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Physiological and behavioural responses of a small heterothermic mammal to fire stimuli

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HIGHLIGHTS

- We report behavioural and physiological responses of a mammal to fire cues.
- Smoke exposure caused immediate arousal in dunnarts (*Sminthopsis crassicaudata*).
- After smoke exposure torpor use decreased and activity increased.
- Charcoal/ash substrate resulted in a decrease in torpor use and activity.
- Food withdrawal reduced the impacts of smoke and charcoal/ash substrate.

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ABSTRACT

The predicted increase of the frequency and intensity of wildfires as a result of climate change could have a devastating impact on many species and ecosystems. However, the particular physiological and behavioural adaptions of animals to survive fires are poorly understood. We aimed to provide the first quantitative data on physiological and behavioural mechanisms used by a small heterothermic marsupial mammal, the fat-tailed dunnart (*Sminthopsis crassicaudata*), that may be crucial for survival during and immediately after a fire. Specifically, we aimed to determine (i) whether captive torpid animals are able to respond to fire stimuli and (ii) which energy saving mechanisms are used in response to fires. The initial response of torpid dunnarts to smoke exposure was to arouse immediately and therefore express shorter and shallower torpor bouts. Dunnarts also increased activity after smoke exposure when food was provided, but not when food was withheld. A charcoal/ash substrate, imitating post-fire conditions, resulted in a decrease in torpor use and activity, but only when food was available. Our novel data suggests that heterothermic mammals are able to respond to fire stimuli, such as smoke, to arouse from torpor as an initial response to fire and adjust torpor use and activity levels according to food availability modulated by fire cues.

1. Introduction

Changes in ambient temperatures (T_a) are only one of the many predicted outcomes of climate change and one of the consequences that is already being observed worldwide is an increase in intensity and frequency of wildfires [1,13,20,36,38,46,53]. Australia is particularly susceptible to fires [4,47] and the effect of climate change in Australia is apparent by the recent early starts to the fire season. While fires are a natural part of the Australian landscape, a shift in the timing and an increase in the frequency of fires may negatively impact on a range of plants and animals, even those that are adapted to fire, making correct management of prescribed fires vitally important [6,47,58].

Ecological data on how animal populations recover from wild and prescribed fires are available to some extent [1,3,9,11,15,27,36,47]. In contrast, data on how individuals cope behaviourally and physiologically during and also after a fire in the subsequent denuded landscape are scant [14,45,47]. Obviously, an understanding of the interactions between behaviour and physiology is important in general [49], but it also has been identified as being fundamentally vital in regard to the sustainable management of fires [13–15,38,45].

Emerging research indicates that many species, especially small mammals that shelter in burrows and rock crevices, are able to survive fire [19,25,45]. As far as insectivorous mammals and birds are concerned, insect abundance is often significantly reduced after a fire, but foraging might become easier [8,12,41,47,54,59]. Along with possible changes in food availability, another important issue in Australia is the presence of introduced predators that hunt more successfully in the open environments created by the fire and, therefore, post-fire predation of small vertebrates can be dramatically increased [23,25,30].

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Therefore, the response of individuals to fire is dependent on the particularities of the fire itself, habitat, life history traits and most importantly how a species manage their daily energy budget [16,26,27,32,45,59].

Energy expenditure in small mammals is generally high but can be substantially decreased by the use of torpor, which is characterised by a reduction in metabolic rate, body temperature (T_b) and water loss and is often used in times of energetic stress to conserve energy [37,40,44]. Clearly, in the aftermath of a fire torpor would be advantageous because it enables small mammals to conserve large amounts of energy and perhaps survive until conditions become more favourable. However, torpor could potentially also be detrimental if it prevents an animal from evading an approaching fire front and the individual is torpid in a location susceptible to destruction by a fire. Surprisingly, quantitative data on the use of torpor directly in relation to fire are scant [45], but torpor has been linked to the survival of many species dealing with environmental challenges in general and in Australia recent mammalian extinctions encompassed mainly homeotherms that are unable to use torpor [18].

The purpose of our study was to examine torpor and activity patterns in fat-tailed dunnarts (*Sminthopsis crassicaudata*; henceforth referred to as ‘dunnarts’) in relation to the effects of fire. We examined whether dunnarts are able to detect smoke during torpor, how dunnarts respond to smoke exposure after torpor, and how torpor and activity are modified on a charcoal/ash substrate as in post-fire environments when resources and refuges are likely to be limited. Dunnarts belong to the marsupial family Dasyuridae and are nocturnal carnivores/insectivores that live in a range of habitats throughout southern Australia, many of which periodically experience fires (*e.g.* hummock grassland) [31]. They use daily torpor throughout most of the year, but increase torpor use during winter [17,51]. Dunnart species are under pressure from a range of native and introduced predators such as feral cats and European foxes [35,42]. As dunnarts often take refuge under fallen woody debris, rocks, cracks in the soil or Spinifex hummocks, they also appear to be vulnerable to fires [33,52]. Importantly, in Australia many small mammals including a number of dunnart species live in particularly fire-prone habitats [24–27,32]. Considering the ecology and biology of dunnarts and other small mammals, we hypothesised that adjustments of activity and torpor patterns during and after a fire event will be important for their long-term survival.

2. Material and methods

2.1. Animals

Captive-bred dunnarts were used for our study and were housed individually in cages (35 × 27 × 21 cm) that were lined with wood shavings and cleaned regularly. Dunnarts were also provided with a nest box containing shredded paper, 2 cardboard rolls and a running wheel. Water was always provided ad libitum, whereas food was provided ad libitum on most days, but was withheld during the experiments for a maximum of one day at a time. Dunnarts were fed once daily in the late afternoon with a mixture of canned cat food and dry cat food soaked in water, supplemented with mealworms and minced meat. The room used for both experimental procedures was kept on a short photoperiod of L:D 10:14 h to simulate natural winter conditions and T_a was maintained at 18.0 ± 0.9 °C (recorded at 10 min intervals using a calibrated iButton Thermochron DS1921G, resolution 0.5 °C, Maxim Integrated Products, Inc., USA). Dunnarts were housed in these conditions for two to four weeks prior to commencement of the experiments. Throughout experiments animals were weighed weekly to the nearest 0.1 g with an electronic balance.

2.2. Smoke treatment

To record T_b throughout the smoke treatment dunnarts ($n = 5$ adult females) were implanted with temperature-sensitive radio-transmitters (1.25 to 1.44 g, Sirtrack, Havelock North, New Zealand). Before implantation these transmitters were coated with inert wax (Paraffin/Elvax) and calibrated in a water bath in a temperature range of 14 to 43 °C to the nearest 0.1 °C. For each individual a transmitter was chosen that was <10% of body mass as recommended by Rojas *et al.* [39]. General isoflurane/oxygen anaesthesia was used for surgery and 70% alcohol for sterilisation of the skin, transmitters and surgical instruments. Transmitters were implanted intraperitoneally and the surgical incisions to the muscle and skin layers were closed using coated Vicryl (3.0 metric, Ethicon Inc.). A topical anaesthetic (Xylocaine, AstraZeneca Pty Ltd., North Ryde, NSW, Australia) and Leuko Spray Bandage (BSN medical (Aust) Pty Ltd., Clayton, Vic, Australia) was applied to the surgery site following the completion of the surgery to promote wound healing. Children's Panadol (Ermington, NSW, Australia) was also provided for post-surgery recovery.

After two weeks of recovery from surgery and acclimation to their new surroundings, the experimental smoke treatment began and lasted for four weeks. Two feeding regimes were used, one involved food ad libitum and the other was no food. On a weekly basis food was withheld on two days, one with smoke and one without smoke, with at least two days of recovery with ad libitum food between these days. By burning 50 g of *Eucalyptus* leaves in a fireproof container, smoke was introduced into the room twice weekly at 8:00 h for 15 min: (i) following a night where food was provided ad libitum and (ii) following a night when food was withheld. A smoke spot tester kit (Testo 308, Testo AG, Lenzkirch, Germany) was used to measure the density of smoke particles in the air. The smoke number scale ranges from zero (clean air) to six (thick smoke) and a measurement was taken prior to lighting the fire and then at 5 min intervals throughout the experiment. During the experiment the smoke number was maintained around the approved midrange of three, which mimicked a control burn, but was enough to elicit sustained discomfort in the experimenter. The fire was controlled by replacing or removing the lid of the fireproof container.

Throughout the four weeks of the experiment we continuously recorded T_b and activity patterns of dunnarts. A remote receiver/data logger system [22] was placed in the room to record the T_b of the animals every 10 min. Activity was measured continuously with passive infrared sensors, which are triggered by movements from an object with a temperature different from the surrounding temperature [21]. These sensors were attached to the top of each cage and activity was summed over 10 min periods and stored on a custom-made logger (Electronic Services Unit, UNE, Armidale). Activity data induced by experimenters entering the room, usually for feeding at 15:00–16:00 h, were removed. Additionally, an experimenter entered the room on days without smoke at the same time as when smoke would be introduced (8:00 h) to determine whether any responses observed were due solely to smoke or to perhaps the presence of an experimenter.

2.3. Substrate treatment

For the substrate treatment, dunnarts ($n = 7$ adult females) were acclimated to the conditions of a new holding room for two weeks. The animals had been implanted previously with subcutaneous transponders (IPTT-300 Bio Medic Data Systems Implantable Programmable Temperature Transponder, Delaware, 0.13 g, 14 mm × 2 mm, for details see [50]). The subcutaneous temperatures (T_{sub}) of dunnarts were scanned (DAS-7006/7R/S Handheld Reader, Bio Medic Data Systems) daily between 9:00 and 10:00 h, during which time torpor in dunnarts is usually most pronounced. Nevertheless, since it is unlikely that this single daily measurement would have recorded the minimum T_{sub} for every day, we only analysed the absolute minimum for each animal per treatment.

Once acclimated, individuals were exposed to a charcoal/ash substrate for a period of four days and this was repeated two weeks later using the same method although for a period of eight days.

Charcoal/ash (80 g) was created by burning dry *Eucalyptus* leaves and twigs and was mixed with 50 g of wood shavings and placed as a substrate in each of the enclosures. Once again, two feeding regimes were used, one involved food ad libitum and the other was no food. On the third experimental day, food was withheld for 24 h to simulate an unpredictable post-fire environment. Animals were weighed before and 24 h after food was withheld. Food was also withheld on the third day of control (usual substrate) conditions for comparison. Activity was measured continuously as described above for the smoke treatment. To ensure that any differences in total daily activity between the control and charcoal/ash substrate was not caused by changing from old to new substrate, total daily activity was measured before (1749.0 ± 810.8 counts/day, $n = 7$, $N = 14$) and after (1885.3 ± 923.4 counts/day, $n = 7$, $N = 14$) changing the control substrate from old to new and no difference was found ($t_{20} = 0.4$, $p = 0.7$).

2.4. Defining torpor bouts

Dunnarts were considered to be torpid when $\mathrm{T_b}$ decreased below 32.5 °C, the calculated torpor onset $\mathrm{T_b}$ ($\mathrm{T_b}$-onset) value (equation 3, [55]):

$$T_b\!-\!onset\text{–}1\ \ \mathrm{SE} = (0.055 \pm 0.014)\mathrm{BM} + (0.071 \pm 0.031)\mathrm{T_a} + (31.823 \pm 0.740)$$
$$\text{when BM (body mass)} = 18.0 \pm 2.8\mathrm{g}(n = 5)\ \text{and}\ \mathrm{T_a} = 18.0 \pm 0.9^{\circ}C\ (\text{mean daily } T_a)$$

As this formula provides a threshold estimate that detects shallow torpor bouts it was preferred over the widely used threshold of 30.0 °C [2], which may overlook decreases in $\mathrm{T_b}$ that are energetically important [5]. Therefore, torpor bout entry and arousal were calculated from times that $\mathrm{T_b}$ decreased below and above 32.5 °C. As $\mathrm{T_{sub}}$ is usually somewhat lower than core $\mathrm{T_b}$, we used a more conservative threshold of 30 °C. Rewarming rates were calculated from the maximum recorded over a period of 10 min for each arousal from torpor.

2.5. Statistical analysis

Statistical tests were performed in R (R version 3.0.1, The R Foundation for Statistical Computing, 2013). The best model for each treatment was determined using ΔAICc values (package 'MuMIn'). The two feeding regimes (food ad libitum and no food) were analysed separately and linear mixed-effects models (package 'nlme') were then fitted for the following variables (tested treatments for each variable are shown in the brackets):

1. Proportion of all study days torpor was used (smoke or control)
2. Torpor bout duration (smoke or control, charcoal/ash or control)
3. Arousal rates from torpor bouts (smoke or control)
4. Daily minimum $\mathrm{T_b}/\mathrm{T_{sub}}$ (smoke or control, charcoal/ash or control)
5. Total daily activity (smoke or control, charcoal/ash or control)
6. Mass loss (charcoal/ash or control)

To account for repeated measures individuals were entered as a random effect. The proportion of study days on which torpor was used were arcsine transformed. Rayleigh tests were used to determine whether the timing of torpor entries and arousals differed from random and Watson-Williams *f*-test was used to compare arousal times between treatments (package 'circular'). Means are represented as the mean of the mean of each individual with ±1 standard deviation. Differences were considered meaningful at a significance level (p) of < 0.05.

3. Results

3.1. Smoke treatment

Irrespective of smoke exposure food withdrawal significantly increased torpor expression in female dunnarts to 92.5 ± 16.9% of days over a background level of spontaneous torpor of 22.5 ± 35.7% of days (i.e. when food was provided ad libitum; Fig. 1). While smoke exposure apparently did not influence torpor frequency, it nevertheless significantly shortened bout duration of spontaneous torpor to 19% of control conditions (Table 1). A similar trend was evident when food was withheld, but in this case the decrease was only moderate with a 30% reduction and therefore not significant. This observed effect on torpor duration was mainly due to premature arousal during smoke treatment (Fig. 1). As such, in dunnarts, timing of torpor entry remained unchanged under all experimental conditions (Watson-Williams *f*-test: smoke: $f_{1,18} = 2.5$, $p = 0.1$; control: $f_{1,38} = 0.8$, $p = 0.4$) and occurred on average a few hours before lights-on at 5:51 ± 6:10 h (Rayleigh test: $r = 0.3$, $z = 7.3$, $p < 0.001$; Fig. 2). In contrast, when exposed to smoke arousals occurred significantly earlier, about 40 min after the introduction of smoke (Rayleigh test: 8:38 ± 1:32 h, $r = 0.9$, $z = 16.9$, $p < 0.001$; Watson-Williams *f*-test: $f_{1,59} = 6.9$, $p = 0.01$), than on days without smoke (Rayleigh test: 9:44 ± 1:29 h, $r = 0.9$, $z = 35.2$, $p < 0.001$; Fig. 2). Despite the "smoke-induced" arousal, rewarming rates remained unchanged at 0.43 ± 0.11 °C/min for all treatments ($p = 0.124$).

Furthermore, smoke significantly elevated daily minimum $\mathrm{T_b}$ (including days with and without torpor), but matching the effect on torpor bout duration this was only significant when food was provided (Table 1). Mean daily minimum $\mathrm{T_b}$ was 2.5 °C higher on days with smoke exposure when food was available (Table 1), but only 1.1 °C higher when food was withheld (Table 1). Smoke exposure also significantly increased total daily activity by 75% when animals were fed, but again not when food was withheld (Table 1).

3.2. Substrate treatment

On both substrates, wood shavings and charcoal/ash/wood shaving mix, withdrawal of food induced torpor in all animals except for one individual on the charcoal/ash substrate (Fig. 3b). When food was provided, however, differences in the expression of spontaneous torpor became apparent. Six out of seven female dunnarts entered spontaneous torpor on the control substrate, whereas only three did on the charcoal/ash substrate (Fig. 3a). Such differences in torpor propensity had significant effects on mean minimum $\mathrm{T_{sub}}$, which on the charcoal/ash substrate was elevated on average by 9.1 °C when food was provided, and still by 2.7 °C when food was withheld (Table 2).

Total daily activity was also influenced by substrate treatment, but the effects appeared to be opposing depending on food availability. When food was provided dunnarts significantly reduced total daily activity on the charcoal substrate (Table 2). However, when food was withheld animals tended to become more active on the same substrate and, although this difference was statistically not significant (Table 2), body mass loss on days without food was still on average 23% higher on the charcoal/ash substrate (2.2 ± 0.3 g) than on the control substrate (1.7 ± 0.4 g, $p = 0.005$).

4. Discussion

Our study provides the first quantitative data on behavioural and physiological responses of a mammal to immediate- and post-fire cues. Most importantly, torpid female dunnarts were able to detect smoke and arouse from torpor. Hence, torpid animals have a similar chance of evading an approaching fire front as their normothermic counterparts. Subsequently, when presented with a charcoal ash substrate, dunnarts became reluctant to enter spontaneous torpor and also reduced overall activity, but continued to resort to torpor when food was withdrawn. Obviously, food shortage remained the primary torpor trigger, but fire cues modified torpor response and activity patterns and under laboratory conditions these effects were most evident when animals were not energetically challenged.

In contrast to normothermic individuals, which are fully alert to environmental stimuli, reactions of torpid individuals are often attenuated

Table 1
Summary statistics from the smoke treatment. Means are shown with ± standard deviation. A significant effect of the smoke treatment is represented by * (from LME).

Dunnart females	Food ad libitum (spontaneous torpor)			Food withheld (induced torpor)		
	Control	Smoke	*p*-Values	Control	Smoke	*p*-Values
Mean torpor bout duration (min)	92.4 ± 173.7	17.5 ± 44.8	0.009*	582.0 ± 231.4	408.0 ± 278.2	0.104
Mean minimum T_b (°C)	31.7 ± 6.9	34.2 ± 4.1	0.008*	20.7 ± 2.7	21.8 ± 5.5	0.507
Mean total daily activity (counts/day)	1193.9 ± 109.3	1592.5 ± 184.6	0.007*	1253.5 ± 204.6	1213.3 ± 316.6	0.279

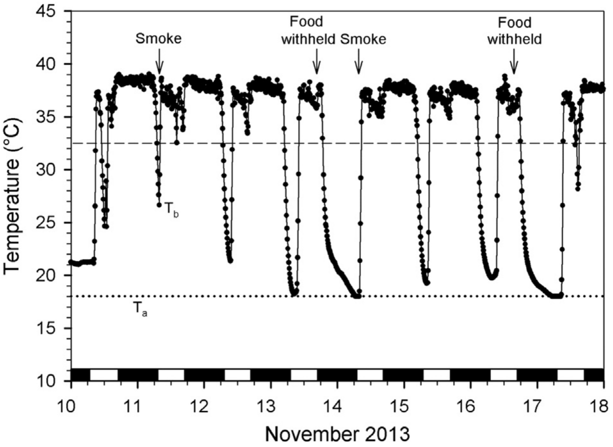

Fig. 1. A T_b trace from one dunnart over eight days. The dashed line represents the torpor threshold and the dotted line represents average T_a. The black and white bars at the bottom of the graph represent night and day, respectively.

although they remain responsive [29,43,48]. Torpid animals often arouse in response to disturbances, but this appears to depend on the nature of the disturbance. For example, hibernating cave bats rarely showed increases in energy use in response to non-tactile human disturbances, whereas tactile disturbances regularly produced an effect [43]. In another study bat flight activity increased in a cave following human intrusion [48] and torpid bats also elevated T_b in response to noise stimuli [29]. In our study torpid dunnarts did not arouse from torpor due to the presence of a person in the room (i.e. days without smoke), but they did respond to a smoke stimulus by arousing from torpor early, on average within 40 min of the introduction of smoke. Even individuals that had not entered torpor maintained an elevated resting T_b when exposed to smoke. This demonstrates firstly that torpid mammals can be responsive also to olfactory stimuli and secondly, that in the case of an approaching fire, smoke provides an early warning signal that could enable normothermic as well as torpid animals to seek shelter. This is particularly important for animals that regularly den above ground and are vulnerable to fire, such as the dunnarts [16,42,52]. In contrast, animals that reside deep underground are obviously not as endangered by a fire front, but those are probably also less exposed to smoke and therefore might remain torpid. Whether hibernating species, which often reduce T_b to near 0 °C, can also react to olfactory stimuli like smoke remains to be tested.

The charcoal ash substrate, simulating the aftermath of a fire, reduced spontaneous torpor and also overall activity. This effect might be specific to the experimental substrate or reflect a more general neo-phobic reaction to an unfamiliar environment. Similarly, the induced arousal could be smoke-specific or perhaps other air-born irritants can elicit a similar response. In either case the observed responses appear to be advantageous for a small animal in a fire scenario. For example, the activity index we derived summarises amongst others foraging/feeding, locomotor activity and perhaps attempts to escape. Consequently, at least when not energetically challenged, activity increased with the induction of smoke when an escape from a fire appears to be paramount, but subsequently was reduced on the charcoal/ash substrate when unfamiliarity with the environment would reduce foraging efficiency and increase predation risk. Hence, the two fire cues cause opposite effects on locomotor activity. However, the effects of either cue were overwritten by food withdrawal, clearly a dominant stimulus for torpor, depressant of activity and a major factor changing a range of behavioural and physiological variables [40]. If food becomes scarce, dunnarts with their minimal energy reserves and high metabolic rate probably have to resort to torpor even in an unfamiliar

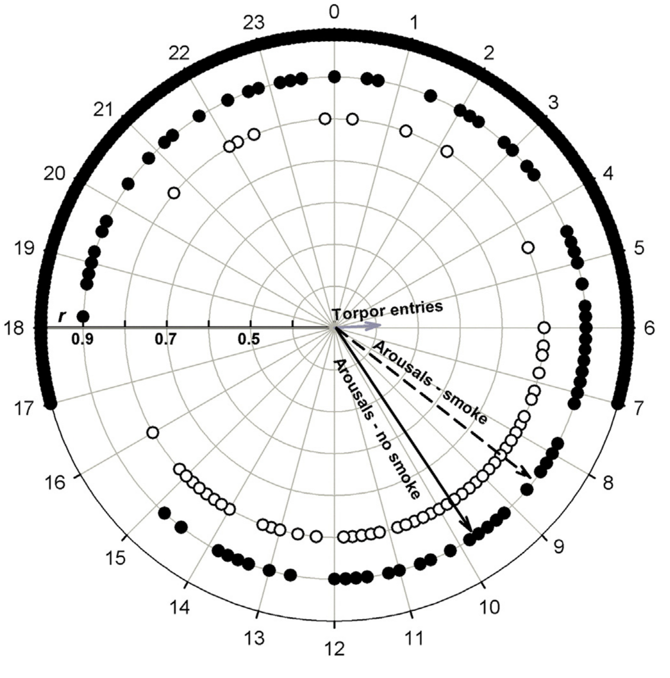

Fig. 2. Circular distribution of the time of day (24 h) for entry into torpor (filled circles) and arousal from torpor (circles) for all animals. Vectors of the means derived from Rayleigh's test for all torpor entry times (grey solid arrow; $r = 0.3$, $z = 7.3$, $p < 0.001$), arousal times on days with smoke exposure (black dashed arrow; $r = 0.9$, $z = 16.9$, $p < 0.001$) and arousal times on control days (black solid arrow; $r = 0.9$, $z = 35.2$, $p < 0.001$). A longer arrow indicates a stronger clustering of events. The scotophase is indicated by the thick black solid line on the outer circle.

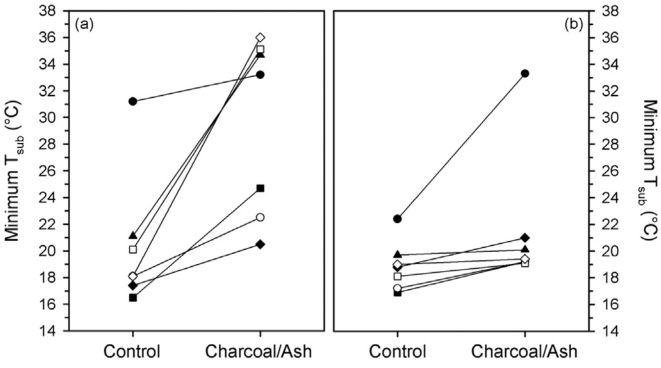

Fig. 3. Lowest recorded subcutaneous temperatures (T_{sub}) of individual dunnarts (represented by different symbols) on a charcoal/ash substrate and on a control substrate for spontaneous torpor (a) and induced torpor (b).

Table 2
Summary statistics from the charcoal/ash treatment. Means are shown with ± standard deviation. A significant effect of the charcoal/ash treatment is represented by * (from LME).

Dunnart females	Food ad libitum (spontaneous torpor)			Food withheld (induced torpor)		
	Control	Charcoal/Ash	*p*-Values	Control	Charcoal/Ash	*p*-Values
Mean minimum T_{sub} (°C)	20.4 ± 5.0	29.5 ± 6.7	0.005*	18.9 ± 1.8	21.6 ± 5.2	0.05*
Mean total daily activity (counts/day)	1876.4 ± 74.3	1508.9 ± 131.1	< 0.0001*	1540.7 ± 488.4	1700.3 ± 163.5	0.084

environment provided there is no immediate threat. Therefore, if food resources have been depleted in the aftermath of a fire torpor remains a viable option to reduce energy expenditure.

Nevertheless, the reaction of dunnarts to the more challenging and complex scenario of a ‘real’ fire in the wild remains to be investigated. What has been verified in the field, however, is that dunnarts use daily torpor year-round, although torpor use is more pronounced during winter than in summer [17,51]. In fact, in the wild dunnarts enter torpor daily during autumn/winter indicating substantially reduced food resources and thermoregulatory stress [51]. Hazard reduction burns are usually conducted during this time of the year when small insectivorous mammals are already energetically challenged. On the other hand, in the grasslands of Australia's interior wildfires generally occur during summer and can burn over many hundred thousands of square kilometres [34]. Consequently, the predicted increase of the frequency and intensity of wildfires as a result of climate change may have a devastating impact on many species and ecosystems [1,4,20,38,46,58], but for small mammals such as dunnarts so could regular hazard reduction burns during winter. Importantly, data from our study and previous studies suggest that many small animals are able to survive a fire front, likely by using smoke as an early cue to arouse from torpor if necessary and then seek secure shelters, such as large trees or, even better, deep burrows [10,11,19,28,45]. During the aftermath of a fire torpor then is a viable strategy to reduce energy expenditure and minimise exposure to predators, as shown in a recent study on brown antechinus (*Antechinus stuartii*; [45]), a close relative of dunnarts. At least in the arid zone, increased activity that translates into long distance movements towards more favourable habitats appears to be also part of the equation [24,25]. Consequently, some dunnart species will disappear from sites shortly after a fire, but can recolonise these habitats ~3–10 years after a fire [7,56,57]. Obviously, laboratory experiments cannot replicate the complexity of a fire in the wild, but our data suggest that the immediate danger of a fire is not increased for torpid animals because smoke can act as a warning signal, and during the fire's aftermath the energy savings afforded by torpor will permit survival on limited resources.

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