

Research



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Physiology

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

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To cope with the post-fire challenges of decreased availability of food and shelter, brown antechinus (*Antechinus stuartii*), a small marsupial mammal, increase the use of energy-conserving torpor and reduce activity. However, it is not known how long it takes for animals to resume pre-fire torpor and activity patterns during the recovery of burnt habitat. Therefore, we tested the hypothesis that antechinus will adjust torpor use and activity after a fire depending on vegetation recovery. We simultaneously quantified torpor and activity patterns for female antechinus from three adjacent areas: (i) the area of a management burn 1 year post-fire, (ii) an area that was burned 2 years prior, and (iii) a control area. In comparison to shortly after the management burn, antechinus in all three groups displayed less frequent and less pronounced torpor while being more active. We provide the first evidence that only 1 year post-fire antechinus resume pre-fire torpor and activity patterns, probably in response to the return of herbaceous ground cover and foraging opportunities.

1. Introduction

As large and destructive wildfires are increasing worldwide [1], management burns are employed in many forested areas with the aim of reducing fire fuel loads. However, the time between fires and their intensity can alter assemblages of plant and animal species [2,3]. Importantly, while leaf litter and some grasses/herbs often reappear quickly after a fire, others, such as woody vegetation and tree hollows, can take up to 30–40 years to re-establish [4].

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

Given the slow recovery of some habitat features it remains unclear over what time period such behavioural and physiological adjustments have to be employed for individuals and populations to survive. While an increase in torpor use is beneficial during detrimental conditions, it may reduce fitness by curtailing territorial defence and reproduction. Therefore, as conditions improve animals should employ less torpor. We tested the hypothesis that following the recovery of an herbaceous understory after a management burn, torpor use and activity in brown antechinus (*Antechinus stuartii*), a

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

group name	group description	individuals	animal days
pre-fire 2014	individuals measured in 2014 before the burn	4	25
post-fire 2014	individuals measured in 2014 after the burn	4	56
control 2014	individuals measured in 2014 in an unburnt area	2	17
1 year post-fire 2015	individuals measured in 2015, 1 year after the management burn in 2014	7	136
2 years post-fire 2015	individuals measured in 2015 in an area that was burnt 2 years prior in 2013	4	89
control 2015	individuals measured in 2015 in an unburnt area	6	135

small heterothermic terrestrial marsupial [10], will return to pre-fire levels in response to more profitable and safer foraging opportunities.

2. Material and methods

Our work was undertaken during May–June 2015, 1 year after a management burn at Guy Fawkes River National Park, Australia (30°04'58.6" S, 152°20'0.9" E). We compared data collected during the current study with those from our previous study in 2014 [9], with a total of six groups of female antechinus (defined in table 1). All groups were measured in areas that were in close proximity, ensuring that the general habitat and climate of the sites was the same. The areas that burnt in 2013 and 2014 are burnt regularly to reduce fuel levels and the intensity of wildfires, whereas the control area last burnt in 1994 due to a wildfire, and no management burns have been implemented since [11]. Ambient temperatures (T_a) were recorded with data loggers ($\pm 0.5^\circ\text{C}$, iButton thermochron DS1921G, Maxim Integrated Products, Inc., Sunnyvale, CA, USA). We visually determined the percentage of ground cover in 12 randomly selected 1 m² quadrats in each of the three study areas (36 quadrats total).

To measure T_b patterns including torpor and also to infer activity, we implanted temperature-sensitive radio transmitters (2 g, Sirtrack, Havelock North, New Zealand) into the intraperitoneal cavity of each animal (for surgical details, see [12]). A receiver/data logger [13] was placed near each nest to record the presence/absence of animals and their T_b . Throughout the study each individual used between one and eight nest sites (mean = 3.7 nests) and loggers were repositioned whenever antechinus moved to a new nest. Activity periods within 24 h (sunrise to sunrise) were calculated as the time animals spent away from the nest site/logger for greater than 30 min. Days when an individual moved nests were excluded, as the time the animal arrived at the new nest was unknown. We calculated the torpor threshold of 31.5°C using equation 4 [14] as previously [9]; torpor bouts were calculated from the time T_b fell below and rose above this threshold for greater than 30 min.

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

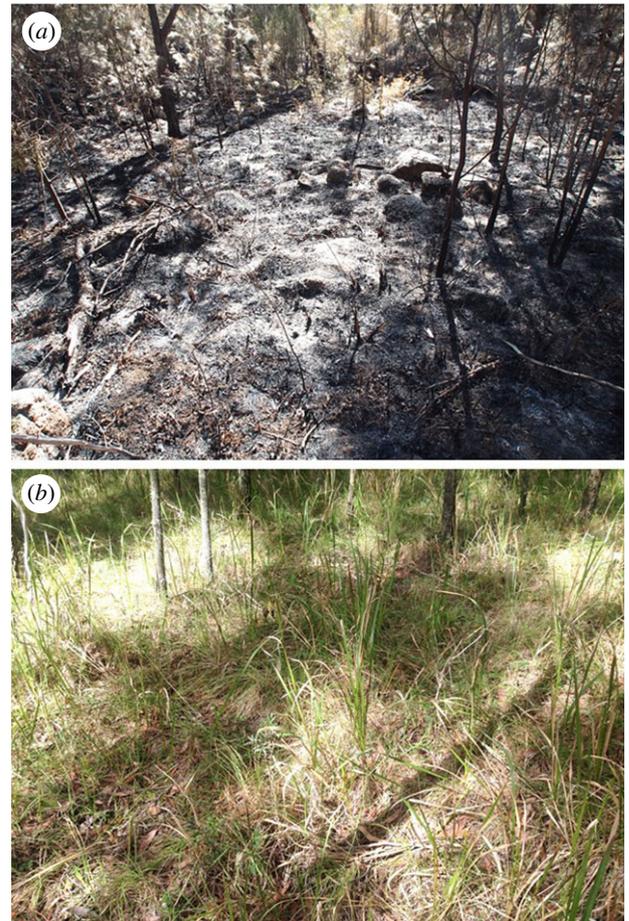


Figure 1. Photos of the study site depicting ground cover in the same area shortly after the management burn in 2014 (a) and 1 year later in 2015 when *Lomandra* had recovered (b).

3. Results

While ground cover had somewhat recovered a year after the burn in 2014 (figure 1), it was patchy in those areas where the 1 year post-fire 2015 (range = 10–100%, mean = 50%, $n = 12$) and 2 years post-fire 2015 (range = 5–100%, mean = 39%, $n = 12$) groups were measured. By contrast, the area where the control 2015 group was measured consisted of thick and even ground cover unchanged from 2014 (range = 60–100%, mean = 87%, $n = 12$).

In all 2015 groups, torpor was employed approximately half as often as by the post-fire 2014 group, and torpor frequency was, therefore, statistically identical to the pre-fire 2014 and control 2014 groups (figure 2a and table 2). Furthermore, in all 2015 groups mean torpor bout durations and the longest torpor bouts recorded per individual were

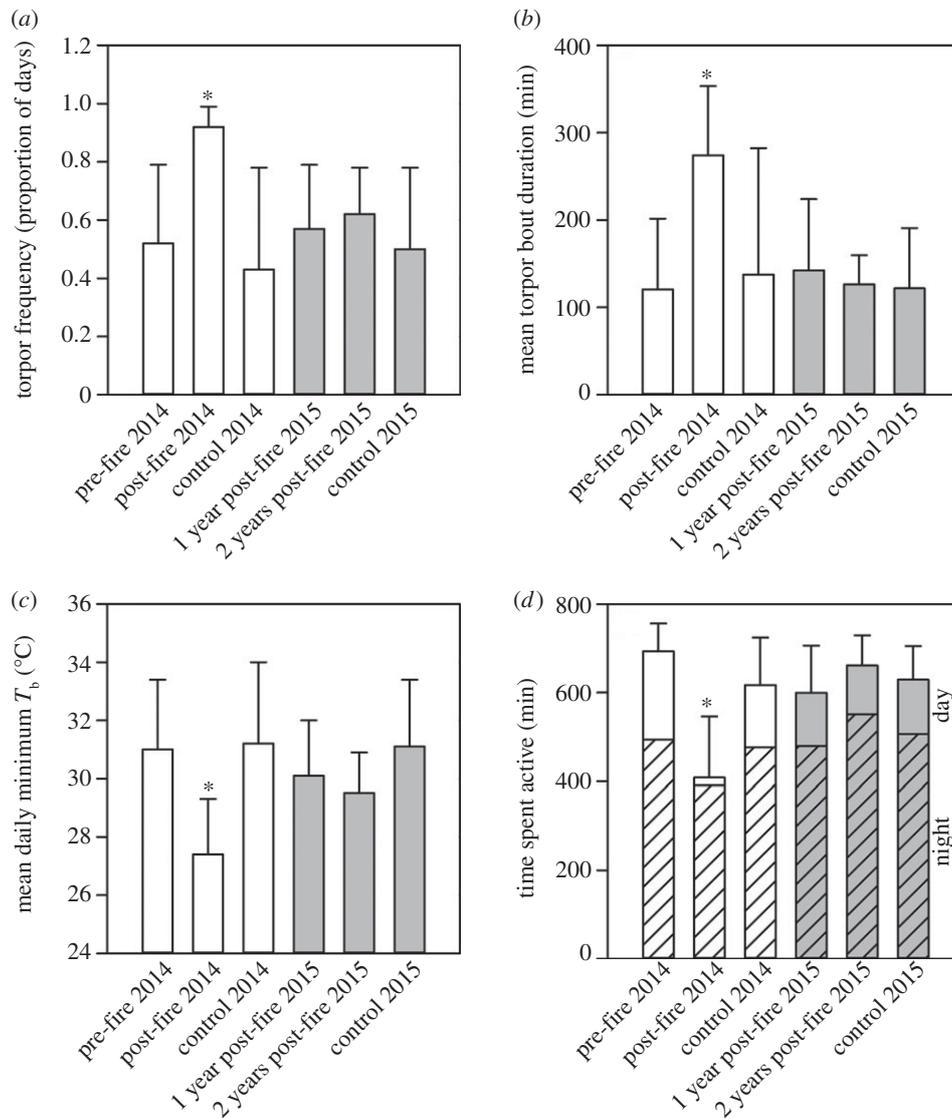


Figure 2. Comparison of variables for female *Antechinus stuartii* from 2014 (white bars) and 2015 (grey bars). (a) torpor frequency (number of days with torpor/days measured), (b) mean torpor bout duration (min), (c) mean daily minimum T_b ($^{\circ}$ C) and (d) time spent active (min). For activity (d) the solid portion of the bar represents daytime (sunrise–sunset) activity and the hatched portion nocturnal (sunset–sunrise) activity. Means are shown ± 1 s.d., which for (d) represents whole day (24 h, sunrise–sunset) activity. Only the post-fire 2014 group differed significantly, denoted by the asterisk.

significantly shorter (approx. 50%) compared with the post-fire 2014 group (figure 2b and table 2). The mean daily minimum T_b displayed by groups in the 2015 study was approximately 3° C higher, and the lowest T_b recorded 3.4° C greater, than that of the post-fire 2014 group (figure 2c and table 2).

Antechinus from all three groups measured in 2015 spent an additional 3 h active each day in comparison to individuals from the post-fire 2014 group (figure 2d and table 2). Further, while daytime activity was almost absent in the post-fire 2014 group (4.4% of total daily activity), it encompassed approximately 20% of the total daily activity of *antechinus* in 2015 and of those in the pre-fire 2014 and control 2014 groups (figure 2d).

4. Discussion

Our study provides the first evidence that within 1 year after a management burn a population of brown antechinus had resumed pre-fire torpor and activity patterns. Torpor bouts were shorter and shallower in individuals in the post-fire

recovered landscape in comparison to shortly after the fire, when ground cover was largely absent. Further, this decrease in torpor use 1 year after the fire was accompanied by an increase in total and especially daytime activity over levels measured just after the burn.

The late autumn management burns employed for our study were of low intensity, but inflicted some mortality among *antechinus* nevertheless [9]. As the fires primarily consumed dead vegetation and dry leaf litter leaving the mid and upper storeys largely intact, a relatively quick recovery of some vegetative ground cover ensued. In particular *Lomandra* spp. (native Australian perennial herbs) had re-sprouted vigorously in the areas that had burned both 1 and 2 years prior (figure 1). However, *Lomandra* is encouraged by fire, and other types of ground cover such as small shrubs and decaying timber were still largely absent. Yet brown antechinus persisted and during early winter resumed daily torpor and activity patterns similar to those recorded at the same time 1 year before the fire and in unburnt habitat [9].

Firstly, it therefore appears that even sparse vegetation of limited diversity is sufficient for *antechinus* to manage their daily energy needs without extensive torpor use. This

Table 2. Torpor variables, body temperatures (T_b) and time spent active (whole day) of female *Antechinus stuartii* and ambient temperatures (T_a). Means are shown ± 1 s.d. and significant differences between groups are identified by different letters.

	pre-fire 2014	post-fire 2014	control 2014	1 year post-fire 2015	2 years post-fire 2015	control 2015
torpor frequency (proportion of days)	0.52 \pm 0.27 ^a	0.92 \pm 0.07 ^b	0.43 \pm 0.35 ^a	0.57 \pm 0.22 ^a	0.62 \pm 0.16 ^a	0.50 \pm 0.28 ^a
torpor bout duration (min)	120.8 \pm 80.8 ^a	274.2 \pm 79.2 ^b	137.5 \pm 102.5 ^a	142.6 \pm 81.4 ^a	126.7 \pm 33.1 ^a	121.9 \pm 69.1 ^a
longest torpor bout recorded (min)	330	650	310	380	340	340
minimum T_b ($^{\circ}$ C)	31.3 \pm 2.2 ^a	27.4 \pm 1.9 ^b	31.2 \pm 2.8 ^a	30.1 \pm 1.9 ^a	29.5 \pm 1.4 ^a	31.1 \pm 2.3 ^a
lowest T_b recorded ($^{\circ}$ C)	24.3	19.8	27.6	24.0	23.2	25.1
time spent active (min)	693.2 \pm 62.7 ^a	408.2 \pm 137.6 ^b	617.1 \pm 107.0 ^a	599.6 \pm 106.6 ^a	661.2 \pm 68.1 ^a	629.3 \pm 75.7 ^a
daily T_a ($^{\circ}$ C)	8.3 \pm 2.8 ^a	11.1 \pm 1.2 ^b	10.9 \pm 1.1 ^b	9.6 \pm 1.1 ^b	9.9 \pm 1.0 ^b	9.9 \pm 1.3 ^b
maximum T_a ($^{\circ}$ C)	13.5 \pm 2.6 ^a	16.5 \pm 1.7 ^b	16.3 \pm 2.0 ^b	15.8 \pm 0.8 ^b	15.4 \pm 1.2 ^b	15.7 \pm 1.3 ^b
absolute highest maximum T_a ($^{\circ}$ C)	17.5	20.0	19.5	18	18.5	18
minimum T_a ($^{\circ}$ C)	4.8 \pm 2.8 ^a	7.4 \pm 1.4 ^b	7.0 \pm 1.4 ^b	6.8 \pm 1.5 ^b	7.1 \pm 1.4 ^b	7.1 \pm 1.7 ^b
absolute lowest minimum T_a ($^{\circ}$ C)	2.0	5.5	5.0	5.5	5.5	5.0

vegetative cover probably aids in protecting antechinus from predation while foraging. Secondly, as the abundance of terrestrial arthropods often increases in the year following a fire [6], for antechinus the prey base might have been elevated. Thirdly, it is likely that the insulating properties of a tussock ground cover alters the microclimate of foraging areas. For example, the retention of a boundary layer of warm air near the ground during the night would reduce thermoregulatory costs while foraging, further decreasing the need to save energy via torpor.

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

Nevertheless, it is evidently possible that fires do not pose a significant challenge for some mammals, especially those that can avoid fires like volant bats [21]. Indeed, the only other study we are aware of focusing on how individuals

recover physiologically and behaviourally in the years after a fire was conducted on bats [21]. Therefore, further studies on different mammals are needed to understand how other species on other continents respond physiologically and behaviourally to fires, including severe wildfires, in the short to long term. In particular, data would be valuable on longer-lived and homeothermic species that do not have the ability to employ torpor for energy conservation.

Ethics. Permits for 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).

Data accessibility. Data can be accessed from Dryad Digital Repository (<http://dx.doi.org/10.5061/dryad.m76ks>) [17].

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

Competing interests. The authors declare no competing interests.

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