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

2

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10

11 **Abstract**

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

31

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

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36 **1. Introduction**

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

46 Small terrestrial mammals are generally not able to flee from a fire, but they have
47 been shown to survive *in situ* (Quinn 1979; Banks et al. 2011; Stawski et al. 2015a). Fire-
48 proof refugia, such as deep burrows and rock crevices, are vital to the persistence of small
49 terrestrial mammals not only during, but also after a fire when the absence of ground cover
50 increases predation pressure (Banks et al. 2011; Diffendorfer et al. 2012; Robinson et al.
51 2013; Stawski et al. 2015a). Therefore, small mammal populations often do not require
52 recolonisation after a fire, provided the remaining individuals are able to survive in a habitat
53 that is usually depleted of food, water, vegetative cover and refuges (Friend 1993; Banks et
54 al. 2011; Zwolak et al. 2012; Stawski et al. 2015a; VanTassel et al. 2015). Indeed, many
55 individuals that survive a fire are often subsequently killed by predators or starve to death
56 (Sutherland & Dickman 1999; McGregor et al. 2014). The behavioural and physiological
57 responses of individuals to fire-modified habitat and the subsequent reduction in vegetative
58 cover will determine whether or not a population can persist and an enhanced phenotypic
59 plasticity in any of these traits would be of great advantage (Nussey et al. 2007; Canale &
60 Henry 2010).

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

71 Behavioural and physiological responses of individuals to changes in their
72 environment vary among species, which can greatly influence survival. Specifically,
73 heterothermy has been posited to have enabled small mammals to survive the meteorite
74 impact that decimated dinosaurs and also the current high levels of mammalian extinctions in
75 Australia (Geiser and Turbill 2009; Lovegrove et al. 2014). Therefore, the physiological
76 flexibility afforded to heterotherms is likely advantageous in a rapidly changing environment
77 (Canale & Henry 2010). These responses can also differ within a species and can be highly
78 variable among different populations, individuals or even within an individual under different
79 conditions (Nussey et al. 2007; Canale & Henry 2010; McKechnie & Mzilikazi 2011). For
80 example, the duration and depth of torpor bouts as well as activity patterns have been
81 observed to be different between sexes in a number of heterothermic mammals (Geiser 1988;
82 Körtner et al. 2010; Sheriff et al. 2013; Rojas et al. 2014). Some of these differences can be
83 attributed to sexual dimorphism in body size and/or reproductive effort, which is
84 energetically costly in both sexes. Males often have to invest more time in searching for a
85 mate whereas females spend more energy on pregnancy and raising young (Körtner et al.
86 2010). Whether or not the sexes have varying adaptations in response to environmental
87 catastrophes, such as fires, is largely unknown.

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

106 pressure to increase their chance of survival. However, we also expected that females would
107 express more torpor than males as is typical in this species (Geiser 1988; Rojas et al. 2014).

108

109 **2. Material and methods**

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

113

114 *2.1. Study site*

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

126 Throughout the study period T_a was measured at 10min intervals at both the
127 prescribed fire site and the control site using temperature data loggers ($\pm 0.5^\circ\text{C}$, iButton
128 thermochron DS1921G, Maxim Integrated Products, Inc., Sunnyvale, California, USA).
129 These loggers were suspended in trees ~1m off the ground and placed in inverted Styrofoam
130 cups to prevent direct sun exposure.

131

132 *2.2. Study protocol*

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

141 g ($n = 8$). Individuals were implanted intraperitoneally with temperature-sensitive radio-
142 transmitters that had individual frequencies (1.8 to 2.1 g, Sirtrack, Havelock North, New
143 Zealand). Before implantation, transmitters were coated in inert wax (Paraffin/Elvax, Mini
144 Mitter, Respironics Inc. OR, USA) and then calibrated in a water bath over a temperature
145 range of 10 to 45°C to the nearest 0.1°C. All antechinus were weighed using an electronic
146 balance to the nearest 0.1 g and a transmitter <10% of body mass was chosen for each
147 individual (Rojas et al. 2010). For details on the surgical procedure see Stawski et al.
148 (2015b).

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

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

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

168

169 *2.3. Torpor and activity definitions*

170 The torpor onset T_b value of antechinus in the current study was calculated as 31.5°C from
171 equation 4 by Willis (2007). For antechinus this formula is particularly important as it
172 provides a threshold estimate that detects shallow torpor bouts. Therefore, a T_b of 31.5°C was
173 used to calculate torpor bout entries and arousals for those that lasted longer than 30min. The
174 proportion of day spent torpid was calculated as the amount of time (min/per day, sunrise-
175 sunrise) each individual spent below the torpor onset T_b , but only for days when individuals

176 did not change nests (i.e. the logger recorded the complete rest phase of an animal).
177 Additionally, the depth of torpor bouts was measured as the absolute minimum T_b of each
178 bout.

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

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

186

187 *2.4. Data analysis*

188 Statistical tests were undertaken in R (R v. 3.0.1, R Core Team, 2014) and StatistiXL (v 1.10,
189 2015). Means for each measured variable were first calculated for each individual and then an
190 overall mean was derived from these individual means and are represented with ± 1 standard
191 deviation (SD); n = the number of individuals, N = the number of observations. A
192 significance level (p) of <0.05 was assumed. An analysis of variance (ANOVA; function
193 'aov') was undertaken to establish if T_a variables differed among the three sites. Linear
194 mixed-effects models (package 'nlme') were fitted to test for differences among the treatment
195 groups (pre-fire, post-fire and control) for the measured variables (activity, torpor bout
196 duration, proportion of day spent torpid, minimum torpor T_b), with sex and daily minimum T_a
197 as covariates, treatment:sex as an interaction term and individuals were included as a random
198 factor. As a significant interaction was found between treatment and sex for all the measured
199 variables ($p < 0.0001$) we performed separate analyses for males and females for each
200 variable using the model stated above, but removing sex and the interaction term. For all
201 models body mass was initially included, however, there was no significant effect of body
202 mass on any of the variables so it was removed. Percentages for the proportion of day spent
203 torpid were arcsine transformed for analyses. Further, a residual plot to test for
204 homoscedasticity and a normal Q-Q plot to test for normal distribution were used for all
205 models. If there was a significant difference among the groups a post-hoc Tukey test
206 (package 'multcomp') was performed to determine which groups were significantly different
207 from each other. An analysis of covariance (ANCOVA; function 'aov') was performed
208 separately for each of the groups to determine if any of the measured variables varied
209 between the sexes, with daily minimum T_a as a covariate and individuals as a random factor.
210 Least square linear regressions (activity and torpor bout duration against daily minimum T_a ;

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

219

220 3. Results

221 3.1. Habitat variables and predator numbers

222 Significant differences among the sites were found for mean ($p = 0.002, f_{2,31} = 8.0$),
223 maximum ($p = 0.006, f_{2,31} = 6.1$) and minimum ($p = 0.008, f_{2,31} = 5.7$) daily T_a (Fig. 3).
224 However, for the post-fire and control animals that were measured at the same time in
225 adjacent areas, all T_a variables were statistically indistinguishable between the two sites
226 (mean = $11.1 \pm 1.2^\circ\text{C}$, $n = 15$; maximum = $16.5 \pm 1.7^\circ\text{C}$, $n = 15$; minimum = $7.4 \pm 1.4^\circ\text{C}$, $n =$
227 15 ; Fig. 3). Conversely, the pre-fire group was measured before the burn when mean ($8.3 \pm$
228 2.8°C , $n = 8$), maximum ($13.5 \pm 2.6^\circ\text{C}$, $n = 8$) and minimum ($4.8 \pm 2.8^\circ\text{C}$, $n = 8$) daily T_a
229 were all on average $\sim 3^\circ\text{C}$ lower (Fig. 3). Similar significant differences in mean (day: $p =$
230 $0.0004, f_{2,31} = 10.0$; night: $p = 0.004, f_{2,30} = 6.7$), maximum (day: $p = 0.006, f_{2,31} = 6.0$; night:
231 $p = 0.005, f_{2,30} = 6.2$) and minimum (day: $p = 0.04, f_{2,31} = 3.2$; night: $p = 0.006, f_{2,30} = 6.1$)
232 daytime and night-time T_a were found between the pre-fire site (mean day = $10.2 \pm 2.6^\circ\text{C}$, $n =$
233 8 ; mean night = $6.4 \pm 3.1^\circ\text{C}$, $n = 7$; maximum day = $13.5 \pm 2.6^\circ\text{C}$, $n = 8$; maximum night =
234 $9.1 \pm 3.1^\circ\text{C}$, $n = 7$; minimum day = $5.4 \pm 3.1^\circ\text{C}$, $n = 8$, minimum night = $4.6 \pm 2.9^\circ\text{C}$, $n = 7$)
235 and the other two sites (mean day = $13.6 \pm 1.4^\circ\text{C}$, $n = 15$; mean night = $9.3 \pm 1.4^\circ\text{C}$, $n = 15$;
236 maximum day = $16.5 \pm 1.7^\circ\text{C}$, $n = 15$; maximum night = $11.8 \pm 1.4^\circ\text{C}$, $n = 15$; minimum day
237 = $8.0 \pm 1.9^\circ\text{C}$, $n = 15$, minimum night = $7.6 \pm 1.8^\circ\text{C}$, $n = 15$).

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

244 No mammalian predators were recorded by the trail cameras along the border of the
245 prescribed area before the fire. During the first week after the fire three feral cats, two wild

246 dogs and one fox were recorded, suggesting an influx of predators after the burn.
247 Nevertheless, before the fire one male and one female antechinus from the pre-fire group
248 were killed by a predator, most likely by a cat. However, after the fire no predation events
249 were recorded in either the post-fire or control groups. Further, only one of the tagged
250 individuals perished as a direct result of the fire.

251

252 3.2. Activity

253 Importantly, none of the individuals tracked in the burn site left the area after the fire.
254 Antechinus were active on average between 6 and 13 hours per day, with about a third of the
255 activity occurring during the daytime and the remainder at night for individuals in the pre-fire
256 and control groups (Fig. 4a,b). Radio-tracking revealed that when active during daytime
257 hours animals regularly foraged in patches of matted grass and *Lomandra* where they could
258 not be seen. Interestingly, the amount of time male antechinus spent active significantly
259 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
260 significant relationship for females ($p = 0.585$, $R^2 = 0.01$, $f_{1,74} = 0.3$). Consequently, when T_a
261 was lower in the pre-fire group females were active significantly longer over the whole day in
262 comparison to males ($p = 0.003$, $f_{1,25} = 10.7$), whereas when T_a was warmer in the control
263 group males were active significantly longer than females ($p = 0.019$, $f_{1,33} = 6.0$; Fig. 4a,b).

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

268 For male antechinus the time spent active during the whole day differed significantly
269 among the groups ($p < 0.0001$, $t_{6,63} = 17.3$; Fig. 4a) and activity duration was ~1.7-fold longer
270 for animals at the control (12.6 ± 3.5 h, $n = 4$, $N = 28$) site than individuals in both the pre-
271 (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
272 fire site whole day activity did not change between before and after the fire. However, the
273 partitioning between daytime and night time activity shifted after the fire. While males in the
274 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
275 one third of their total activity during the day, in the post-fire (0.4 ± 0.5 h, $n = 3$, $N = 31$)
276 group this was reduced to 5.3% (Fig. 4a).

277 In females, whole day activity also differed significantly among the three groups ($p <$
278 0.0001 , $t_{6,67} = 6.4$; Fig. 4b), but they decreased total activity time by 60% after the fire in the
279 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
280 $= 4$, $N = 16$) and control (10.3 ± 1.8 h, $n = 2$, $N = 14$) groups. This reduced level of activity

281 encompassed both daytime and night time activity, but daytime activity more so. While pre-
282 fire (3.3 ± 0.4 h, $n = 4$, $N = 16$) and control (2.4 ± 0.7 h, $n = 2$, $N = 14$) animals spent on
283 average 28.2% and 23.4% of the total activity time during the day, respectively, diurnal
284 activity was reduced to 4.4% in post-fire (0.3 ± 0.3 h, $n = 4$, $N = 45$) animals (Fig. 4b).

285

286 3.3. Torpor

287 After the fire, antechinus in the post-fire group expressed longer torpor bouts in comparison
288 to the pre-fire and control groups (Fig. 5a,b). However, in all groups females were torpid
289 longer than males (pre-fire: $p < 0.0001$, $f_{1,16} = 173.1$; post-fire: $p < 0.0001$, $f_{1,67} = 495.4$;
290 control: $p < 0.0001$, $f_{1,21} = 145.5$) and torpor bouts were generally shallower in males than in
291 females (pre-fire: $p = 0.039$, $f_{1,18} = 4.9$; post-fire: $p < 0.0001$, $f_{1,64} = 67.4$; control: $p = 0.154$,
292 $f_{1,26} = 2.2$; Fig. 6a,b). Furthermore, in both males ($p = 0.037$, $R^2 = 0.4$, $f_{1,8} = 5.3$, $y = -15.5x +$
293 159.7) and females ($p = 0.011$, $R^2 = 0.5$, $f_{1,12} = 9.3$, $y = -29.4x + 285.0$) torpor bout duration
294 in the pre-fire group increased as daily minimum T_a decreased.

295 Over the study period for males the proportion of day spent torpid ($p < 0.0001$, $t_{6,88} =$
296 5.2 ; Fig. 5a) as well as mean torpor bout duration ($p < 0.0001$, $t_{6,88} = 5.2$) differed
297 significantly among the groups. Males from the post-fire group were torpid ~ 2.2 -fold more
298 each day in comparison to both of the other groups and torpor bouts were also ~ 1.5 -fold
299 longer in the post-fire group (127.3 ± 38.4 min, $n = 3$, $N = 26$), in comparison to torpor bouts
300 expressed by males from both the pre-fire (84.6 ± 37.1 min, $n = 4$, $N = 11$) and control ($84.3 \pm$
301 26.8 min, $n = 4$, $N = 20$) groups. However, the depth of torpor bouts was the same for all
302 groups ($p = 0.228$, $t_{6,41} = 1.2$; pre-fire = $31.0 \pm 0.2^\circ\text{C}$, $n = 4$, $N = 8$; post-fire = $30.8 \pm 0.3^\circ\text{C}$, n
303 = 3 , $N = 22$; control = $30.4 \pm 0.6^\circ\text{C}$, $n = 4$, $N = 21$; Fig. 6).

304 Similarly to the males, for females the proportion of day spent torpid differed
305 significantly among the groups ($p < 0.0001$, $t_{6,89} = 7.0$; Fig. 5b) and females from the post-
306 burn group were torpid ~ 3.4 -fold more each day in comparison to both of the other groups.
307 Mean torpor bout duration of all bouts recorded for female antechinus also differed among
308 the groups ($p < 0.0001$, $t_{6,89} = 6.9$) and torpor bouts were ~ 2.5 -fold longer in the post-fire
309 (267.5 ± 61.9 min, $n = 4$, $N = 57$) group in comparison to torpor bouts expressed by females
310 from both the pre-fire (118.0 ± 76.1 min, $n = 4$, $N = 15$) and control (94.2 ± 83.7 min, $n = 2$, N
311 = 8) groups. Importantly, mean minimum torpor T_b of female antechinus was 4°C lower in
312 the post-fire ($26.0 \pm 1.3^\circ\text{C}$, $n = 4$, $N = 44$) group in comparison to both the pre-fire ($29.7 \pm$
313 1.7°C , $n = 4$, $N = 14$) and control ($30.2 \pm 1.3^\circ\text{C}$, $n = 2$, $N = 21$) groups ($p < 0.0001$, $t_{6,55} =$
314 45.3 ; Fig. 6).

315

316 4. Discussion

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

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

350 Whereas females reduced overall activity, males in the post-fire group shifted their
351 activity into the night and in comparison to pre-fire conditions males in both the post-fire and
352 control groups maintained a high level of night-time activity. This was likely facilitated by
353 the warmer T_a , as activity in males increased with T_a which was possibly a response to higher
354 food availability as they primarily feed on insects that often become more prevalent at
355 warmer temperatures (Stawski 2012). The overall higher levels of activity seen in males in
356 the current study may be related to pre-mating season preparation to establish home ranges
357 and indeed an increase in movements by male brown antechinus have been recorded as early
358 as May (Wood 1970), which corresponds to the timeframe of the current study. However,
359 while a shift towards nocturnal activity somewhat reduces predation risk in comparison to
360 diurnal activity, physical protection at night is still limited after fire. Therefore, an overall
361 reduction of both daytime and night time activity as observed in female antechinus appears to
362 be a prudent strategy since animals resting in a secure location are less exposed to predation
363 than when active (Turbill et al. 2011). Further, the major food resource of antechinus, insects,
364 is often significantly reduced after a fire (Coleman and Rieske 2006; VanTassel et al. 2015),
365 suggesting that increasing energy savings is paramount. Importantly, this can only be
366 achieved if daily energy demands can be lowered substantially, and in heterothermic
367 endotherms an avenue for accomplishing this effectively is the use of torpor (Ruf & Geiser
368 2015).

369 Torpor not only reduces energy demands, it also enhances predator avoidance
370 (Stawski & Geiser 2010; Turbill et al. 2011; Geiser & Brigham 2012; Vuarin & Henry 2014).
371 This in turn appears to contribute to the lower extinction rates in heterothermic compared to
372 homeothermic mammals (Geiser & Turbill 2009; Hanna & Cardillo 2014). While individual
373 survival and longevity increase with the amount of time spent torpid (Turbill et al. 2011), the
374 state of torpor cannot continue forever, but must be interrupted for activity and especially
375 reproduction (Sheriff et al. 2013; Lovegrove et al. 2014). Although torpor and reproduction
376 are not mutually exclusive, certain phases during the reproductive cycle are often
377 incompatible with entering torpor (McAllan & Geiser 2014). For example, in many species
378 the hibernation season is often shorter in males, as they need to emerge earlier from
379 hibernation to commence spermatogenesis and to secure territories for the mating period
380 (Barnes et al. 1986). Similarly, male antechinus show increased levels of activity and
381 metabolism, continue to grow and generally enter torpor rarely throughout winter (June-July),
382 when the size of testes is greatest (Woolley 1966; Geiser 1988; Rojas et al. 2014). The sexual
383 differences for torpor use and activity patterns observed here are therefore not unexpected.
384 The unusual reproductive strategy of male antechinus entails a high level of energy turnover

385 that eventually culminates in complete male die-off (Woolley 1966; Wood 1970) and
386 therefore the time leading up to reproduction likely influences the behavioural and
387 physiological responses to a catastrophic event such as fire. Consequently, while female
388 antechinus minimised energy expenditure as well as predator exposure by considerably
389 increasing torpor use after the fire, males increased torpor use only marginally, confirming
390 our prediction that females would express more torpor than males. Nevertheless, the
391 strategies employed by both sexes were successful at least in the short to medium term, as no
392 deaths were recorded in the weeks after the fire event. Obviously, flexibility in behavioural
393 and physiological traits in individuals of both sexes is advantageous, as it allows a population
394 to respond to sudden changes in environmental conditions and food supply (Nussey et al.
395 2007; Canale & Henry 2010; Stawski & Geiser 2012; Nowack et al. 2015).

396 Even though the present study involved only a low-intensity burn, a large proportion
397 of the habitat was severely degraded. Fires leave a fragmented patchwork of more or less
398 suitable habitats that at least temporarily results in a significant reduction in habitat size and
399 food availability, leading to increased levels of stress and decreased health in antechinus
400 (Dickman 1989; Johnstone et al. 2012). Fire regimes in Australia have been altered for
401 millennia, with Aborigines regularly burning patches to maintain a variety of habitats for
402 animals they could hunt (Bowman 1998). However, these fire regimes have been radically
403 changed since European settlement with drastic impacts on ecosystems contributing to the
404 exceptionally high rate of mammal extinctions in Australia's recent history (Woinarski et al.
405 2015). While the negative impacts of modified fire regimes have also occurred in other parts
406 of the world (Stephens et al. 2013; Kelly et al. 2014; VanTassel et al. 2015), in Australia such
407 changes were confounded by the introduction of new predators, namely feral cats and
408 European red fox (Woinarski et al. 2015). Importantly, after a fire an influx of predators is
409 common, as the removal of ground cover facilitates their hunting effort (Quinn 1979;
410 McGregor et al. 2014). It is this outcome of fires that often results in more deaths and decline
411 in small mammal populations than the fire itself (Quinn 1979).

412 Habitat structure is vitally important for the survival of animals during a fire and to
413 their recovery after a fire, thus understanding the relationships between individuals and
414 aspects of their environment is paramount (Friend 1993; Diffendorfer et al. 2012). Therefore,
415 maintaining a mosaic of habitats through varying fire regimes and intensities also appears to
416 be important to conserving biodiversity and, in particular, ensuring that some old vegetation
417 remains intact to provide refuges, cover for foraging and food resources (Coleman and Rieske
418 2006; Robinson et al. 2013; Stephens et al. 2013; Kelly et al. 2014; Stawski et al. 2015a;
419 VanTassel et al. 2015). Fortunately, in an undulating forested landscape characteristic for the

420 east coast of Australia, even severe wildfires leave pockets of unburned vegetation often
421 along wet gullies. These remnants constitute vital refuge areas for small mammal
422 populations, as during previous research following a wildfire most agile (*A. agilis*) and dusky
423 antechinus (*A. swainsonii*) were trapped along such drainage lines (Davies and Drew 2014).
424 Interestingly, during our study radio-tagged antechinus were never observed to move into
425 such refugia, even though the low intensity control burn left about 30% of the area untouched
426 and further unburned habitat could be found in the control site just across a narrow forest
427 trail. This could be a result of the unburnt areas already being occupied and defended, or a
428 risk of venturing too far in the newly created open habitat and brown antechinus do generally
429 show strong site fidelity (Wood 1970). Understanding the phenotypic plasticity of these
430 mechanisms linking the fate of individuals with changes seen on a population level is vitally
431 important for understanding fire ecology and to effectively manage fires in a conservation
432 context.

433

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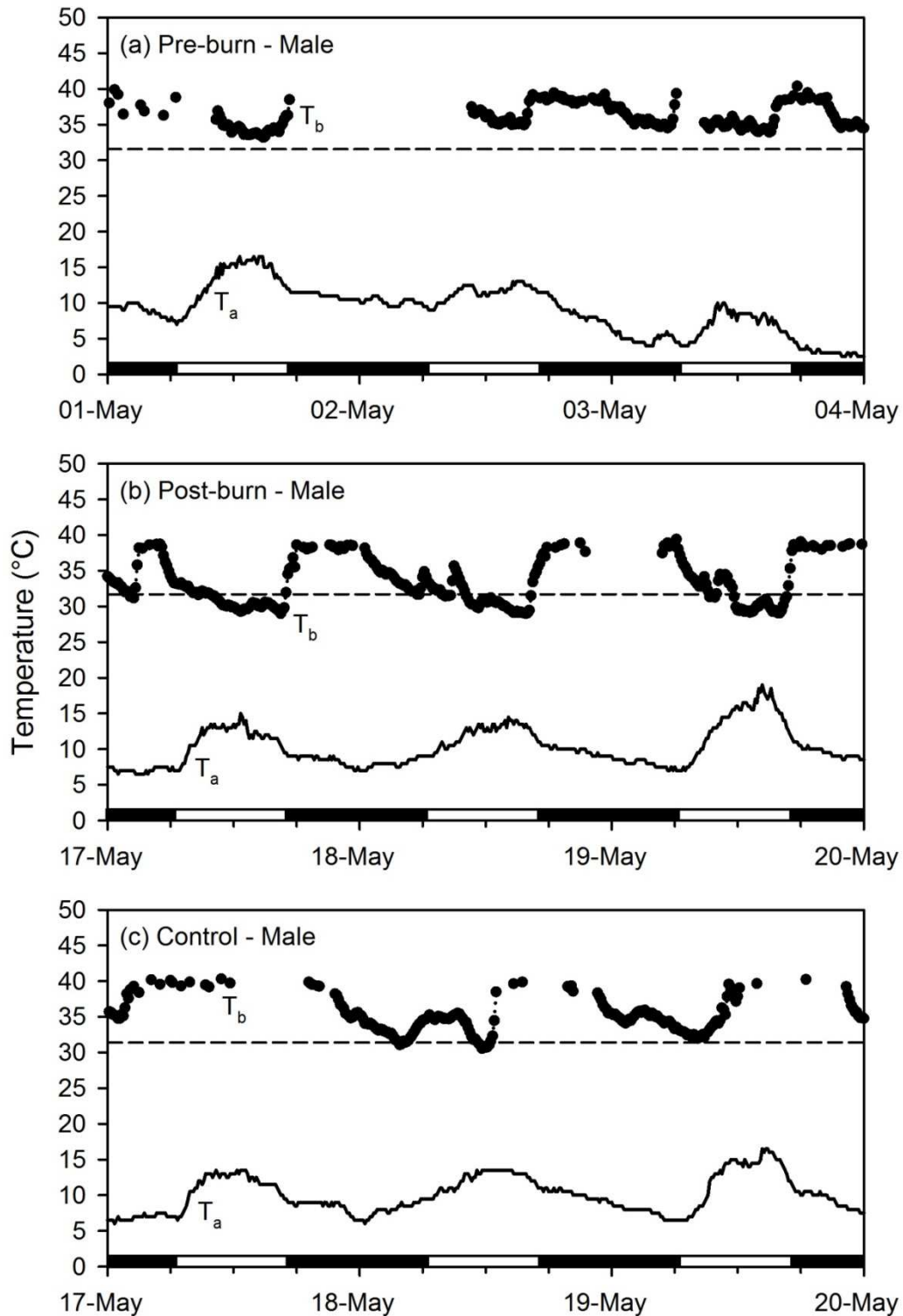
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572 **Table 1.** The number of days data was recorded for each individual in all three groups: pre-
 573 fire, post-fire and control. Also shown are the total (n = the number of individuals) and mean
 574 number of days of data for each group.
 575

	Pre-fire		Post-fire		Control	
	(Days recorded)		(Days recorded)		(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

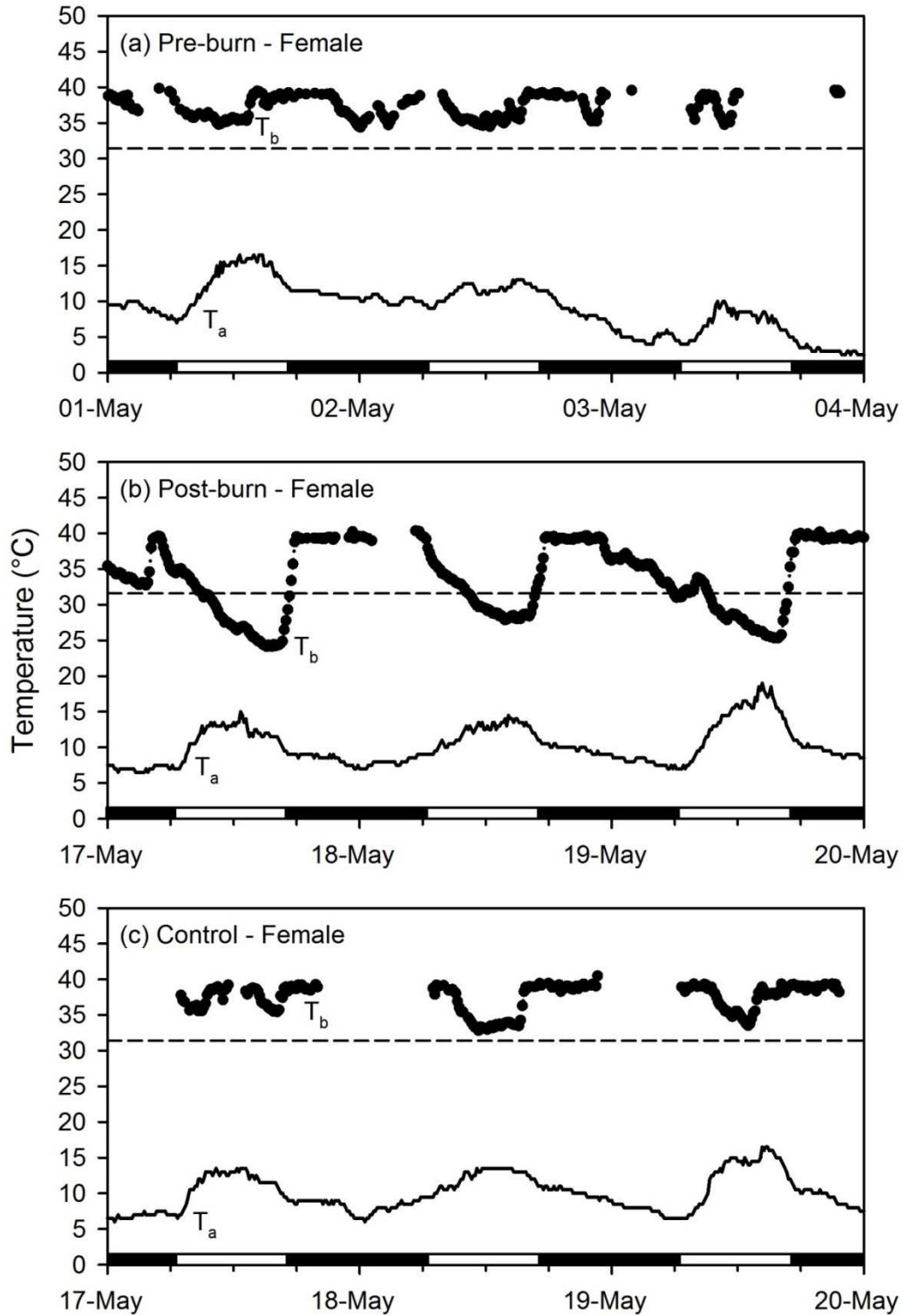
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2014

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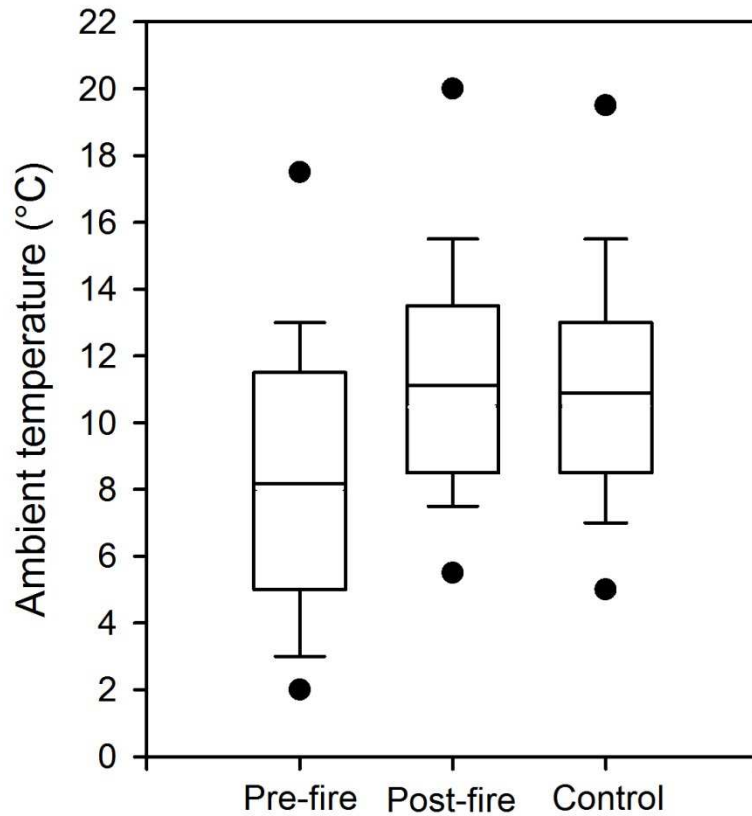
578 **Fig. 1.** Examples of T_b (dotted line) and T_a (solid line) data for male brown antechinus over a
 579 three day period during the study for an individual from the (a) pre-burn, (b) post-burn and
 580 (c) control groups. The dashed line represents the torpor onset T_b and times when T_b data are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



2014

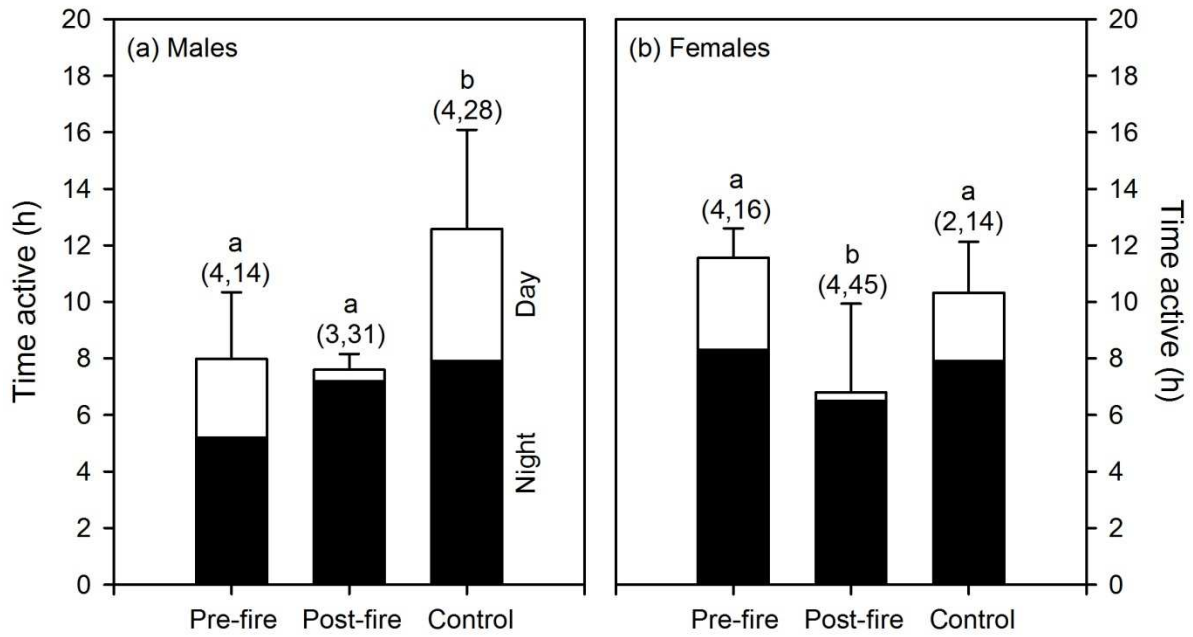
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584 **Fig. 2.** Examples of T_b (dotted line) and T_a (solid line) data for female brown antechinus over
 585 a three day period during the study for an individual from the (a) pre-burn, (b) post-burn and
 586 (c) control groups. The dashed line represents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



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



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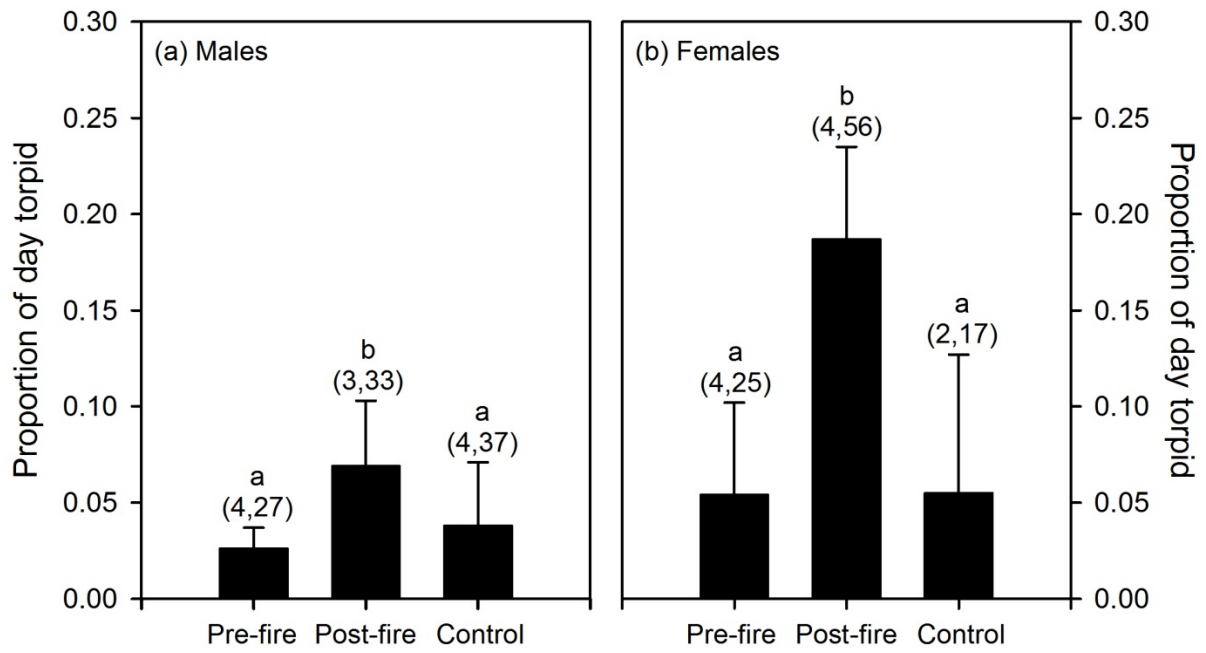
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600 **Fig. 4.** The amount of time (h) male (a) and female (b) antechinus spent active throughout the
 601 whole day (24h, sunrise-sunrise) for the pre-fire, post-fire and control groups. Means for
 602 whole day activity are shown with ± 1 SD (n =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

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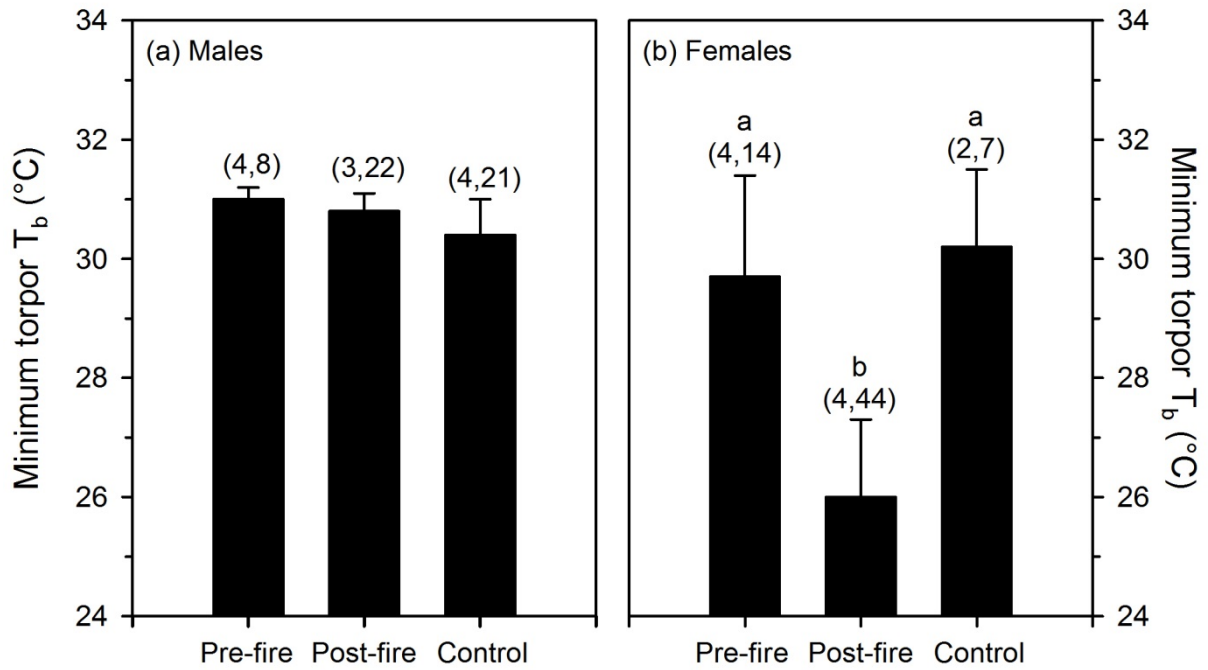
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Fig. 5. The mean proportion of time each day male (a) and female (b) antechinus spent torpid over the entire study period for the pre-fire, post-fire and control groups. Means are shown with ± 1 SD (n = the number of individuals, N = the number of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



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