011; Zwolak et al. 2012; Stawski et al. 2015*a*; VanTassel et al. 2015). Indeed, many individuals that survive a fire are often subsequently killed by predators or starve to death (Sutherland & Dickman 1999; McGregor et al. 2014). The behavioural and physiological responses of individuals to fire-modified habitat and the subsequent reduction in vegetative cover will determine whether or not a population can persist and an enhanced phenotypic plasticity in any of these traits would be of great advantage (Nussey et al. 2007; Canale & Henry 2010).

Unfortunately, our understanding of how small mammals deal with post-fire challenges is limited. Some recent evidence suggests that heterothermic mammals, with fluctuating body temperatures (T_b) and adjustable energy expenditures, may have an adaptive advantage over homeothermic mammals that maintain a stable and high T_b and have continuously high energy requirements (Banks et al. 2011; Stawski et al. 2015*a*). Heterothermic endotherms can save large amounts of energy and water by employing torpor, a controlled reduction of T_b and metabolic rate (Ruf & Geiser 2015). While mobility is generally reduced in torpor, in the context of fire, torpid animals are able to respond to smoke, an early warning cue to an approaching fire front, by arousing from torpor to find or remain in a suitable refuge (Stawski et al. 2015*b*).

Behavioural and physiological responses of individuals to changes in their environment vary among species, which can greatly influence survival. Specifically, heterothermy has been posited to have enabled small mammals to survive the meteorite impact that decimated dinosaurs and also the current high levels of mammalian extinctions in Australia (Geiser and Turbill 2009; Lovegrove et al. 2014). Therefore, the physiological flexibility afforded to heterotherms is likely advantageous in a rapidly changing environment (Canale & Henry 2010). These responses can also differ within a species and can be highly variable among different populations, individuals or even within an individual under different conditions (Nussey et al. 2007; Canale & Henry 2010; McKechnie & Mzilikazi 2011). For example, the duration and depth of torpor bouts as well as activity patterns have been observed to be different between sexes in a number of heterothermic mammals (Geiser 1988; Körtner et al. 2010; Sheriff et al. 2013; Rojas et al. 2014). Some of these differences can be attributed to sexual dimorphism in body size and/or reproductive effort, which is energetically costly in both sexes. Males often have to invest more time in searching for a mate whereas females spend more energy on pregnancy and raising young (Körtner et al. 2010). Whether or not the sexes have varying adaptations in response to environmental catastrophes, such as fires, is largely unknown.

To reveal the key adaptations used by small mammals to survive a controlled fire we studied the brown antechinus (*Antechinus stuartii*), a small dasyurid marsupial mammal that occurs in south-eastern Australia, forages terrestrially and arboreally and also use nests in a variety of locations such as tree hollows, rock crevices and logs (Wood 1970; Crowther & Braithwaite 2013). Brown antechinus have an unusual life history; after a short two week mating period during the austral late winter (August-early September) all of the males die whereas most females survive until after the young have been weaned in summer and some will live for a second breeding season (Woolley 1966; Wood 1970; McAllan et al. 2006). Brown antechinus can use daily torpor throughout most of the year, often in response to unfavourable environmental conditions (Rojas et al. 2014; Stawski et al. 2015*a*). As brown antechinus typically consume insects (Crowther & Braithwaite 2013) their food source is likely to become limited with cold ambient conditions and also after a fire (Coleman and Rieske 2006; Stawski 2012; VanTassel et al. 2015), times when torpor expression would be beneficial. Because of the unique life history of this species, we aimed to determine whether and how male and female brown antechinus differ behaviourally and physiologically in dealing with the thermal and energetic challenges in a post-fire environment. We hypothesised that both sexes would show phenotypic plasticity and increase torpor use and decrease activity in response to a prescribed burn to save energy and ameliorate predation pressure to increase their chance of survival. However, we also expected that females would express more torpor than males as is typical in this species (Geiser 1988; Rojas et al. 2014).

2. Material and methods

Permits to conduct this study were issued by the University of New England Animal Ethics Committee (AEC13-088) and the New South Wales National Parks and Wildlife Service (SL100791).

2.1. Study site

This study was undertaken during April-May 2014 (austral autumn), ~3 months before the breeding season, at Guy Fawkes River National Park (30°04'58.6"S, 152°20'0.9"E) in Australia. A hazard-reduction burn was performed by New South Wales National Parks and Wildlife Service (NSW NPWS) on 8-9 May 2014. The affected area (our prescribed fire site) was 379 hectares and was bordered by an escarpment and dirt roads. Our control site was situated in the unburned forest beyond these roads. Three treatment regimes were investigated in the study: (i) pre-fire group: prescribed area before the fire, (ii) post-fire group: prescribed area after the fire and (iii) control group: control area after the fire. As we were only given two weeks' notice prior to the prescribed fire we only had time to capture and undertake surgeries on a limited number of individuals from the treatment site only. The amount of time for data collection in the pre-fire group was obviously also limited.

Throughout the study period T_a was measured at 10min intervals at both the prescribed fire site and the control site using temperature data loggers (± 0.5°C, iButton thermochron DS1921G, Maxim Integrated Products, Inc., Sunnyvale, California, USA). These loggers were suspended in trees ~1m off the ground and placed in inverted Styrofoam cups to prevent direct sun exposure.

2.2. Study protocol

Brown antechinus were captured using aluminium box traps (Elliott Scientific Equipment, Upwey, Australia) baited with oats, peanut butter and honey. Bedding material was provided to prevent hypothermia in animals confined to traps overnight. Before the prescribed fire four male and four female antechinus were trapped in the prescribed fire site and immediately following the fire another four male and two female antechinus were captured in the control site. As one male and two females in the pre-fire group perished before/during the fire, we captured an additional two females just prior to the fire, which were included in the post-fire group only. Mean body mass of males was 27.7 ± 2.3 g (n = 8) and of females was 25.6 ± 4.2

g (*n* = 8). Individuals were implanted intraperitoneally with temperature-sensitive radio-transmitters that had individual frequencies (1.8 to 2.1 g, Sirtrack, Havelock North, New Zealand). Before implantation, transmitters were coated in inert wax (Paraffin/Elvax, Mini Mitter, Respironics Inc. OR, USA) and then calibrated in a water bath over a temperature range of 10 to 45°C to the nearest 0.1°C. All antechinus were weighed using an electronic balance to the nearest 0.1 g and a transmitter <10% of body mass was chosen for each individual (Rojas et al. 2010). For details on the surgical procedure see Stawski et al. (2015*b*).

Field data were collected from four male brown antechinus in the pre-fire group, three males in the post-fire group and four males in the control group (Table 1). For the females, field data were collected from four females in the pre-fire group, four females in the post-fire group and two females in the control group (Table 1). Some of the collected data from the female brown antechinus have been published previously (Stawski et al. 2015*a*), but these are not included here and in the current study we present new physiological and behavioural data with an emphasis on phenotypic plasticity and comparing differences between sexes.

Each individual was radio-tracked daily to its nest except for four days during and after the fire as the study site was inaccessible. Coordinates of every nest site were recorded with a GPS. Once an individual was found a remote receiver/data logger and an antenna were placed in range of the transmitter signal (Körtner & Geiser 2000). Each logger was programmed to record the pulse rate of the transmitter once every 10min, which was then converted into T_b using the calibration equations for each individual transmitter. Whenever animals moved nests the loggers were transferred to the new location to ensure they were in range of the transmitter signal.

Four remote cameras (HC600 Hyperfire, Reconyx, Inc., Wisconsin, USA) were placed along the road bordering the prescribed fire site closest to the nests of the study antechinus, recording the presence of predators (i.e. foxes, feral cats and wild dogs) along the road for three days before the fire and for eight days after the fire.

2.3. Torpor and activity definitions

The torpor onset T_b value of antechinus in the current study was calculated as 31.5°C from equation 4 by Willis (2007). For antechinus this formula is particularly important as it provides a threshold estimate that detects shallow torpor bouts. Therefore, a T_b of 31.5°C was used to calculate torpor bout entries and arousals for those that lasted longer than 30min. The proportion of day spent torpid was calculated as the amount of time (min/per day, sunrise-sunrise) each individual spent below the torpor onset T_b, but only for days when individuals did not change nests (i.e. the logger recorded the complete rest phase of an animal). Additionally, the depth of torpor bouts was measured as the absolute minimum T_b of each bout.

Activity periods were calculated from the time the individual's transmitter signal was absent on the logger to the time the signal returned for periods of longer than 30min. These were calculated for three time frames: (i) whole day = 24 h from sunrise-sunrise, (ii) daytime = sunrise-sunset, (iii) night time = sunset-sunrise. Days when an individual changed nests and the logger did not record the end of the activity phase were excluded.

Figures 1 (males) and 2 (females) provide example traces of recorded T_b and T_a over three days of the study period for an individual from each of the groups.

2.4. Data analysis

Statistical tests were undertaken in R (R v. 3.0.1, R Core Team, 2014) and StatistiXL (v 1.10, 2015). Means for each measured variable were first calculated for each individual and then an overall mean was derived from these individual means and are represented with ± 1 standard deviation (SD); n = the number of individuals, N = the number of observations. A significance level (p) of <0.05 was assumed. An analysis of variance (ANOVA; function 'aov') was undertaken to establish if T_a variables differed among the three sites. Linear mixed-effects models (package 'nlme') were fitted to test for differences among the treatment groups (pre-fire, post-fire and control) for the measured variables (activity, torpor bout duration, proportion of day spent torpid, minimum torpor T_b), with sex and daily minimum T_a as covariates, treatment:sex as an interaction term and individuals were included as a random factor. As a significant interaction was found between treatment and sex for all the measured variables ($p < 0.0001$) we performed separate analyses for males and females for each variable using the model stated above, but removing sex and the interaction term. For all models body mass was initially included, however, there was no significant effect of body mass on any of the variables so it was removed. Percentages for the proportion of day spent torpid were arcsine transformed for analyses. Further, a residual plot to test for homoscedasticity and a normal Q-Q plot to test for normal distribution were used for all models. If there was a significant difference among the groups a post-hoc Tukey test (package 'multcomp') was performed to determine which groups were significantly different from each other. An analysis of covariance (ANCOVA; function 'aov') was performed separately for each of the groups to determine if any of the measured variables varied between the sexes, with daily minimum T_a as a covariate and individuals as a random factor. Least square linear regressions (activity and torpor bout duration against daily minimum T_a;

function ‘Linear Regression’) for each of the treatment groups were compared using an ANOVA (function ‘Compare Linear Regressions’), separately for males and females. Data were pooled and regressed together if no significant differences were found in the slope and intercept among the treatment groups. As T_a was lower and more variable before the fire than after (Fig. 3), a significant relationship between torpor bout duration and daily minimum T_a could be established in the pre-fire group in both sexes. However, the narrower T_a range after the fire precluded a comparable analysis and therefore daily minimum T_a was included as a covariate when comparing torpor bout durations among all treatment groups as stated above.

3. Results

3.1. Habitat variables and predator numbers

Significant differences among the sites were found for mean ($p = 0.002, f_{2,31} = 8.0$), maximum ($p = 0.006, f_{2,31} = 6.1$) and minimum ($p = 0.008, f_{2,31} = 5.7$) daily T_a (Fig. 3). However, for the post-fire and control animals that were measured at the same time in adjacent areas, all T_a variables were statistically indistinguishable between the two sites (mean = 11.1 ± 1.2°C, $n = 15$; maximum = 16.5 ± 1.7°C, $n = 15$; minimum = 7.4 ± 1.4°C, $n = 15$; Fig. 3). Conversely, the pre-fire group was measured before the burn when mean (8.3 ± 2.8°C, $n = 8$), maximum (13.5 ± 2.6°C, $n = 8$) and minimum (4.8 ± 2.8°C, $n = 8$) daily T_a were all on average ~3°C lower (Fig. 3). Similar significant differences in mean (day: $p = 0.0004, f_{2,31} = 10.0$; night: $p = 0.004, f_{2,30} = 6.7$), maximum (day: $p = 0.006, f_{2,31} = 6.0$; night: $p = 0.005, f_{2,30} = 6.2$) and minimum (day: $p = 0.04, f_{2,31} = 3.2$; night: $p = 0.006, f_{2,30} = 6.1$) daytime and night-time T_a were found between the pre-fire site (mean day = 10.2 ± 2.6°C, $n = 8$; mean night = 6.4 ± 3.1°C, $n = 7$; maximum day = 13.5 ± 2.6°C, $n = 8$; maximum night = 9.1 ± 3.1°C, $n = 7$; minimum day = 5.4 ± 3.1°C, $n = 8$, minimum night = 4.6 ± 2.9°C, $n = 7$) and the other two sites (mean day = 13.6 ± 1.4°C, $n = 15$; mean night = 9.3 ± 1.4°C, $n = 15$; maximum day = 16.5 ± 1.7°C, $n = 15$; maximum night = 11.8 ± 1.4°C, $n = 15$; minimum day = 8.0 ± 1.9°C, $n = 15$, minimum night = 7.6 ± 1.8°C, $n = 15$).

Ground cover in the prescribed area before the fire and also the control area consisted of herbs, grass, *Lomandra* (a monocod with grass-like appearance), shrubs and also fallen timber. Especially along drainage lines, grasses and *Lomandra* formed dense mats totally obscuring the ground and any small animals underneath. After the fire about 70% of the ground cover was obliterated (NSW NPWS, personal communication) leaving only bare ground, but the mid- and upper-layers of the forest remained intact.

No mammalian predators were recorded by the trail cameras along the border of the prescribed area before the fire. During the first week after the fire three feral cats, two wild dogs and one fox were recorded, suggesting an influx of predators after the burn. Nevertheless, before the fire one male and one female antechinus from the pre-fire group were killed by a predator, most likely by a cat. However, after the fire no predation events were recorded in either the post-fire or control groups. Further, only one of the tagged individuals perished as a direct result of the fire.

3.2. Activity

Importantly, none of the individuals tracked in the burn site left the area after the fire. Antechinus were active on average between 6 and 13 hours per day, with about a third of the activity occurring during the daytime and the remainder at night for individuals in the pre-fire and control groups (Fig. 4a,b). Radio-tracking revealed that when active during daytime hours animals regularly foraged in patches of matted grass and *Lomandra* where they could not be seen. Interestingly, the amount of time male antechinus spent active significantly increased at higher T_a ($p = 0.005$, $R^2 = 0.2$, $f_{1,72} = 8.4$, $y = 0.5x + 3.2$), whereas there was no significant relationship for females ($p = 0.585$, $R^2 = 0.01$, $f_{1,74} = 0.3$). Consequently, when T_a was lower in the pre-fire group females were active significantly longer over the whole day in comparison to males ($p = 0.003$, $f_{1,25} = 10.7$), whereas when T_a was warmer in the control group males were active significantly longer than females ($p = 0.019$, $f_{1,33} = 6.0$; Fig. 4a,b).

Both males and females in the post-fire group significantly reduced daytime activity, which did not differ between the sexes ($p = 0.851$, $f_{1,73} = 0.04$; Fig. 4a,b). However, while females in the post-fire group also reduced nocturnal activity, males in this group did not and therefore were active longer than females ($p = 0.0002$, $f_{1,69} = 15.2$; Fig. 4a,b).

For male antechinus the time spent active during the whole day differed significantly among the groups ($p < 0.0001$, $t_{6,63} = 17.3$; Fig. 4a) and activity duration was ~1.7-fold longer for animals at the control (12.6 ± 3.5 h, $n = 4$, $N = 28$) site than individuals in both the pre- (7.9 ± 2.4 h, $n = 4$, $N = 14$) and post-fire (7.6 ± 0.6 h, $n = 3$, $N = 31$) sites. Importantly, at the fire site whole day activity did not change between before and after the fire. However, the partitioning between daytime and night time activity shifted after the fire. While males in the pre-fire (2.7 ± 2.2 h, $n = 4$, $N = 14$) and control (4.7 ± 1.5 h, $n = 4$, $N = 28$) groups spent about one third of their total activity during the day, in the post-fire (0.4 ± 0.5 h, $n = 3$, $N = 31$) group this was reduced to 5.3% (Fig. 4a).

In females, whole day activity also differed significantly among the three groups ($p < 0.0001$, $t_{6,67} = 6.4$; Fig. 4b), but they decreased total activity time by 60% after the fire in the post-fire (6.8 ± 3.1 h, $n = 4$, $N = 45$) group in comparison to both the pre-fire (11.6 ± 1.1 h, $n = 4$, $N = 16$) and control (10.3 ± 1.8 h, $n = 2$, $N = 14$) groups. This reduced level of activity encompassed both daytime and night time activity, but daytime activity more so. While pre-fire (3.3 ± 0.4 h, $n = 4$, $N = 16$) and control (2.4 ± 0.7 h, $n = 2$, $N = 14$) animals spent on average 28.2% and 23.4% of the total activity time during the day, respectively, diurnal activity was reduced to 4.4% in post-fire (0.3 ± 0.3 h, $n = 4$, $N = 45$) animals (Fig. 4b).

3.3. Torpor

After the fire, antechinus in the post-fire group expressed longer torpor bouts in comparison to the pre-fire and control groups (Fig. 5a,b). However, in all groups females were torpid longer than males (pre-fire: $p < 0.0001, f_{1,16} = 173.1$; post-fire: $p < 0.0001, f_{1,67} = 495.4$; control: $p < 0.0001, f_{1,21} = 145.5$) and torpor bouts were generally shallower in males than in females (pre-fire: $p = 0.039, f_{1,18} = 4.9$; post-fire: $p < 0.0001, f_{1,64} = 67.4$; control: $p = 0.154$, $f_{1,26} = 2.2$; Fig. 6a,b). Furthermore, in both males ($p = 0.037$, $R^2 = 0.4, f_{1,8} = 5.3$, $y = -15.5x + 159.7$) and females ($p = 0.011$, $R^2 = 0.5, f_{1,12} = 9.3$, $y = -29.4x + 285.0$) torpor bout duration in the pre-fire group increased as daily minimum T_a decreased.

Over the study period for males the proportion of day spent torpid ($p < 0.0001$, $t_{6,88} = 5.2$; Fig. 5a) as well as mean torpor bout duration ($p < 0.0001$, $t_{6,88} = 5.2$) differed significantly among the groups. Males from the post-fire group were torpid ~2.2-fold more each day in comparison to both of the other groups and torpor bouts were also ~1.5-fold longer in the post-fire group (127.3 ± 38.4 min, $n = 3$, $N = 26$), in comparison to torpor bouts expressed by males from both the pre-fire (84.6 ± 37.1 min, $n = 4$, $N = 11$) and control (84.3 ± 26.8 min, $n = 4$, $N = 20$) groups. However, the depth of torpor bouts was the same for all groups ($p = 0.228$, $t_{6,41} = 1.2$; pre-fire = 31.0 ± 0.2°C, $n = 4$, $N = 8$; post-fire = 30.8 ± 0.3°C, $n = 3$, $N = 22$; control = 30.4 ± 0.6°C, $n = 4$, $N = 21$; Fig. 6).

Similarly to the males, for females the proportion of day spent torpid differed significantly among the groups ($p < 0.0001$, $t_{6,89} = 7.0$; Fig. 5b) and females from the post-burn group were torpid ~3.4-fold more each day in comparison to both of the other groups. Mean torpor bout duration of all bouts recorded for female antechinus also differed among the groups ($p < 0.0001$, $t_{6,89} = 6.9$) and torpor bouts were ~2.5-fold longer in the post-fire (267.5 ± 61.9 min, $n = 4$, $N = 57$) group in comparison to torpor bouts expressed by females from both the pre-fire (118.0 ± 76.1 min, $n = 4$, $N = 15$) and control (94.2 ± 83.7 min, $n = 2$, $N = 8$) groups. Importantly, mean minimum torpor T_b of female antechinus was 4°C lower in the post-fire (26.0 ± 1.3°C, $n = 4$, $N = 44$) group in comparison to both the pre-fire (29.7 ± 1.7°C, $n = 4$, $N = 14$) and control (30.2 ± 1.3°C, $n = 2$, $N = 21$) groups ($p < 0.0001$, $t_{6,55} = 45.3$; Fig. 6).

4. Discussion

The results of our study support our hypothesis and reveal that individual male and female brown antechinus responded behaviourally and physiologically to fire and the removal of ground cover. Antechinus reduced diurnal activity and increased torpor use to save energy and likely to avoid predation by foxes, wild dogs and feral cats. This flexibility in behavioural and physiological traits suggests that brown antechinus, and presumably other small heterothermic mammals, are able to adapt readily to sudden environmental changes and therefore enables them to survive catastrophic events. Indeed, phenotypic plasticity has been previously proposed to play an important role in vertebrate resilience in the light of climate change and habitat degradation (Nussey et al. 2007; Canale & Henry 2010).

Although the fire did not significantly change climate conditions in comparison to the control area and therefore thermoregulatory demands, the obliteration of ground cover increased visibility and thus exposure to predators. It is therefore not surprising that fire changed the activity patterns of brown antechinus in the post-fire group and both sexes reduced daytime activity to as little as 5% pre-fire levels. Brown antechinus, like most small mammals, have been considered to be strictly nocturnal in the past (Woolley 1966; Körtner & Geiser 1995). However, from a thermoregulatory point of view activity during the daytime has energetic advantages especially in a cold climate, as the warmer temperatures and solar radiation from the sun reduces the amount of energy needed for thermoregulation while foraging (Scholander et al. 1950). Accordingly, our study clearly shows that male and female antechinus were active for 23 to 37%, respectively, during the daytime when ground cover was available in the pre-fire and control groups. Daytime activity in other small dasyurids has been reported, but usually occurs in species that inhabit complexly structured habitats with shelters from visually hunting predators (Pavey & Geiser 2008). The kaluta (*Dasykaluta rosamondae*), for example, is currently the only known small dasyurid that is strictly diurnal in winter (Körtner et al. 2010) and it occurs in areas densely covered with spinifex, a spikey grass that not only offers a visual but also a physical shield against most predators. Apparently, the presence of abundant ground cover is also important for brown antechinus (Crowther & Braithwaite 2013), as they are often only found in habitats with low burn frequencies (Mowat et al. 2015). Our data suggest that this dense cover can be especially important during winter when shifting the activity period into the daytime can reduce thermoregulatory costs. However, since predator avoidance becomes crucial in a burnt landscape with limited protection, daytime activity would be risky and the observed reduction in daytime activity seen in the post-fire group would account for this.

Whereas females reduced overall activity, males in the post-fire group shifted their activity into the night and in comparison to pre-fire conditions males in both the post-fire and control groups maintained a high level of night-time activity. This was likely facilitated by the warmer T_a, as activity in males increased with T_a which was possibly a response to higher food availability as they primarily feed on insects that often become more prevalent at warmer temperatures (Stawski 2012). The overall higher levels of activity seen in males in the current study may be related to pre-mating season preparation to establish home ranges and indeed an increase in movements by male brown antechinus have been recorded as early as May (Wood 1970), which corresponds to the timeframe of the current study. However, while a shift towards nocturnal activity somewhat reduces predation risk in comparison to diurnal activity, physical protection at night is still limited after fire. Therefore, an overall reduction of both daytime and night time activity as observed in female antechinus appears to be a prudent strategy since animals resting in a secure location are less exposed to predation than when active (Turbill et al. 2011). Further, the major food resource of antechinus, insects, is often significantly reduced after a fire (Coleman and Rieske 2006; VanTassel et al. 2015), suggesting that increasing energy savings is paramount. Importantly, this can only be achieved if daily energy demands can be lowered substantially, and in heterothermic endotherms an avenue for accomplishing this effectively is the use of torpor (Ruf & Geiser 2015).

Torpor not only reduces energy demands, it also enhances predator avoidance (Stawski & Geiser 2010; Turbill et al. 2011; Geiser & Brigham 2012; Vuarin & Henry 2014). This in turn appears to contribute to the lower extinction rates in heterothermic compared to homeothermic mammals (Geiser & Turbill 2009; Hanna & Cardillo 2014). While individual survival and longevity increase with the amount of time spent torpid (Turbill et al. 2011), the state of torpor cannot continue forever, but must be interrupted for activity and especially reproduction (Sheriff et al. 2013; Lovegrove et al. 2014). Although torpor and reproduction are not mutually exclusive, certain phases during the reproductive cycle are often incompatible with entering torpor (McAllan & Geiser 2014). For example, in many species the hibernation season is often shorter in males, as they need to emerge earlier from hibernation to commence spermatogenesis and to secure territories for the mating period (Barnes et al. 1986). Similarly, male antechinus show increased levels of activity and metabolism, continue to grow and generally enter torpor rarely throughout winter (June-July), when the size of testes is greatest (Woolley 1966; Geiser 1988; Rojas et al. 2014). The sexual differences for torpor use and activity patterns observed here are therefore not unexpected. The unusual reproductive strategy of male antechinus entails a high level of energy turnover that eventually culminates in complete male die-off (Woolley 1966; Wood 1970) and therefore the time leading up to reproduction likely influences the behavioural and physiological responses to a catastrophic event such as fire. Consequently, while female antechinus minimised energy expenditure as well as predator exposure by considerably increasing torpor use after the fire, males increased torpor use only marginally, confirming our prediction that females would express more torpor than males. Nevertheless, the strategies employed by both sexes were successful at least in the short to medium term, as no deaths were recorded in the weeks after the fire event. Obviously, flexibility in behavioural and physiological traits in individuals of both sexes is advantageous, as it allows a population to respond to sudden changes in environmental conditions and food supply (Nussey et al. 2007; Canale & Henry 2010; Stawski & Geiser 2012; Nowack et al. 2015).

Even though the present study involved only a low-intensity burn, a large proportion of the habitat was severely degraded. Fires leave a fragmented patchwork of more or less suitable habitats that at least temporarily results in a significant reduction in habitat size and food availability, leading to increased levels of stress and decreased health in antechinus (Dickman 1989; Johnstone et al. 2012). Fire regimes in Australia have been altered for millennia, with Aborigines regularly burning patches to maintain a variety of habitats for animals they could hunt (Bowman 1998). However, these fire regimes have been radically changed since European settlement with drastic impacts on ecosystems contributing to the exceptionally high rate of mammal extinctions in Australia's recent history (Woinarski et al. 2015). While the negative impacts of modified fire regimes have also occurred in other parts of the world (Stephens et al. 2013; Kelly et al. 2014; VanTassel et al. 2015), in Australia such changes were confounded by the introduction of new predators, namely feral cats and European red fox (Woinarski et al. 2015). Importantly, after a fire an influx of predators is common, as the removal of ground cover facilitates their hunting effort (Quinn 1979; McGregor et al. 2014). It is this outcome of fires that often results in more deaths and decline in small mammal populations than the fire itself (Quinn 1979).

Habitat structure is vitally important for the survival of animals during a fire and to their recovery after a fire, thus understanding the relationships between individuals and aspects of their environment is paramount (Friend 1993; Diffendorfer et al. 2012). Therefore, maintaining a mosaic of habitats through varying fire regimes and intensities also appears to be important to conserving biodiversity and, in particular, ensuring that some old vegetation remains intact to provide refuges, cover for foraging and food resources (Coleman and Rieske 2006; Robinson et al. 2013; Stephens et al. 2013; Kelly et al. 2014; Stawski et al. 2015*a*; VanTassel et al. 2015). Fortunately, in an undulating forested landscape characteristic for the east coast of Australia, even severe wildfires leave pockets of unburned vegetation often along wet gullies. These remnants constitute vital refuge areas for small mammal populations, as during previous research following a wildfire most agile (*A. agilis*) and dusky antechinus (*A. swainsonii*) were trapped along such drainage lines (Davies and Drew 2014). Interestingly, during our study radio-tagged antechinus were never observed to move into such refugia, even though the low intensity control burn left about 30% of the area untouched and further unburned habitat could be found in the control site just across a narrow forest trail. This could be a result of the unburnt areas already being occupied and defended, or a risk of venturing too far in the newly created open habitat and brown antechinus do generally show strong site fidelity (Wood 1970). Understanding the phenotypic plasticity of these mechanisms linking the fate of individuals with changes seen on a population level is vitally important for understanding fire ecology and to effectively manage fires in a conservation context.

Acknowledgments

For help with the logistics of the study and fieldwork we would like to thank A. Bondarenco, Anna Doty, Geoffrey James, Arne Müller, Margaret Stawski, Lihong Yuan and NSW NPWS staff. Funding for this research was granted to C.S. by a University of New England Postdoctoral Research Fellowship, to J.N. from the German Academic Exchange Service (DAAD) and the Schimper Stiftung für ökologische Forschung and to F.G. from the Australian Research Council (DP130101506).

References

Alencar AA, Brando PM, Asner GP, Putz FE. 2015. Landscape fragmentation, severe drought, and the new Amazon forest fire regime. Ecological Applications **25**:1493-1505.

Banks SC, Dujardin M, McBurney L, Blair D, Barker M, Lindenmayer DB. 2011. Starting points for small mammal population recovery after wildfire: recolonization or residual populations? Oikos **120**:26-37.

Barnes BM, Kretzmann M, Licht P, Zucker I. 1986. The influence of hibernation on testis growth and spermatogenesis in the golden-mantled ground squirrel, *Spermophilus lateralis*. Biology of Reproduction **35**:1289-1297.

Bowman DMJS. 1998. Tansley Review No. 101: The impact of Aboriginal landscape burning on the Australian biota. New Phytology **140**:385-410.

Canale CI, Henry P-Y. 2010. Adaptive phenotypic plasticity and resilience of vertebrates to increasing climatic unpredictability. Climate Research **43**:135-147.

Coleman TW, Rieske LK. 2006. Arthropod response to prescription burning at the soil-litter interface in oak-pine forests. Forest Ecology and Management **233**:52-60.

Crowther MS, Braithwaite RW. 2013. Brown Antechinus *Antechinus stuartii*. Page 51 in Van Dyck S, Gynther I, Baker A, editors. Field companion to the mammals of Australia. New Holland Publishers, Australia.

Davies MJ, Drew A. 2014. Monitoring of small mammal populations in the Brindabella Ranges after fire. Australian Mammalogy **36**:103-107.

Dickman CR. 1989. Demographic responses of *Antechinus stuartii* (Marsupialia) to supplementary food. Australian Journal of Ecology **14**:387-398.

Diffendorfer J, Fleming GM, Tremor S, Spencer W, Beyers JL. 2012. The role of fire severity, distance from fire perimeter and vegetation on post-fire recovery of small-mammal communities in chaparral. International Journal of Wildland Fire **21**:436-448.

Friend GR. 1993. Impact of fire on small vertebrates in mallee woodlands and heathlands of temperate Australia: a review. Biological Conservation **65**:99-114.

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, Brigham RM. 2012. The other functions of torpor. Pages 109-121 in Ruf T, Bieber C, Arnold W, Millesi E, editors. Living in a seasonal world. Springer-Verlag, Germany.

Geiser F, Turbill C. 2009. Hibernation and daily torpor minimize mammalian extinctions. Naturwissenschaften **96**:1235-1240.

Hanna E, Cardillo M. 2014. Clarifying the relationship between torpor and anthropogenic extinction risk in mammals. Journal of Zoology **293**:211-217.

Johnstone CP, Lill A, Reina RD. 2012. Does habitat fragmentation cause stress in agile antechinus? A haematological approach. Journal of Comparative Physiology B **182**:139-155.

Kelly LT, Bennett AF, Clarke MF, McCarthy MA. 2014. Optimal fire histories for biodiversity conservation. Conservation Biology **29**:473-481.

Körtner G, Geiser F. 1995. Body temperature rhythms and activity in reproductive *Antechinus* (Marsupialia). Physiology and Behavior **58**:31-36.

Körtner G, Geiser F. 2000. Torpor and activity patterns in free-ranging sugar gliders *Petaurus breviceps* (Marsupialia). Oecologia **123**:350-357.

Körtner G, Rojas AD, Geiser F. 2010. Thermal biology, torpor use and activity patterns of a small diurnal marsupial from a tropical desert: sexual differences. Journal of Comparative Physiology B **180**:869-876.

Lovegrove BG, Lobban KD, Levesque DL. 2014. Mammal survival at the Cretaceous-Palaeogene boundary: metabolic homeostasis in prolonged tropical hibernation in tenrecs. Proceedings of the Royal Society B **281**:20141304.

McAllan BM, Geiser F. 2014. Torpor during reproduction in mammals and birds: dealing with an energetic conundrum. Integrative and Comparative Biology **54**:516-532.

McAllan BM, Dickman CR, Crowther MS. 2006. Photoperiod as a reproductive cue in the marsupial genus *Antechinus*: ecological and evolutionary consequences. Biological Journal of the Linnean Society **87**:365-379.

McGregor HW, Legge S, Jones ME, Johnson CN. 2014. Landscape management of fire and grazing regimes alters the fine-scale habitat utilisation by feral cats. PLoS ONE **9**:e109097.

McKechnie AE, Mzilikazi N. 2011. Heterothermy in Afrotropical mammals and birds: a review. Integrative and Comparative Biology **51**:349-363.

McKenzie D, Gedalof Z, Peterson DL, Mote P. 2004. Climatic change, wildfire, and conservation. Conservation Biology **18**:890-902.

Mowat EJ, Webb JK, Crowther MS. 2015. Fire-mediated niche-separation between two sympatric small mammal species. Austral Ecology **40**:50-59.

Nowack J, Rojas AD, Körtner G, Geiser F. 2015. Snoozing through the storm: torpor use during a natural disaster. Scientific Reports **5**:11243.

Nussey DH, Wilson AJ, Brommer JE. 2007. The evolutionary ecology of individual phenotypic plasticity in wild populations. Journal of Evolutionary Biology **20**:831-844.

Pavey CR, Geiser F. 2008. Basking and diurnal foraging in the dasyurid marsupial *Pseudantechinus macdonnellensis*. Australian Journal of Zoology **56**:129-135.

Quinn RD. 1979. Effects of fire on small mammals in the chaparral. Cal-Neva Wildlife Transactions **1979**:125-133.

R Development Core Team. 2014. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Robinson NM, Leonard SWJ, Ritchie EG, Bassett M, Chia EK, Buckingham S, Gibb H, Bennett AF, Clarke MF. 2013. Refuges for fauna in fire-prone landscapes: their ecological function and importance. Journal of Applied Ecology **50**:1321-1329.

Rojas AD, Körtner G, Geiser F. 2010. Do implanted transmitters affect maximum running speed of two small marsupials? Journal of Mammalogy **91**:1360-1364.

Rojas AD, Körtner G, Geiser F. 2014. Torpor in free-ranging antechinus: does it increase fitness? Naturwissenschaften **101**:105-114.

Ruf T, Geiser F. 2015. Daily torpor and hibernation in birds and mammals. Biological Reviews **90**:891-926.

Scholander PF, Hock R, Walters V, Johnson F, Irving L. 1950. Heat regulation in some arctic and tropical mammals and birds. The Biological Bulletin **99:**237-258.

Sheriff MJ, Richter MM, Buck CL, Barnes BM. 2013. Changing seasonality and phenological responses of free-living male arctic ground squirrels: the importance of sex. Philosophical Transactions of the Royal Society B **368**:20120480.

Stawski C. 2012. Capture and care of northern long-eared bats (*Nyctophilus bifax)* and seasonal changes in insect abundance. Australian Mammalogy **34**:245-250.

Stawski C, Geiser F. 2010. Fat and fed: frequent use of torpor in a subtropical bat. Naturwissenschaften **97**:29-35.

Stawski C, Geiser F. 2012. Will temperature effects or phenotypic plasticity determine the thermal response of a heterothermic tropical bat to climate change? PLoS ONE **7**:e40278.

Stawski C, Körtner G, Nowack J, Geiser F. 2015*a*. The importance of mammalian torpor for survival in a post-fire landscape. Biology Letters **11**:20150134.

Stawski C, Matthews JK, Körtner G, Geiser F. 2015*b*. Physiological and behavioural responses of a small heterothermic mammal to fire stimuli. Physiology and Behavior **151**:617-622.

Stephens SL, Agee JK, Fulé PZ, North MP, Romme WH, Swetnam TW, Turner MG. 2013. Managing forests and fire in changing climates. Science **342**:41-42.

Sutherland EF, Dickman CR. 1999. Mechanisms of recovery after fire by rodents in the Australian environment: a review. Wildlife Research **26**:405-419.

Turbill C, Bieber C, Ruf T. 2011. Hibernation is associated with increased survival and the evolution of slow life histories among mammals. Proceedings of the Royal Society of London B **278**:3355-3363.

VanTassel HLH, Barrows CW, Anderson KE. 2015. Post-fire spatial heterogeneity alters ground-dwelling arthropod and small mammal community patterns in a desert landscape experiencing a novel disturbance regime. Biological Conservation **182**:117-125.

Vuarin P, Henry P-Y. 2014. Field evidence for a proximate role of food shortage in the regulation of hibernation and daily torpor: a review. Journal of Comparative Physiology B **184**:683-697.

Willis CKR. 2007. An energy-based body temperature threshold between torpor and normothermia for small mammals. Physiological and Biochemical Zoology **80**:643-651.

Woinarski JCZ, Burbidge AA, Harrison PL. 2015. Ongoing unravelling of a continental fauna: Decline and extinction of Australian mammals since European settlement. Proceedings of the National Academy of Sciences **112**:4531-4540.

Wood DF. 1970. An ecological study of *Antechinus stuartii* (Marsupialia) in a south-east Queensland rain forest. Australian Journal of Zoology **18**:185-207.

Woolley P. 1966. Reproduction in *Antechinus* spp. and other dasyurid marsupials. Symposia of the Zoological Society of London **15**:281-294.

Zwolak R, Pearson DE, Ortega YK, Crone EE. 2012. Mechanisms driving postfire abundance of a generalist mammal. Canadian Journal of Zoology **90**:51-60.

Table 1. The number of days data was recorded for each individual in all three groups: pre-fire, post-fire and control. Also shown are the total (*n* = the number of individuals) and mean number of days of data for each group.

	Pre-fire (Days recorded)		**Post-fire (Days recorded)**		**Control (Days recorded)**	
	Females	**Males**	**Females**	**Males**	**Females**	**Males**
	7	7	15	11	7	11
	6	7	15	11	10	9
	7	7	12	11		10
	5	6	14			7
Total	25 (4)	27 (4)	56 (4)	33 (3)	17 (3)	37 (4)
Mean	6.3 ± 0.9	6.8 ± 0.5	14.0 ± 1.4	11.0 ± 0.0	8.5 ± 2.1	9.3 ± 2.1

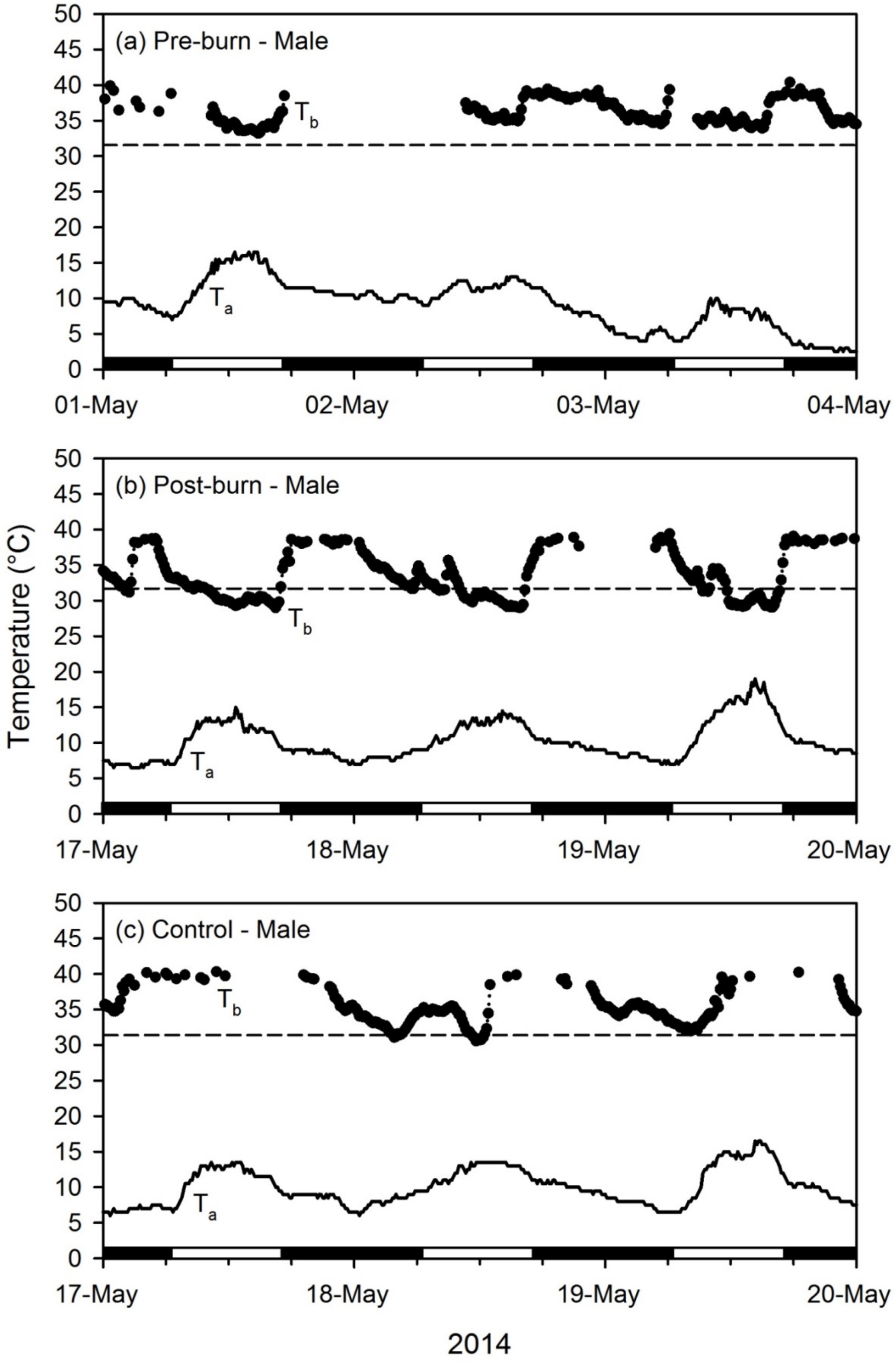

Fig. 1. Examples of T_b (dotted line) and T_a (solid line) data for male brown antechinus over a three day period during the study for an individual from the (a) pre-burn, (b) post-burn and (c) control groups. The dashed line represents the torpor onset T_b and times when T_b data are missing represent activity periods. The black and white bars along the bottom of the graphs represent night and day, respectively.

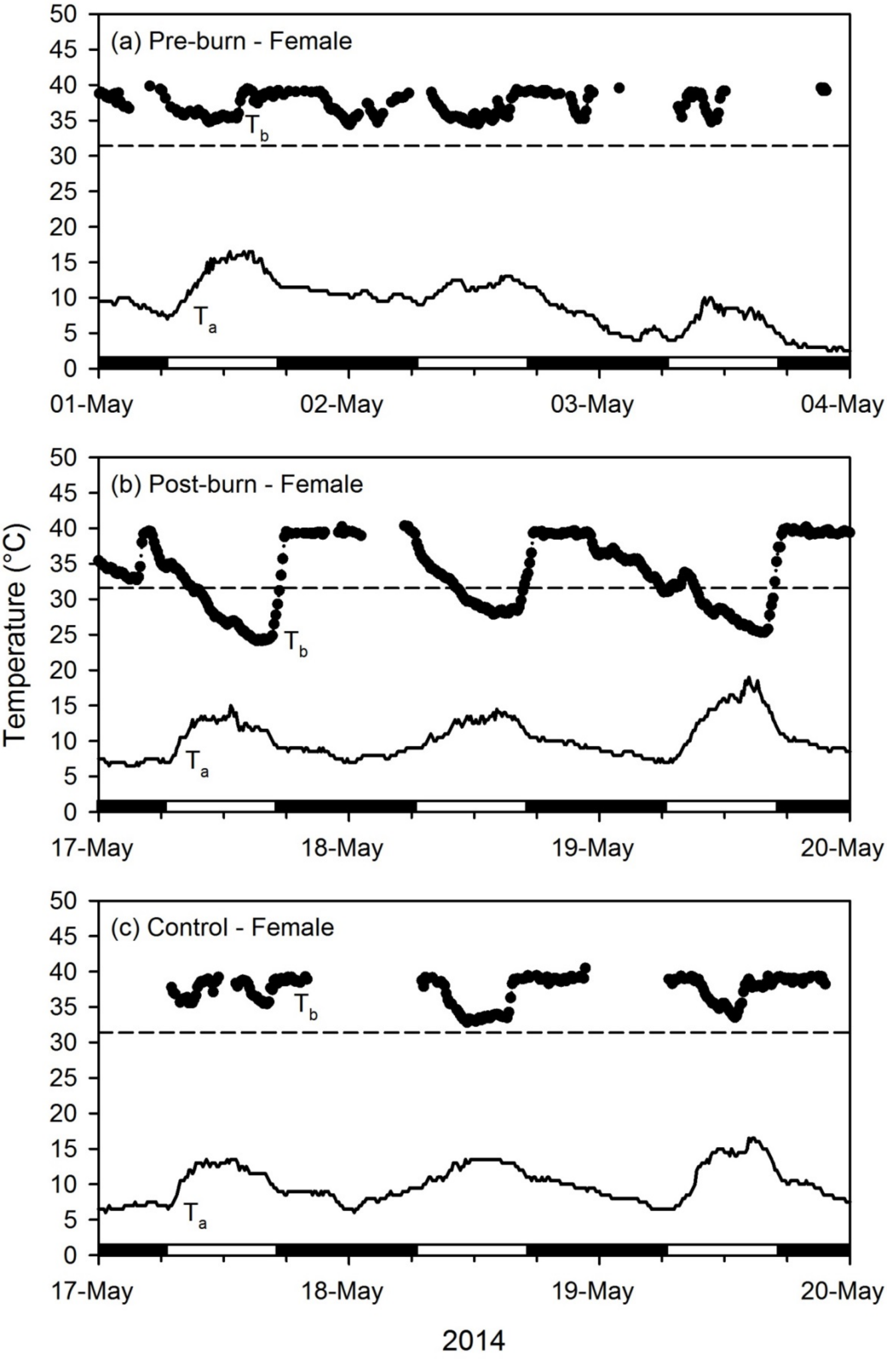

Fig. 2. Examples of T_b (dotted line) and T_a (solid line) data for female brown antechinus over a three day period during the study for an individual from the (a) pre-burn, (b) post-burn and (c) control groups. The dashed line represents the torpor onset T_b and times when T_b data are missing represent activity periods. The black and white bars along the bottom of the graphs represent night and day, respectively.

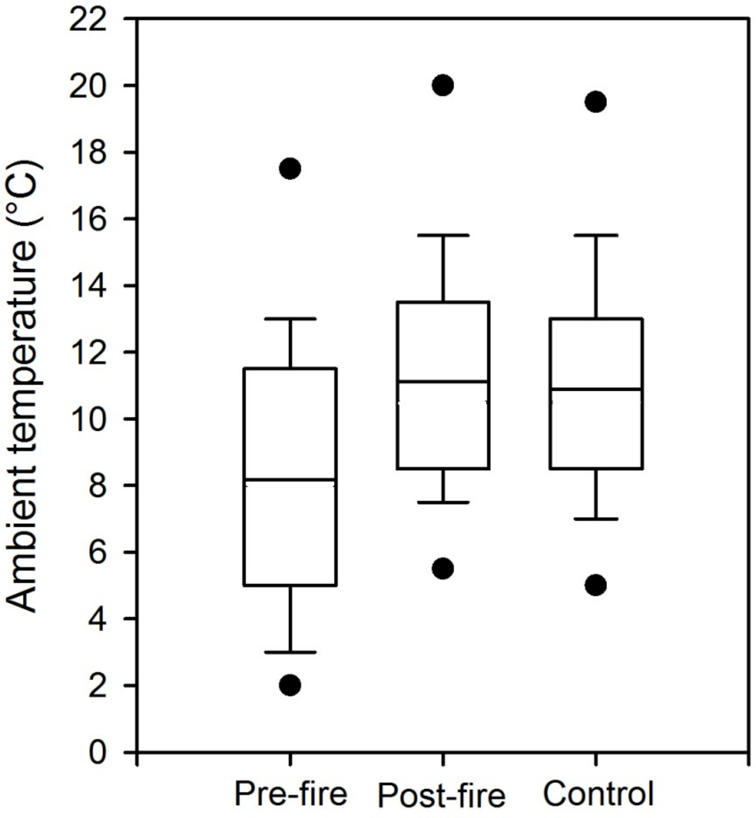

Fig. 3. All ambient temperatures (°C) recorded throughout the study period in each of the sites: the pre-fire site that was measured before the fire (*n* = 9 days) and the post-fire (*n* = 15 days) and control (*n* = 15 days) sites which were measured concurrently after the fire. The middle line in the boxes is the mean daily T_a, whereas the bottom of the box is the 25th percentile and the top is the 75th percentile. The lower error bar represents the 10th percentile and the upper error bar the 90th percentile. The lower and upper dots denote the absolute minimum and maximum T_a recorded in each of the sites, respectively.

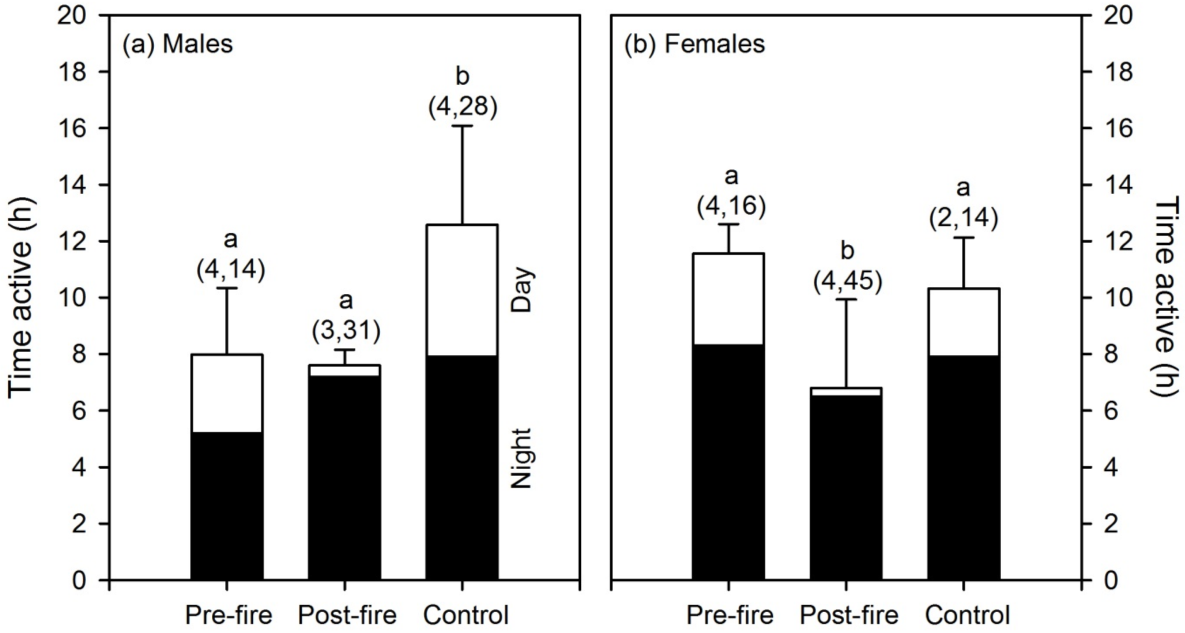

Fig. 4. The amount of time (h) male (a) and female (b) antechinus spent active throughout the whole day (24h, sunrise-sunrise) for the pre-fire, post-fire and control groups. Means for whole day activity are shown with ± 1 SD (*n* = the number of individuals, *N* = the number of observations) and significant differences are represented by different letters. Night time activity (sunset-sunrise) is represented by the black and daytime activity (sunrise-sunset) by the white portion of each bar.

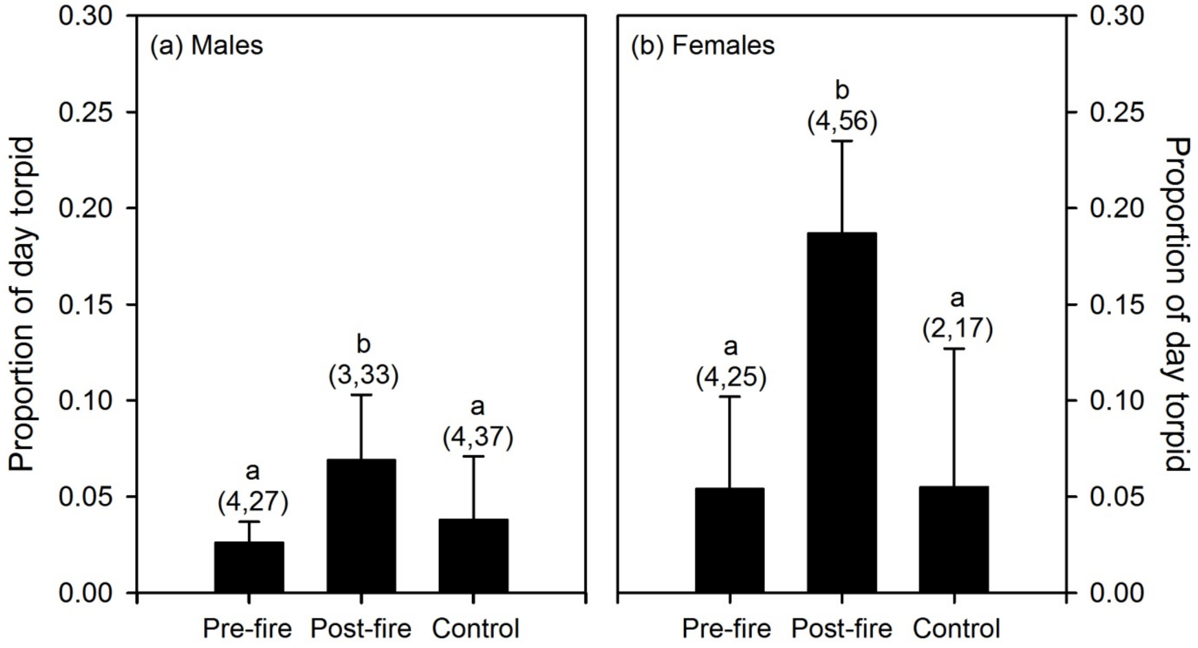

Fig. 5. The mean proportion of time each day male (a) and female (b) antechinus spent torpid over the entire study period for the pre-fire, post-fire and control groups. Means are shown with ± 1 SD (*n* = the number of individuals, *N* = the number of observations) and significant differences are represented by different letters.

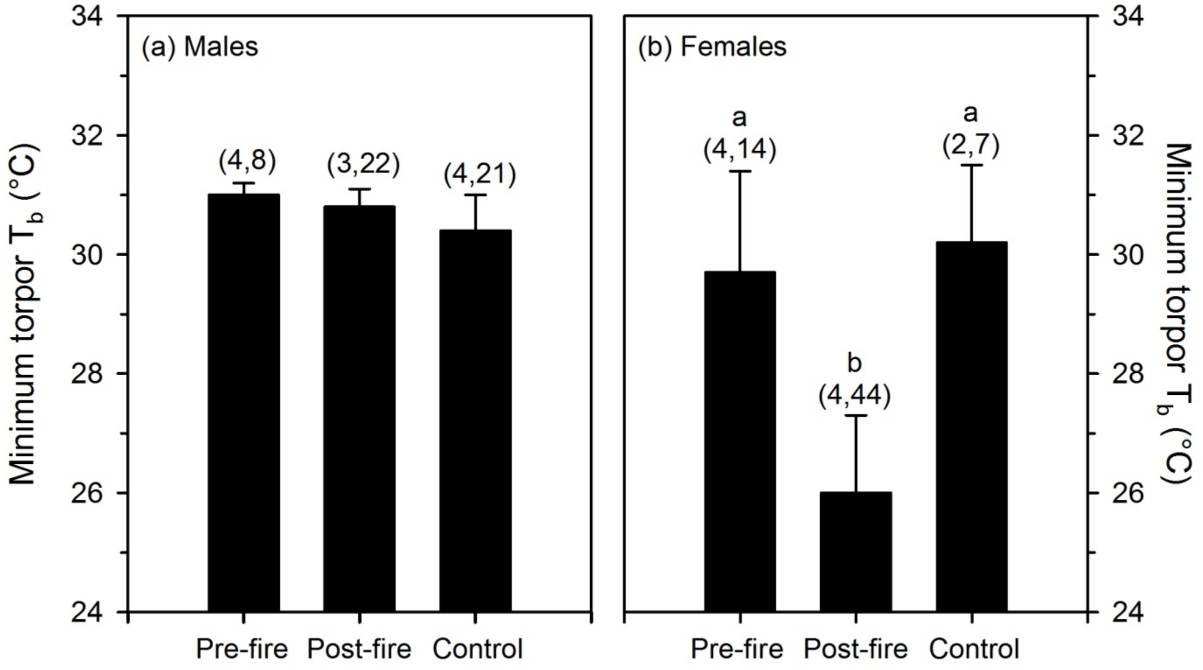

Fig. 6. Torpor bout depth shown as mean minimum torpor T_b (°C) of male (a) and female (b) antechinus for the pre-fire, post-fire and control groups. Means are shown with ± 1 SD (*n* = the number of individuals, *N* = the number of observations) and significant differences for the females are represented by different letters; no significant differences were found for the males.