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1 **Post-fire recovery of torpor and activity patterns of a small mammal**

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16

17 **Abstract**

18 To cope with the post-fire challenges of decreased availability of food and shelter, brown

19 antechinus (*Antechinus stuartii*), a small marsupial mammal, increase the use of energy

20 conserving torpor and reduce activity. However, it is not known how long it takes for animals

21 to resume pre-fire torpor and activity patterns during the recovery of burnt habitat. Therefore,

22 we tested the hypothesis that antechinus will adjust torpor use and activity after a fire

23 depending on vegetation recovery. We simultaneously quantified torpor and activity patterns

24 for female antechinus from three adjacent areas: (i) the area of a management burn one year

25 post-fire, (ii) an area that was burned two years prior and (iii) a control area. In comparison to

26 shortly after the management burn, antechinus in all three groups displayed less frequent and  
27 less pronounced torpor while being more active. We provide the first evidence that only one  
28 year post-fire antechinus resume pre-fire torpor and activity patterns, likely in response to the  
29 return of herbaceous ground cover and foraging opportunities.

30

31 **Keywords:** antechinus, behaviour, heterothermy, marsupial, physiology, predation

32

### 33 **1. Introduction**

34 As large and destructive wildfires are increasing worldwide [1], management burns are  
35 employed in many forested areas with the aim of reducing fire fuel loads. However, the time  
36 between fires and their intensity can alter assemblages of plant and animal species [2,3].

37 Importantly, while leaf litter and some grasses/herbs often reappear quickly after a fire,  
38 others, such as woody vegetation and tree hollows, can take up to 30-40 years to re-establish  
39 [4].

40 In the long-term fires can help to increase habitat complexity, which is beneficial for  
41 many small terrestrial mammals [2]. However, the initial loss of ground cover after a fire can  
42 be detrimental because it leads to reduced foraging opportunities due to increased predation  
43 pressure [5]. This is exacerbated for insectivorous mammals, as the abundance of ground-  
44 dwelling arthropods often decreases after fire [6]. Hence, in the short to medium-term after  
45 fire, some terrestrial mammals have been found to substantially curtail activity and enhance  
46 the use of torpor - a pronounced reduction in energy expenditure via a controlled fall of  
47 metabolic rate and body temperature ( $T_b$ ) [6-9].

48 Given the slow recovery of some habitat features it remains unclear over what time  
49 period such behavioural and physiological adjustments have to be employed for individuals  
50 and populations to survive. While an increase in torpor use is beneficial during detrimental

51 conditions, it may reduce fitness by curtailing territorial defence and reproduction. Therefore,  
52 as conditions improve animals should employ less torpor. We tested the hypothesis that  
53 following the recovery of an herbaceous understory after a management burn, torpor use and  
54 activity in brown antechinus (*Antechinus stuartii*), a small heterothermic terrestrial marsupial  
55 [10], will return to pre-fire levels in response to more profitable and safer foraging  
56 opportunities.

57

## 58 **2. Material and methods**

59 Our work was undertaken during May-June 2015, one year after a management burn at Guy  
60 Fawkes River National Park, Australia (30°04'58.6"S, 152°20'0.9"E). We compared data  
61 collected during the current study to those from our previous study in 2014 [9], with a total of  
62 six groups of female antechinus (defined in table 1). All groups were measured in areas that  
63 were in close proximity, ensuring that the general habitat and climate of the sites was the  
64 same. The areas that burnt in 2013 and 2014 are burnt regularly to reduce fuel levels and the  
65 intensity of wildfires, whereas the control area last burned in 1994 due to a wildfire and no  
66 management burns have been implemented since [11]. Ambient temperatures ( $T_a$ ) were  
67 recorded with data loggers ( $\pm 0.5^\circ\text{C}$ , iButton thermochron DS1921G, Maxim Integrated  
68 Products, Inc., Sunnyvale, California, USA). We visually determined the percentage of  
69 ground cover in 12 randomly selected  $1\text{m}^2$  quadrats in each of the three study areas (36  
70 quadrats total).

71 To measure  $T_b$  patterns including torpor and also to infer activity we implanted  
72 temperature-sensitive radio-transmitters (2g, Sirtrack, Havelock North, New Zealand) into the  
73 intraperitoneal cavity of each animal (for surgical details see [12]). A receiver/data logger  
74 [13] was placed near each nest to record the presence/absence of animals and their  $T_b$ .

75 Throughout the study each individual used between 1 and 8 nest sites (mean = 3.7 nests) and

76 loggers were repositioned whenever antechinus moved to a new nest. Activity periods within  
77 24 h (sunrise to sunrise) were calculated as the time animals spent away from the nest  
78 site/logger for >30min. Days when an individual moved nests were excluded as the time the  
79 animal arrived at the new nest was unknown. We calculated the torpor threshold of 31.5°C  
80 using equation 4 [14] as previously [9]; torpor bouts were calculated from the time  $T_b$  fell  
81 below and rose above this threshold for > 30 min.

82 We used R [15] to perform statistical analyses. As the duration of activity and torpor  
83 are significantly correlated with  $T_a$  in antechinus [10], only data recorded when  $T_a$  was within  
84 daily maxima (20.0°C) and minima (2.0°C) of our previous study were included [9]. We  
85 employed linear mixed-effects models [16] to test for differences among the six groups for  
86 the measured variables: torpor frequency, torpor bout duration, daily minimum  $T_b$ , time spent  
87 active [17]. We used body mass and daily minimum  $T_a$  as covariates, individuals were  
88 included as a random effect to account for repeated measures and we accounted for temporal  
89 autocorrelation [17]. We used a residual plot to test for homoscedasticity and a normal Q-Q  
90 plot to test for normal distribution. We employed a post-hoc Tukey test [18] to determine  
91 which groups differed from each other. All proportions were arcsine transformed before  
92 analysis. We assumed significance at  $p < 0.05$ .

93

### 94 **3. Results**

95 While ground cover had somewhat recovered a year after the burn in 2014 (figure 1), it was  
96 patchy in those areas where the one year post-fire 2015 (range = 10-100%, mean = 50%,  $n =$   
97 12) and two years post-fire 2015 (range = 5-100%, mean = 39%,  $n = 12$ ) groups were  
98 measured. In contrast, the area where the control 2015 group was measured consisted of thick  
99 and even ground cover unchanged from 2014 (range = 60-100%, mean = 87%,  $n = 12$ ).

100 In all 2015 groups torpor was employed approximately half as often as by the post-  
101 fire 2014 group, and torpor frequency was therefore statistically identical to the pre-fire 2014  
102 and control 2014 groups (figure 2a; table 2). Furthermore, in all 2015 groups mean torpor  
103 bout durations and the longest torpor bouts recorded per individual were significantly shorter  
104 (~50%) compared to the post-fire 2014 group (figure 2b; table 2). The mean daily minimum  
105  $T_b$  displayed by groups in the 2015 study was  $\sim 3^\circ\text{C}$  higher, and the lowest  $T_b$  recorded  
106  $>3.4^\circ\text{C}$  greater, than that of the post-fire 2014 group (figure 2c; table 2).

107 Antechinus from all three groups measured in 2015 spent an additional three hours  
108 active each day in comparison to individuals from the post-fire 2014 group (figure 2d; table  
109 2). Further, while daytime activity was almost absent in the post-fire 2014 group (4.4% of  
110 total daily activity), it encompassed  $\sim 20\%$  of the total daily activity of antechinus in 2015 and  
111 of those in the pre-fire 2014 and control 2014 groups (figure 2d).

112

#### 113 **4. Discussion**

114 Our study provides the first evidence that within one year after a management burn a  
115 population of brown antechinus had resumed pre-fire torpor and activity patterns. Torpor  
116 bouts were shorter and shallower in individuals in the post-fire recovered landscape in  
117 comparison to shortly after the fire when ground cover was largely absent. Further, this  
118 decrease in torpor use one year after the fire was accompanied by an increase in total and  
119 especially daytime activity over levels measured just after the burn.

120 The late autumn management burns employed for our study were of low-intensity, but  
121 inflicted some mortality amongst antechinus nevertheless [9]. As the fires primarily  
122 consumed dead vegetation and dry leaf litter leaving the mid and upper storeys largely intact,  
123 a relatively quick recovery of some vegetative ground cover ensued. In particular *Lomandra*  
124 spp. (native Australian perennial herbs) had re-sprouted vigorously in the areas that had

125 burned both one and two years prior (figure 1). However, *Lomandra* is encouraged by fire,  
126 and other types of ground cover such as small shrubs and decaying timber were still largely  
127 absent. Yet, brown antechinus persisted and during early winter resumed daily torpor and  
128 activity patterns similar to those recorded at the same time of year before the fire and in  
129 unburnt habitat [9].

130 Firstly, it therefore appears that even sparse vegetation of limited diversity is  
131 sufficient for antechinus to manage their daily energy needs without extensive torpor use.  
132 This vegetative cover likely aids in protecting antechinus from predation while foraging.  
133 Secondly, as the abundance of terrestrial arthropods often increases in the year following a  
134 fire [6], for antechinus the prey base might have been elevated. Thirdly, it is likely that the  
135 insulating properties of a tussock ground cover alters the microclimate of foraging areas. For  
136 example, the retention of a boundary layer of warm air near the ground during the night  
137 would reduce thermoregulatory costs while foraging, further decreasing the need to save  
138 energy via torpor.

139 Our results highlight the importance of even sparse ground cover for small terrestrial  
140 mammals while foraging [19]. The general association of torpor with low  $T_a$  and the  
141 reduction of torpor use as habitat conditions improve suggests that antechinus mostly employ  
142 torpor in response to detrimental conditions, which is similar to other marsupials such as  
143 sugar gliders (*Petaurus breviceps*) [9,10,13]. Importantly, antechinus are somewhat unusual  
144 in being semelparous, reproducing only once a year towards the end of winter [20]. It is  
145 therefore likely vital for them during autumn and early winter to invest time in protecting  
146 resources, such as food and nests, to ensure reproductive success, and torpor decreases the  
147 time available for these activities.

148 Nevertheless, it is evidently possible that fires do not pose a significant challenge for  
149 some mammals, especially those that can avoid fires like volant bats [21]. Indeed, the only

150 other study we are aware of focussing on how individuals recover physiologically and  
151 behaviourally in the years after a fire was conducted on bats [21]. Therefore, further studies  
152 on different mammals are needed to understand how other species on other continents  
153 respond physiologically and behaviourally to fires, including severe wildfires, in the short- to  
154 long-term, particularly on longer-lived and homeothermic species that do not have the ability  
155 to employ torpor for energy conservation.

156

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

160

161 **Data accessibility.** Data can be accessed from Dryad Digital Repository  
162 (doi:10.5061/dryad.m76ks).

163

164 **Authors' contributions.** C.S. and F.G. designed the study. C.S. and T.H. analysed the data.  
165 C.S. drafted the manuscript. All authors collected the data and commented on the manuscript.  
166 All authors agree to be held accountable for the content.

167

168 **Competing interests.** The authors declare no competing interests.

169

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177

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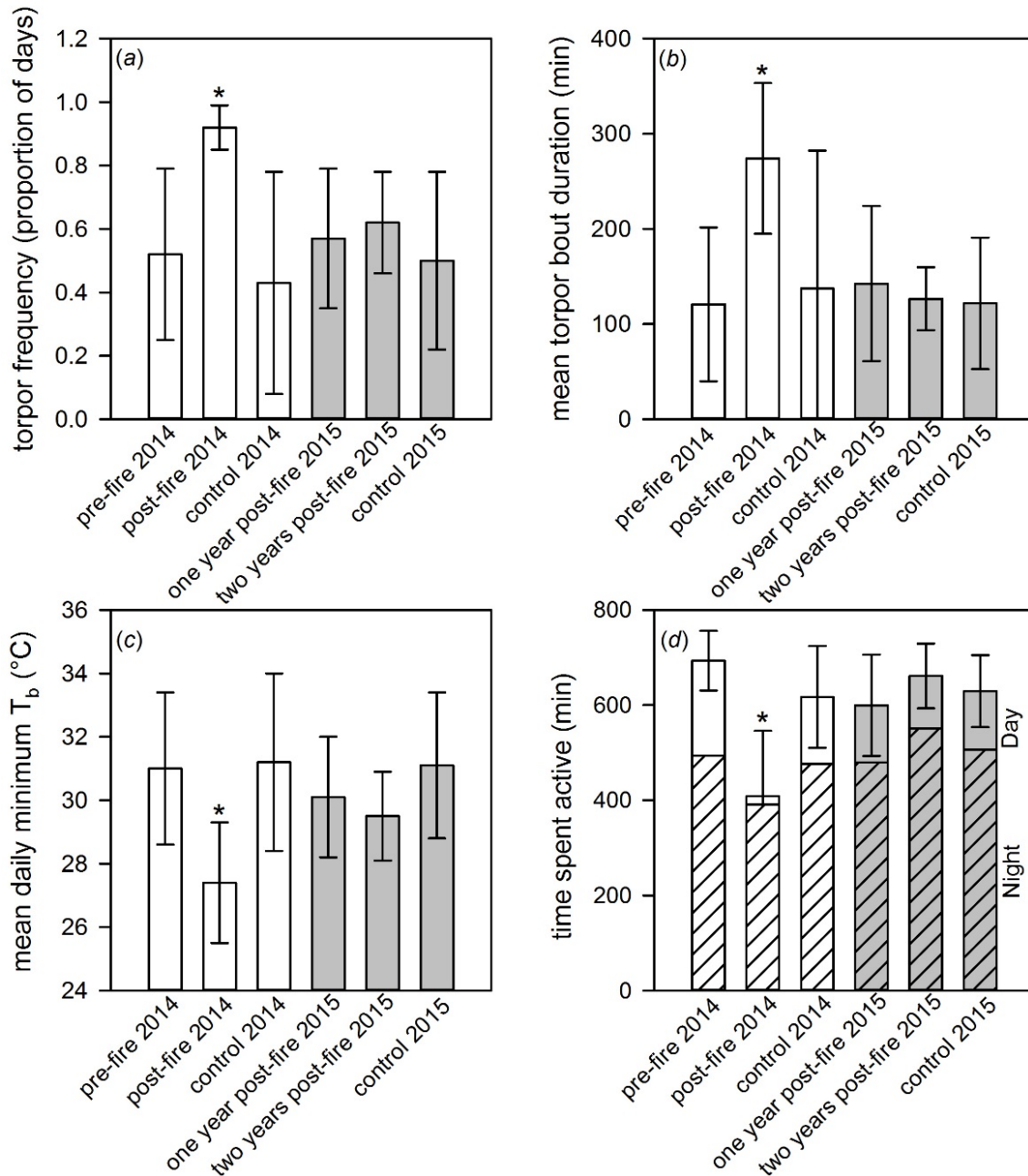
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225

226 **Figure 1.** Photos of the study site depicting ground cover in the same area shortly after the  
227 management burn in 2014 (a) and one year later in 2015 when *Lomandra* had recovered (b).

228



229

230 **Figure 2.** Comparison of variables for female *Antechinus stuartii* from 2014 (white bars) and

231 2015 (grey bars). (a) torpor frequency (number of days with torpor/days measured), (b) mean

232 torpor bout duration (min), (c) mean daily minimum  $T_b$  ( $^{\circ}$ C) and (d) time spent active (min).

233 For activity (d) the solid portion of the bar represents daytime (sunrise-sunset) activity and

234 the hatched portion nocturnal (sunset-sunrise) activity. Means are shown  $\pm 1$  standard

235 deviation, which for (d) represents whole day (24h, sunrise-sunrise) activity. Only the post-

236 fire 2014 group differed significantly, denoted by the asterisk.

237 **Table 1.** Descriptions of each of the groups measured, including number of individuals and  
 238 animal days measured.

| <b>group name</b>               | <b>group description</b>   | <b>individuals</b> | <b>animal days</b> |
|---------------------------------|--|--------------------|--------------------|
| <b>pre-fire 2014</b>            | individuals measured in 2014 before the burn                                   | 4                  | 25                 |
| <b>post-fire 2014</b>           | individuals measured in 2014 after the burn                                    | 4                  | 56                 |
| <b>control 2014</b>             | individuals measured in 2014 in an unburnt area                                | 2                  | 17                 |
| <b>one year post-fire 2015</b>  | individuals measured in 2015 one year after the management burn in 2014        | 7                  | 136                |
| <b>two years post-fire 2015</b> | individuals measured in 2015 in an area that was burnt two years prior in 2013 | 4                  | 89                 |
| <b>control 2015</b>             | individuals measured in 2015 in an unburnt area                                | 6                  | 135                |

239

240 **Table 2.** Torpor variables, body temperatures ( $T_b$ ) and time spent active (whole day) of female *Antechinus stuartii* and ambient temperatures  
 241 ( $T_a$ ). Means are shown  $\pm$  1 standard deviation and significant differences between groups are identified by different letters.

|   | <b>pre-fire<br/>2014</b>      | <b>post-fire<br/>2014</b>      | <b>control<br/>2014</b>        | <b>one year<br/>post-fire<br/>2015</b> | <b>two years<br/>post-fire<br/>2015</b> | <b>control<br/>2015</b>       |
|---|-------------------------------|--------------------------------|--------------------------------|--|---|-------------------------------|
| <b>torpor frequency (proportion of days)</b>          | 0.52 $\pm$ 0.27 <sup>a</sup>  | 0.92 $\pm$ 0.07 <sup>b</sup>   | 0.43 $\pm$ 0.35 <sup>a</sup>   | 0.57 $\pm$ 0.22 <sup>a</sup>           | 0.62 $\pm$ 0.16 <sup>a</sup>            | 0.50 $\pm$ 0.28 <sup>a</sup>  |
| <b>torpor bout duration (min)</b>                     | 120.8 $\pm$ 80.8 <sup>a</sup> | 274.2 $\pm$ 79.2 <sup>b</sup>  | 137.5 $\pm$ 102.5 <sup>a</sup> | 142.6 $\pm$ 81.4 <sup>a</sup>          | 126.7 $\pm$ 33.1 <sup>a</sup>           | 121.9 $\pm$ 69.1 <sup>a</sup> |
| <b>longest torpor bout recorded (min)</b>             | 330                           | 650                            | 310                            | 380                                    | 340                                     | 340                           |
| <b>minimum <math>T_b</math> (°C)</b>                  | 31.3 $\pm$ 2.2 <sup>a</sup>   | 27.4 $\pm$ 1.9 <sup>b</sup>    | 31.2 $\pm$ 2.8 <sup>a</sup>    | 30.1 $\pm$ 1.9 <sup>a</sup>            | 29.5 $\pm$ 1.4 <sup>a</sup>             | 31.1 $\pm$ 2.3 <sup>a</sup>   |
| <b>lowest <math>T_b</math> recorded (°C)</b>          | 24.3                          | 19.8                           | 27.6                           | 24.0                                   | 23.2                                    | 25.1                          |
| <b>time spent active (min)</b>                        | 693.2 $\pm$ 62.7 <sup>a</sup> | 408.2 $\pm$ 137.6 <sup>b</sup> | 617.1 $\pm$ 107.0 <sup>a</sup> | 599.6 $\pm$ 106.6 <sup>a</sup>         | 661.2 $\pm$ 68.1 <sup>a</sup>           | 629.3 $\pm$ 75.7 <sup>a</sup> |
| <b>daily <math>T_a</math> (°C)</b>                    | 8.3 $\pm$ 2.8 <sup>a</sup>    | 11.1 $\pm$ 1.2 <sup>b</sup>    | 10.9 $\pm$ 1.1 <sup>b</sup>    | 9.6 $\pm$ 1.1 <sup>b</sup>             | 9.9 $\pm$ 1.0 <sup>b</sup>              | 9.9 $\pm$ 1.3 <sup>b</sup>    |
| <b>maximum <math>T_a</math> (°C)</b>                  | 13.5 $\pm$ 2.6 <sup>a</sup>   | 16.5 $\pm$ 1.7 <sup>b</sup>    | 16.3 $\pm$ 2.0 <sup>b</sup>    | 15.8 $\pm$ 0.8 <sup>b</sup>            | 15.4 $\pm$ 1.2 <sup>b</sup>             | 15.7 $\pm$ 1.3 <sup>b</sup>   |
| <b>absolute highest maximum <math>T_a</math> (°C)</b> | 17.5                          | 20.0                           | 19.5                           | 18                                     | 18.5                                    | 18                            |
| <b>minimum <math>T_a</math> (°C)</b>                  | 4.8 $\pm$ 2.8 <sup>a</sup>    | 7.4 $\pm$ 1.4 <sup>b</sup>     | 7.0 $\pm$ 1.4 <sup>b</sup>     | 6.8 $\pm$ 1.5 <sup>b</sup>             | 7.1 $\pm$ 1.4 <sup>b</sup>              | 7.1 $\pm$ 1.7 <sup>b</sup>    |
| <b>absolute lowest minimum <math>T_a</math> (°C)</b>  | 2.0                           | 5.5                            | 5.0                            | 5.5                                    | 5.5                                     | 5.0                           |

242